

Short Note

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The Pleistocene record attributed to the cricetid genus *Nectomys* (Rodentia, Sigmodontinae): unexpected connections

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Abstract: *Nectomys* is a cricetid genus of medium-large sized oryzomyines broadly distributed in creeks and rivers of lowland South America. It has been mentioned in two localities, one in Bolivia and another in Argentina in Pleistocene assemblages. After revising the fossils that supported both records we conclude that they are not *Nectomys*. The record from Bolivia is *Reigomys primigenus*. The record from Argentina is attributable to *Scapteromys*. In conclusion, past occurrences of *Nectomys* are restricted to those of undifferentiated Quaternary age from Brazilian caves. The unexpected connections between fossils described here are discussed to explore the rationality behind detected misidentifications.

Keywords: *Holochilus primigenus*; Pleistocene; *Reigomys*; *Scapteromys*.

Within more than 400 living species that compose the cricetid subfamily Sigmodontinae, just a handful developed amphibious adaptations in tropical and temperate lowlands and most of those are concentrated into a single tribe, oryzomyines. *Nectomys* Peters 1861, encompass medium-large bodied rats broadly distributed in tropical and subtropical South American freshwater courses (Bonvicino and Weksler 2015). The alpha-taxonomy of this genus was recently revised and eight living species were recognized including two proposed as new, despite being unnamed (Chiquito 2015). Dental morphology in *Nectomys* is very conservative across the species and easy to recognize at a generic level by the laminated aspect of main occlusal structures, plus a tendency to general

simplification, planation and hypsodonty (Hershkovitz 1944). Therefore, fossil material, if any, can be confidently associated with this genus on morphological grounds.

Nectomys has been mentioned twice in paleontological literature (excluding records from undifferentiated Quaternary deposits in Brazil, see below), although never published in full. The first mention was in a general summary about South American Quaternary vertebrates which were listed as integrating the fossil assemblage recovered in the Bolivian locality of Tarija (cf. Marshall et al. 1984: 19 and 32, Marshall and Sempere 1991: 642, Pardiñas et al. 2002: 220 and 224). The second mention was also first published in Marshall et al. (1984: 27) where *Nectomys squamipes* Brants 1827, was reported for the Mar del Plata-Miramar (Buenos Aires, Argentina) Neogene sequence. This finding was briefly quoted again in Reig (1987: 381–382) when he mentioned that fossils of another sigmodontine, referred to as *Akodon cursor*, were recovered “...in association... with remains of *Reithrodon auritus*, *Nectomys squamipes* and *Ctenomys* sp. in a bone conglomerate probably representing fossil owl pellets... extracted from a rocky block from the Atlantic cliffs 5 km N of Colonia Camet”. The fossil occurrence of *Nectomys* in Southern Buenos Aires province was posteriorly repeated by Pardiñas et al. (2002) and introduced by Pardiñas (2008: 1270) with the goal to discuss oryzomyine evolution indicating that “For the Pampean region of Argentina... the oldest oryzomyines are limited to a presumed Ensenadan record of *Nectomys* (Reig 1987)...”.

Both records of *Nectomys* referred to Middle Pleistocene deposits, the Tarijan and the Pampean, apparently have the same original source in the unpublished dissertation of Reig (1972). In fact, Reig (1972: 100–108) revised the taxonomy of *Nectomys*, described in full the record from Buenos Aires province and also added a brief minute about a collection of fossil cricetids from Tarija where he reported *Nectomys squamipes* (Reig 1972: 379–380). Differing from most of the Reig’s dissertation, these results were never published. Perhaps this was a fortunate situation because according to our conclusions, these presumed

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Nectomys must be referred to other cricetid genera. In the following paragraphs, we present our results based on the inspections of these fossils. Those of Bolivia are housed in the paleontological collections of the Muséum National d'histoire Naturelle (Paris, France; under the acronym F-TAR), together with other cricetids and vertebrates secured by Hoffstetter (1963). Argentinean fossils are deposited in La Plata Museum (La Plata, Buenos Aires, