

A NEW GENUS OF ORYZOMYINE RODENT (CRICETIDAE: SIGMODONTINAE) FROM THE PLEISTOCENE OF ARGENTINA

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Based on a right maxillary with 1st molar recovered in Pleistocene (Ensenadan) deposits from south-central Buenos Aires Province, Argentina, a new genus and species of Oryzomyini (Rodentia, Cricetidae) is named and described. The new taxon is one of the largest known extinct or extant sigmodontines, morphologically related to the marsh rats *Holochilus*, †*Noronhomys*, and *Pseudoryzomys*. It can be differentiated from these taxa by the combination of several traits in the 1st upper molar, in particular a well-developed mesoloph and the free connection of both para- and protoflexus. The occurrence of this sigmodontine suggests warmer and probably moister conditions during deposition times, a hypothesis reinforced by other vertebrates exhumed together (e.g., turtles, coypus, and the giant armadillo †*Propraopus*).

Key words: Argentina, *Holochilus*, mesoloph, †*Noronhomys*, Pleistocene, *Pseudoryzomys*, Sigmodontinae

The oryzomyines are the largest and most widespread tribe of the sigmodontine radiation, including about 26 extant and 2 historical extinct genera (D'Elía et al. 2007; Musser and Carleton 2005; Weksler et al. 2006). However, their fossil record is very scarce. Because oryzomyines are mainly sylvan and perisylvan forms, this absence could be related with taphonomical biases coupled with the general scarcity of fossiliferous deposits in tropical and subtropical environments. For the Pampean region of Argentina, which has the richest sigmodontine fossil record (Pardiñas 1999a, 1999b; Pardiñas et al. 2002), the oldest oryzomyines are limited to a presumed Ensenadan record of *Nectomys* (Reig 1987), *Holochilus* (Pardiñas 2004), and *Oligoryzomys* (Voglino and Pardiñas 2005).

During 1992–2002, I conducted several field trips to look for fossil sigmodontines in the southern province of Buenos Aires along the oceanic coast. One prospected area was the outcrops exposed near the mouth of the arroyo (= creek) de Zavala (San Cayetano County), a discontinuous front (approximately 20 km in extent) of low cliffs and rocky shelf placed at intertidal position. There, the stratigraphical profile is roughly comparable to those exposed in the Punta Negra–Las Grutas (Necochea County) area described by several authors (Bidegain et al. 2005; Tonni et al. 1996; Verzi et al. 2004; Vucetich and Verzi 2002). Fossil vertebrate bones and teeth, including a craniodental remain, of a large oryzomyine were sampled from the

lower levels of this area. Comparisons carried out on this material indicate that it belongs to an undescribed genus that is morphologically related to the *Lundomys*–*Holochilus* clade (sensu Carleton and Olson 1999; Weksler 2006). In this contribution, I describe it as a new taxon and discuss its phylogenetic relationships with other members of Oryzomyini, determination of age of the material, and its significance to the paleoclimatic conditions of the area during depositional times.

MATERIALS AND METHODS

The fossil specimen studied is housed at Museo de La Plata collections (MLP). For descriptive purposes I follow Weksler (2006) regarding Oryzomyini taxonomic contents, general morphology, and phylogeny, and Reig (1977) for occlusal molar topography and terminology. The notations used for upper and lower molars are M1, M2, and M3 and m1, m2, and m3, respectively. Specimens of several taxa examined for comparison are listed in Appendix I.

RESULTS

Family Cricetidae Fischer, 1817

Tribe Oryzomyini Vorontsov, 1959

†*Carletonomys*, new genus

†*Noronhomys* sensu Pardiñas (1999a, 1999b, 2004) and Pardiñas et al. (2002).

Type species.—†*Carletonomys cailoi* new genus and species.

Distribution.—South-central Buenos Aires Province, Argentina, middle Pleistocene (Ensenadan age).

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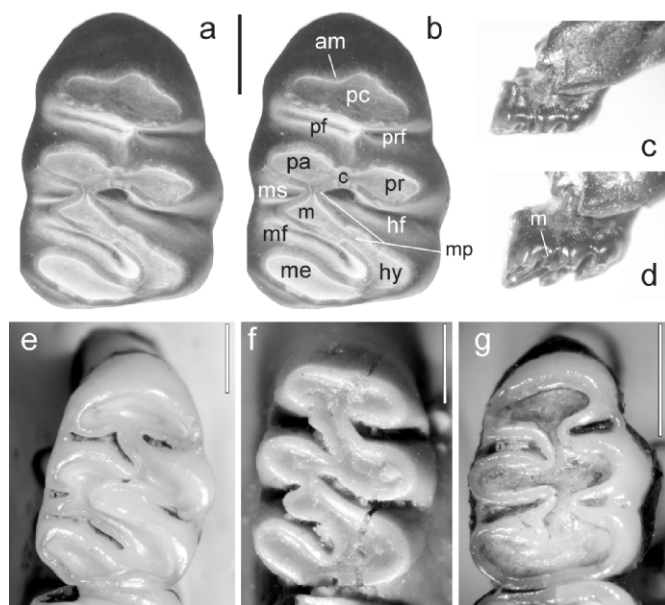


FIG. 1.—Upper row: Holotype of †*Carletonomys cailoi*, new genus and species (MLP 98-I-15-1), right M1 a) in occlusal view and b) the same with nomenclature superimposed. Note c) the plane coronal surface and d) the mesoloph (m) projection on labial side. Other abbreviations used are: am = anteromedian flexus, c = constriction, hf = hypoflexus, hy = hypocone, ma = anterior mure, me = metacone, mf = metafllexus, mp = median mure, ms = mesoflexus, pa = paracone, pc = procingulum, pf = parafllexus, pr = protocone, and prf = protofllexus. Lower row: Occlusal views of right M1 in adult individuals of e) *Holochilus brasiliensis* (CNP-E-72-1), f) †*Noronhomys vespuccii* (USNM 490297), and g) *Pseudoryzomys simplex* (CNP-E 185). Scale = 1 mm.

Etymology.—The generic name honors Dr. Michael Carleton (Smithsonian Institution), gentleman and rigorous student of Muroidea, author of numerous key contributions that are source of inspiration, and a role model for generations of mammalogists.

Morphological diagnosis.—A Sigmodontinae rodent slightly larger than *Holochilus brasiliensis* characterized by a unique combination of molar traits, including 4-rooted, hypsodont, and coronal planate M1 with main cusp arranged in nearly opposite pairs, confluent proto- and parafllexus (at least in adult wear stage), and a conspicuous mesoloph reaching the labial margin of the molar.

Remarks.—The holotype of †*Carletonomys* was previously and erroneously referred to the endemic genus †*Noronhomys*, described from Quaternary deposits of Fernando de Noronha Island by Carleton and Olson (1999). In order to eliminate spurious data in paleontological literature, all mentions of †*Noronhomys* for Argentinean deposits (Pardiñas 1999a, 1999c:18; Pardiñas et al. 2002:224 and figure 3.C; Pardiñas 2004:447) must be referred to †*Carletonomys*.

†*Carletonomys cailoi*, new genus and species

Fig. 1; Table 1

Holotype.—MLP 98-I-15-1, incomplete right maxillary with the M1 and the root of the zygomatic plate belonging to a full adult individual as judged by occlusal wear, collected by Ulyses Pardiñas and Florencia Cremona on 21 January 1998.

Molar measurements (in mm).—M1, alveolar maximum length = 3.59; M1, alveolar maximum width = 2.53; M1, height at protocone = 1.37.

Hypodigm.—The holotype is the only specimen known to date.

Type locality and stratigraphy.—Unnamed sedimentary unit composed of light green silts that form a rocky shelf exposed, situated at 1.13 km SW of the mouth of the arroyo de Zavala and approximately 7.3 km NE Balneario San Cayetano, San Cayetano County, Buenos Aires Province, Argentina, at geographic coordinates 38°44'21"S, 59°20'51"W (Fig. 2). Although at the type locality the bearing deposit is isolated, their stratigraphic relationships can be observed in a profile about 6 km to the northeast. There this layer is located at the bottom, overlaid by a sedimentary pile composed of several tabular banks approximately 7 m in total thickness. This stratigraphic profile can be correlated with those exposed near the Punta Negra locality (Necochea County, about 45 km to the northeast), whose lithology, paleontology, and magnetostratigraphy were described by Tonni et al. (1996; see also Verzi et al. 2004) and Bidegain et al. (2005). I propose a correlation between the deposit that yielded the †*Carletonomys* holotype and the sedimentary unit A of Punta Negra profile (sensu Tonni et al. 1996). Bidegain et al. (2005) found that the sedimentary unit A of Punta Negra was deposited under a normal polarity magnetic excursion (probably Jaramillo), older than 1 million years ago (mya). From these data and the available paleontological evidence at hand, I estimate an antiquity slightly older than 1 mya for †*Carletonomys*.

TABLE 1.—Molar measurements (in mm; mean, sample size in parentheses, and observed range) of †*Carletonomys cailoi*, new genus and species, and other taxa compared (arranged by decreasing M1 length).

	M1, length	M1, width	Source
<i>Lundomys molitor</i>	3.60 (4) 3.56–3.64	2.66 ^a (4) 2.56–2.80	This paper
† <i>Carletonomys cailoi</i>	3.59 (1)	2.53 (1)	This paper
<i>Holochilus brasiliensis</i>	3.24 (15) 3.01–3.34	2.56 (15) 2.39–2.71	This paper
<i>Nectomys squamipes</i>	3.30 (3) 3.24–3.36	2.18 (3) 2.12–2.32	This paper
† <i>Noronhomys vespuccii</i>	3.17 (1)	2.31 ^b (1)	This paper
† <i>Holochilus primigenus</i>	2.67 (2) 2.63–2.70	2.03 (2) 2.03	Steppan (1996:table 1)

^a Voss and Carleton (1993:table 1) reported 2.60 (12) 2.50–2.80 for this measurement.

^b Carleton and Olson (1999:table 1) reported 2.25 (7) 2.16–2.33 for this measurement.

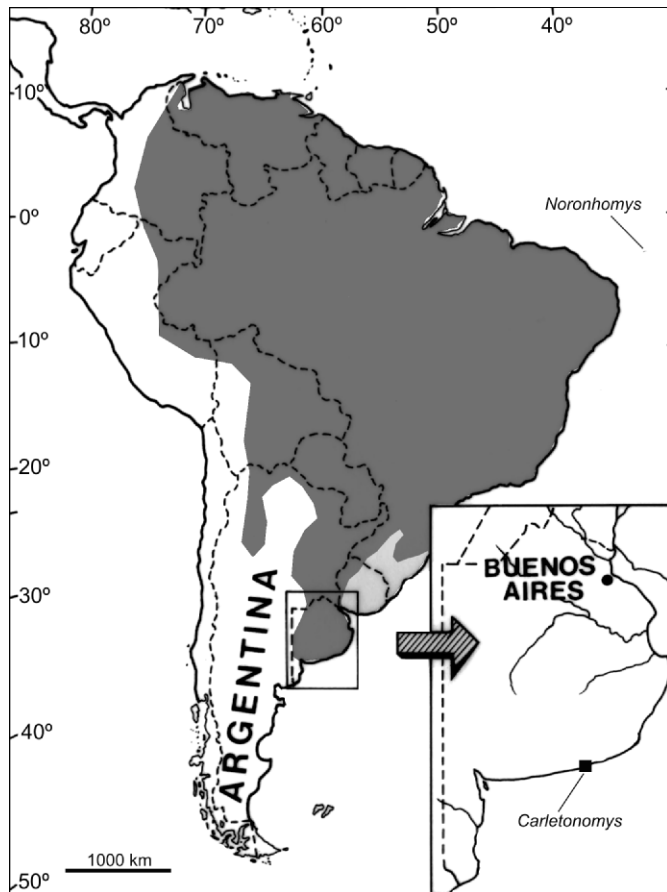


FIG. 2.—Map of South America showing the type locality (inset) of †*Carletonomys cailoi*, new genus and species, and the approximate distributions of *Holochilus* (dark gray), *Lundomys* (light gray), and †*Noronhomys* (compiled from several sources).

Etymology.—The specific epithet “cailoi” is in homage to Carlos “Cailo” Galliari, a biologist and friend with whom I spent many years studying sigmodontine rodents. This somewhat unorthodox etymological practice of forming patronyms from nicknames is in line with previous erections of †*Cholomys* (Reig 1980) and †*Panchomys* (Pardiñas 1997).

Morphological diagnosis.—The same as the genus by monotypy.

Description and comparisons.—The M1 is subeliptical in outline with plane coronal surface (sensu Hershkovitz 1962) and moderate hypsodonty. Bulbous and externally rounded, and nearly coaligned para- and protocone and meta- and hypocone pairs are observed. The anterior face of the molar forms a transverse shelf. The procingulum is narrow and has a shallow indentation on its anterior surface, suggesting an inconspicuous but present anteromedian flexus. Para- and protoflexus are confluent; a small ridge present in the anterior face of the protocone indicates that with more advanced wear the procingulum would attach to the remaining portion of the molar through an anterior mure. The proto- and paracone are subequal in size, transversely oriented, and display a medial constriction. The median mure is 45° oriented with respect to

the longitudinal axis of the tooth and is connected to the paracone through a minute bridge after producing a mesoloph. The latter is subtriangular in outline and laterally reaches the labial margin of the molar. The metaflexus and hypoflexus are opposite and deeply interpenetrate across molar midline. The posteroloph is absent. Four roots are present, including a medium-sized labial accessory root. Little anatomical information can be added from the maxillary portion preserved. The posterior end of incisive foramina is not visible, suggesting their termination at least anterior to the M1 plane. The basal portion of the zygomatic plate indicates a robust structure with their posterior border emerging at <45° at the level of the anterior face of M1.

The few preserved remains of †*Carletonomys* are similar in size and form to those of *Holochilus* (excluding †*H. primigenus*), †*Noronhomys*, and, in minor degree, *Lundomys* and *Pseudoryzomys*. Other extinct and extant oryzomyines and thomomyines are morphologically clearly different, and as such no comparisons need be made.

The following comparisons are structured according to the known anatomy of †*Carletonomys* (see also Table 2).

General M1 morphology and size (Figs. 1 and 3). †*Carletonomys* generally resembles *Holochilus* and †*Noronhomys* in the laminated occlusal pattern and general molar morphology, including subeliptical outline, plane corona, narrower procingulum, interpenetrating flexi, and posteroflexus absence (at least in adults). A more-detailed comparison reveals subtle differences. Adult *Holochilus* has a bell-shaped procingulum without any trace of an anteromedian flexus. In addition, the main cusps are more alternating than those of †*Carletonomys*. *Pseudoryzomys* shares with †*Carletonomys* the vestigial persistence of an anteromedian flexus, but its molars are clearly smaller than those of †*Carletonomys*. The margins of the labial and lingual cusps are bluntly rounded in †*Carletonomys*, †*Noronhomys*, *Lundomys*, and *Pseudoryzomys*; *Holochilus* departs from this condition in its extreme lamination producing more-acute angles (especially in *H. chacarius* and *H. sciureus* species complex). All of these genera have 4-rooted M1s, contrasting with the 3-rooted condition of *Lundomys*.

Regarding size (Table 1), the 1st molar of †*Carletonomys* is longer but as broad as that of *H. brasiliensis*, slightly smaller than that of *L. molitor*, and clearly bigger than those of †*H. primigenus* and †*Noronhomys vespucii*. The M1 measurements indicate that †*Carletonomys* is among the larger extinct or extant oryzomyines, solely surpassed by *L. molitor* and, perhaps, large *Nectomys* species (see Weksler 2006:table 8).

Procingulum isolation. This is an unusual (especially for upper molars) and partially age-related trait in sigmodontines. All examined M1s ($n = 7$) of †*Noronhomys* possess the anterior mure (M. Carleton, pers. comm., 1999). Very young *Holochilus* and *Pseudoryzomys* individuals (e.g., see Voss and Myers 1991:figure 2) sometimes display the proto- and paraflexus confluent. But both genera differ in this condition. In *Holochilus*, the confluence is restricted to a narrow gap, due to the presence of a very short anteroloph. In contrast, individuals of *Pseudoryzomys* with proto- and paraflexus confluent show a large gap between procingulum and para- plus

TABLE 2.—Synthetic comparisons of M1 of †*Carletonomys* and related genera.

	<i>Pseudoryzomys</i>	<i>Lundomys</i>	† <i>Carletonomys</i>	† <i>Noronhomys</i>	<i>Holochilus</i> ^a
Coronal topography	Slightly terraced, higher crowned	Slightly terraced, higher crowned	Plane, moderately hypsodont	Plane, moderately hypsodont	Plane, well hypsodont
Main cusps alignment	Essentially opposite	Essentially opposite	Essentially opposite	Essentially opposite	Slightly alternating
Main cusps outer margins	Rounded	Rounded	Rounded	Rounded	Slightly prismatic
Main folds interpenetration	Slightly	Slightly	Moderately	Moderately	Deeply
Anteromedian flexus persistence in adults	Yes	No	Yes	No	No
Procingulum morphology	Narrow	Narrow	Narrow	Narrow	Bell-shaped
Procingulum isolation in adults	No	No	Yes	No	No
Median mure anteriormost connection	To protocone	To median point between para- and protocone	To paracone	To paracone	To paralophule
Paralophule	Absent	Absent	Absent	Absent	Present
Mesoloph	Short	Short	Large	Medium	Absent
Posteroflexus persistence in adults	Present	Present	Absent	Absent	Absent
Labial accessory root	Absent	Absent	Present	Present	Present

^a Only *H. brasiliensis* was considered.

protocone loph; the same condition is observed in the holotype of †*Carletonomys*.

Mesoloph and mesolophlike structures (Figs. 1, 3, and 4). †*Carletonomys* and †*Noronhomys* share mesolophs that are subtriangular, transverse oriented, and reaching the labial margin; that of the former is slightly larger than that of the latter (see Carleton and Olson 1999:16). Some adult specimens of *H. brasiliensis* display a mesolophlike structure very similar to those of †*Carletonomys* and †*Noronhomys* (Fig. 1). However, after examining several hundred individuals of *H. brasiliensis*, representing very complete ontogenetic series (Fig. 3), I found that the M1 mesolophlike structure of this species is different from that of †*Carletonomys*. In fact, very young individuals clearly reveal that the so-called mesoloph of *H. brasiliensis* (see Massoia 1971; Voss and Carleton 1993; Weksler 2006) is produced by the early coalescence of the anteriormost point of the median mure—almost quite transverse in orientation—with a paralophule (Fig. 4). In the congeneric *H. chacarius*, and in the species of the complex of *H. sciureus*, the paralophule is absent and the anteriormost point of the median mure directly contacts the posterior face of the paracone (Fig. 3). In contrast, both *L. molitor* and *Pseudoryzomys simplex* display a true minute mesoloph arising from the median mure coupled with the absence of a paralophule (Fig. 4). The evaluation of these differences requires consideration of the point where the median mure connects to the middle portion (paracone–protocone) of the molar (Fig. 4). In *L. molitor*, this point is located on the constriction (“enamel bridge” sensu Weksler [2006:45, character 61]) present between the proto- and the paracone. In *P. simplex*, this point is located on the protocone although close to the constriction; in addition, the anterior part of the median mure is parallel to the longitudinal axis of the molar. In *H. chacarius*, this point is located on the interior angle of the paracone, very close to the constriction, and the median mure is diagonally oriented. The

paralophule of *H. brasiliensis* determines that this point rests on the median part of the paracone; the same location is observed in the holotype of †*Carletonomys*. Both differ in the orientation of the minute bridge connecting to the paracone: labially oriented in *H. brasiliensis* versus vertically oriented in †*Carletonomys*. The vertical orientation suggests that †*Carletonomys* has a true mesoloph that arises from the anterior part of the median mure without the participation of the paralophule. The necessary testing of this hypothesis rests on the study of additional fossil material that, unfortunately, currently is not available.

Zygomatic plate (Fig. 5). All the genera under discussion have robust and high zygomatic plates. From the remains of †*Carletonomys* I found some peculiarities with respect to the conformation of the posterior border and the general inclination of this structure. Labially, the maxillary portion of †*Carletonomys* is partially crossed by a “rib” that marks the origin of the posterior border of the zygomatic plate. The same condition is displayed by †*Noronhomys* (see Carleton and Olson 1999:figure 11), *Lundomys* (see Voss and Carleton 1993:figure 4), and *Pseudoryzomys*, but not by *Holochilus* (at least *H. brasiliensis*). Additionally, the position of the posterior border of the zygomatic plate, short before it arches forward in order to connect with the zygomatic arch, is in the plane of the anterior face of the M1 in †*Carletonomys*, *Holochilus*, and †*Noronhomys*, but clearly anterior in *Pseudoryzomys*. In frontal view, the zygomatic plate is more inclined outward in *Pseudoryzomys* and †*Carletonomys* (this trait cannot be checked in †*Noronhomys*) than in *Lundomys* and *Holochilus*.

DISCUSSION

Dental morphology and phylogenetic relationships.—The M1 pattern of †*Carletonomys* resembles that of tetralophodont genera of Oryzomyini with laminate molars such as

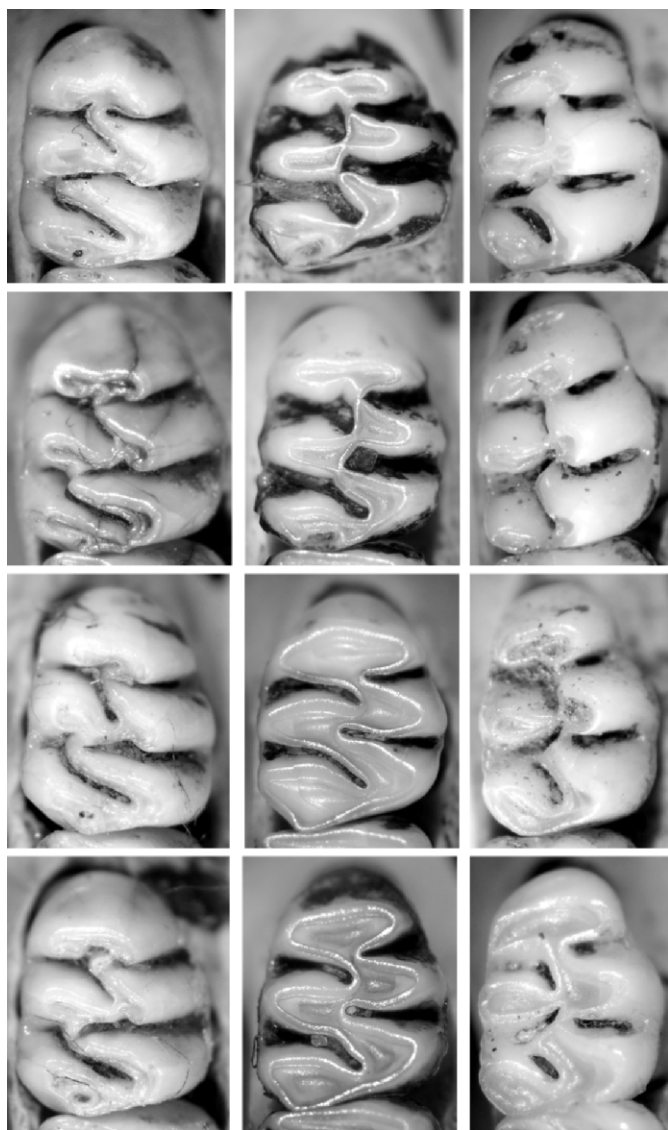


FIG. 3.—Occlusal pattern variation on M1 in young *Holochilus brasiliensis* (left column), *H. chacarius* (middle column), and *Pseudoryzomys simplex* (right column).

Pseudoryzomys, †*Noronhomys*, and *Holochilus*. *Lundomys*, a taxon phylogenetically related to the latter (Carleton and Olson 1999; Stepan 1996; Voss and Carleton 1993; Weksler 2006), displays a markedly different dental pattern. The same is true with respect to the only described extinct species of *Holochilus*, †*H. primigenus* (Stepan 1996).

The differences observed in the formation of the mesoloph and associated occlusal structures indicate a more complex evolutionary scenario for these structures than those traditionally envisioned (cf. Hershkovitz 1955, 1962; Weksler 2006). On one hand, the pattern displayed by *Pseudoryzomys* is not shared by its relative genera, such as *Lundomys*, †*Noronhomys*, and *Holochilus*; on the other hand, *H. brasiliensis* has a unique configuration due to the participation of a paralophule. These findings give additional support to the phylogeny proposed by Carleton and Olson (1999:42) where *Pseudoryzomys* is sister to

the (*Lundomys* (†*Noronhomys*, *Holochilus*)) clade (see also Weksler 2006).

The evolutionary modifications of the M1 (and M2) mesoloph in Oryzomyini clearly deserve a closer inspection. Most oryzomyines possess a well-developed mesoloph that reaches the labial margin of the teeth; in many taxa this structure is associated with a conspicuous paralophule (e.g., *Oecomys trinitatis* and *Oryzomys palustris*—Weksler 2006: figure 25). *H. brasiliensis* displays an extreme modification of this pattern: the anteriormost point of the median mure is “captured” by the paralophule losing its typical oryzomyine connection to the protocone (character 63 of Weksler [2006:45]). Coupled with this new morphological condition the penetration of the hypoflexus is outstanding, practically reaching the lingual margin. Morphological intermediate instances are exemplified by †*Carletonomys* and †*Noronhomys*; these taxa have the paracone connection without paralophule participation and the mesoloph still remains independent. Moreover, the morphology of *Lundomys* is even more generalized: the median mure is placed toward the molar midline, whereas the paralophule is virtually absent (a very short paralophule is present in the *L. molitor* holotype [see Voss and Carleton 1993: figure 5], suggesting some degree of polymorphism in this trait, but its independent nature regarding the mesoloph is clear).

It is important to note that in a detailed inspection of oryzomyine dental morphology, the paralophule on M1 was considered as absent within the tribe (Weksler 2006:117). As was stated above, several taxa (including the recently redescribed *Sigmodontomys*—McCain et al. 2007) show moderate or short lophes arising from the posterior face of the paracone that, at least topographically, are coincident with the structure traditionally regarded as paralophule (e.g., Hershkovitz 1962:71). The paralophule has a particular importance in sigmodontine molar evolution. Hershkovitz (1962:80–82) refers to it as “pseudomesoloph,” indicating that this structure acts as a functional replacement of the mesoloph. The same author stated that “with specialization, mesoloph (-id) and mesostyle (-id) degenerate, lose their triturative function and become obsolete or disappear altogether in hypsodont, laminate, triangulate and all other advanced types of cricetine molars” (Hershkovitz 1962:80; see also Hershkovitz 1955:644). It is not known how the paralophule in *Holochilus* and its ontogenetically early association with the anteriormost portion of the median mure resulted in a mesolophlike structure. The same process appears to have occurred in the dentition of *Sigmodon hispidus*. This convergence—because *Holochilus* and *Sigmodon* are only distant relatives (Weksler 2003)—may represent a stage in sigmodontine molar evolution reached when lamination (sensu Hershkovitz 1962) is achieved, an issue that certainly needs further exploration.

The unique combination of traits displayed by †*Carletonomys* deserves generic recognition. Other arguable classificatory schemes could be to consider this form as an extinct species of *Holochilus* or as a 2nd species of †*Noronhomys*. Inclusion in *Holochilus* can be discarded because living species of this genus have a dental pattern with a marked tendency, seen from *H. brasiliensis* to *H. sciureus* species complex, toward

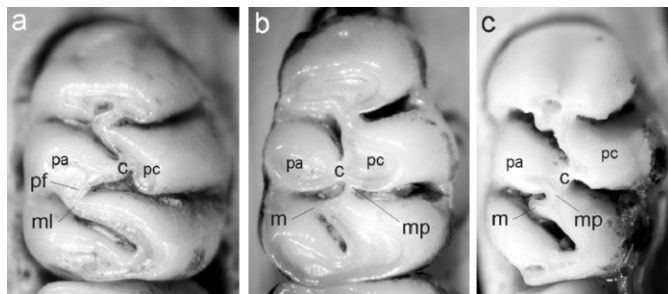


FIG. 4.—Contrasting mesoloph and related occlusal structures in right M1 of young individuals of a) *Holochilus brasiliensis*, b) *Pseudoryzomys simplex*, and c) *Lundomys molitor*. Abbreviations used are: c = constriction, m = mesoloph, ml = mesolophlike, pa = paracone, pc = protocone, pf = paralophule, and mp = median mure contact point.

enhanced lamination (character 19 of Carleton and Olson [1999:39]). †*H. primigenus* displays a different condition; therefore, as Steppan (1996) in its original description and as Carleton and Olson (1999) recognized, the allocation of this species to *Holochilus* is debatable. The remarkable similarity between 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 the radiation of tetralophodont oryzomyines. Taking into consideration the conservative mandible morphology of the living species of *Holochilus*, the mosaic of features shown by †*H. primigenus* (combining *Holochilus*-like mandible with *Lundomys*-like molars) suggest generic distinctiveness. The former consideration of †*Carletonomys* as an undescribed species of †*Noronhomys* (see above) conveys the similarity between these 2 taxa. I concur with the hypothesis of Carleton and Olson (1999), who suggested that †*Noronhomys* represents an insular endemic, probably derived from a continental relative. In this context, some dental traits (e.g., absence of the anterior mure) possessed by †*Carletonomys* can be considered indicators of ancestry (see Schmidt-Kittler [1984] for dental evolution in hypsodont rodents) with respect to †*Noronhomys* or *Holochilus*.

The consideration of at least 3 extant (*Pseudoryzomys*, *Holochilus*, and *Lundomys*) and 3 extinct (†*Carletonomys*, †*Noronhomys*, and putative unnamed genus for *H. primigenus*) genera constituting a clade departs from the prevailing view of the sigmodontine radiation where the extinct diversity is always far less developed than the living one. In fact, the fossil record of Sigmodontinae known to date, and which covers roughly 5 mya, includes only 9 extinct genera (excluding †*Carletonomys*—Pardiñas et al. 2002); whereas the extant diversity includes around 84 genera. Clearly, it is undesirable to produce spurious taxonomic inflation, but, at the same time, morphological diversity must be assessed and accordingly recognized (D'Elia and Pardiñas 2007). In this context, the erection of a new genus is the best choice in line with the present taxonomical paradigm, although with a major nomenclatural impact if, in turn, a new species of †*Noronhomys* was named.

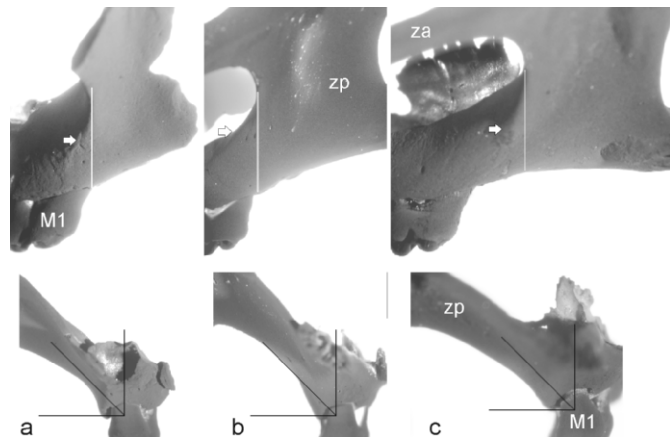


FIG. 5.—Right zygomatic plate (zp) in lateral (upper row) and frontal (lower row) views (not to scale) of a) †*Carletonomys cailoi*, b) *Holochilus brasiliensis*, and c) *Pseudoryzomys simplex*. White line marks the position of the posterior border of the zygomatic plate; arrow points where the zygomatic root arise; diagonal black lines mark 45° angle with respect to alveolar plane. Other abbreviations are: M1 = 1st upper molar and za = zygomatic arch.

Lundomys, †*Carletonomys*, †*Noronhomys*, *Pseudoryzomys*, and *Holochilus* represent a small radiation within the typically sylvan oryzomyine clade that allowed the tribe, in addition to *Oligoryzomys*, to invade perisylvan-temperate habitats. This event gave rise to several morphological modifications linked to dietary changes, including increasing molar hypsodonty and size, coronal flattening, lamination, and simplification (Hershkovitz 1962; Vorontsov 1962).

Age determination of the Oryzomyini fossil record.—Although the stratigraphical correlation and chronological interpretation of the sediments bearing †*Carletonomys* are not free of alternative interpretations (see above), I propose an antiquity >0.78 mya, probably slightly older than 1 mya (Ensenadan; early to middle Pleistocene). Steppan (1996) also stated an Ensenadan age for *H. primigenus* (Tarija, Bolivia), but the fossil remains of this species lack precise stratigraphical information (Steppan 1996:528). The same is true for the *Nectomys* material recovered from a fallen sedimentary block in Camet (north of Mar del Plata, Buenos Aires—Reig 1987). Two other taxa, *Holochilus* cf. *H. brasiliensis* and *Oligoryzomys* cf. *O. flavescens* have been cited for Ensenadan times, being both younger than 0.78 mya (Pardiñas 2004; Voglino and Pardiñas 2005). As so far known, †*C. cailoi* is the oldest known oryzomyine (Table 3).

In view of the recent phylogeny proposed by Weksler (2006), it can be hypothesized that southern latitudes—as those represented by the Pampean fossil record—were reached by oryzomyines in latter stages of their diversification. This coupled with the predominance of arid and semiarid environments during Miocene–Pliocene times (Tonni et al. 1999) could be an explanation of the absence of oryzomyines in pre-Ensenadan times. In fact, the presence of oryzomyines in recent Argentinean Pampean assemblages is poor, especially compared to akodontines, being limited to 2 species of *Holochilus*

TABLE 3.—Pampean fossil record for Oryzomyini and other sigmodontine tribes and taxa (compiled from several sources).

		Pliocene					Pleistocene			Holocene	
		Chapadmalalan		Marplatan							
		Montehermosan	Lower	Upper	Barranculobian	Vorohuean	Sanandresian	Ensenadan	Bonaerian	Lujanian	Platan
Phyllotini											
“Abrotrichini”											
Akodontini	<i>Akodon</i> Division*										
	<i>Bibimys</i> Division										
	<i>Oxymycterus</i> Division										
	<i>Scapteromys</i> Division										
Reithrodontini		?									
Wiedomyini											
Oryzomyini	<i>Holochilus</i>										
	<i>Lundomys</i>										
	† <i>Carletonomys</i>										
	<i>Nectomys</i>							?			
	<i>Oligoryzomys</i>										
	<i>Pseudoryzomys</i>										

* Akodontine division sensu D'Elia (2003).

(1 of marginal distribution) and 2 of *Oligoryzomys* (1 marginal—Pardiñas 1999a).

In summary, the available evidence suggests that the Pampean fossil record provides a limited window to investigate oryzomyine evolution because the main steps of this process were mainly extra-Pampean events, and solely offers patchy evidence restricted to oryzomyine taxa capable of invading marginal perisylvan and temperate habitats (e.g., *Lundomys*, *Holochilus*, *Oligoryzomys*, and, to a lesser extent, *Nectomys*). If this is true, then paleontological efforts focusing on understanding early stages of oryzomyine radiation should be concentrated in northern South American latitudes. This assertion does not neglect the importance of the Pampean fossil record to investigate the evolution of *Lundomys* and *Holochilus* (Teta and Pardiñas 2006).

Paleoenvironmental conditions.—Other vertebrate remains recovered together with †*Carletonomys* include fishes, chelid turtles, birds, frogs, and several mammals. In addition, the bearing sediments contained many freshwater snails belonging to *Biomphalaria* and *Littoridina*. Among the mammals, 3 armadillos were recorded, 1 unidentified pampaterid (cf. *Pampatherium*; MLP 98-I-15-5, dermal scute fragment), the extinct giant †*Propraopus* (several unnumbered dermal scutes), and the extant Chacoan *Tolypeutes matacus* (MLP 98-I-15-4, 1 isolated dermal scute). Rodents present other than †*Carletonomys* are the extant coypu *Myocastor* (MLP 98-I-15-2, incomplete mandible), an unidentified cavy (MLP 98-I-15-7, an isolated molar), an octodontid (MLP 98-I-15-9, isolated incisive), the poorly known echimyid †*Dicolpomys* (MLP 98-I-15-3, incomplete mandible with m1—Vucetich and Verzi 1998), and the widespread sigmodontine *Reithrodon auritus* (MLP 00-V-10-1, maxillary with M1-M2).

Regrettably, almost nothing can be surmised about the natural history of †*Carletonomys* from its anatomy. Considering

the plane molar surface and the moderate hypsodonty, a diet probably focused on green fibrous material can be inferred. The morphological resemblance between †*Carletonomys* and members of the *Lundomys*–*Holochilus* clade (see above), and the adaptation of these to flooded tropical and subtropical environments (e.g., Hershkovitz 1955; Massoia 1971) could be interpreted as indicator of this kind of habitat specialization for the former. Taxa recovered in association support the existence of a freshwater (or moderate saline) body under at least subtropical–temperate conditions during depositional times. Inferred habitats for the giant armadillos are in line with this hypothesis (Vizcaíno 1990); the same is true regarding the extant *Myocastor coypus*.

Several taxa recorded in the fossil assemblage where †*Carletonomys* was gathered also indicate the occurrence of higher temperatures than present ones. Chelid turtles such as *Hydromedusa* (the southernmost taxon of this group) are today absent from southern Buenos Aires Province and their southernmost populations occur by the Salado River (approximately 36°S—Cabrera 1998), about 3° latitude north of the study area. Although almost nothing is known about †*Dicolpomys*, a taxon restricted to its type locality in Lagoa Santa (Minas Gerais, Brazil—Winge 1887), echimyid rats are mainly tropical forms; the southernmost living record of the family, corresponding to *Euryzgomatomys*, lies in central Corrientes Province (approximately 28°30'S—Cabrera 1961), about 1,000 km north of type locality of †*Carletonomys*.

In brief, the fossil assemblage bearing the remains of †*Carletonomys* seems to reflect a freshwater body probably under warmer and moister climatic conditions than those occurring today in the area. This large oryzomyine constitutes another example of primarily Brazilian taxa (sensu Hershkovitz 1958) that, in response to Pleistocene interglacials, invaded austral latitudes (see also Pardiñas 2004; Teta and Pardiñas

2006; Verzi et al. 2004; Vucetich and Verzi 2002; Vucetich et al. 1997). In addition, it also indicates that the Pampean fossil record may still have rich pristine evidence regarding the outstanding sigmodontine radiation.

RESUMEN

Sobre la base de un maxilar derecho con el primer molar exhumado en depósitos del Pleistoceno (Ensenadense) del centro-sur de la provincia de Buenos Aires (Argentina) se describe un nuevo género y especie de Oryzomyini (Rodentia, Cricetidae). El nuevo taxón es uno de los mayores sigmodontinos conocidos, tanto extintos como vivientes y se relaciona morfológicamente con las ratas nutrias *Holochilus*, †*Noronhomys* y *Pseudoryzomys*. Puede ser diferenciado de estos taxones por una combinación de varios rasgos del primer molar superior, en particular un mesolofo bien desarrollado y una conexión libre entre para- y protoflexo. La ocurrencia de este sigmodontino sugiere condiciones ambientales más cálidas y posiblemente más húmedas durante el depósito de los sedimentos portadores, una hipótesis asimismo reforzada por otros vertebrados exhumados conjuntamente (e.g., tortugas, coipos, y el armadillo gigante †*Propraopus*).

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APPENDIX I

Specimens examined.—Acronyms for institutions are as follows: Colección de Material de Egagrópilas y afines del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina (CNP-E); Colección Elio Massoia, Buenos Aires, Argentina (CEM); Museo Nacional de Historia Natural y Antropología, Montevideo, Uruguay (MNHN); Museo de La Plata, La Plata, Argentina (MLP); National Museum of Natural History, Washington, D.C. (USNM).

†*Carletonomys cailoi* ($n = 1$).—Argentina: Buenos Aires, 1.13 km SW arroyo de Zavala mouth (MLP 98-I-15-1).

Holochilus brasiliensis ($n = 15$).—Argentina: Entre Ríos, Villa Elisa (cranial remains from owl pellets [CNP-E 72]).

Holochilus chacarius ($n = 19$).—Argentina: Chaco, Puerto Bermejo (cranial remains from owl pellets [CNP-E 58]).

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

Nectomys squamipes ($n = 3$).—Argentina: Misiones, Campo Viera (CEM 10091-10093).

†*Noronhomys vespucii* ($n = 1$).—Brazil: Fernando de Noronha Island (USNM 490297, cast).

Pseudoryzomys simplex ($n = 12$).—Argentina: Chaco, Lote 16 (cranial remains from owl pellets [CNP-E 185]).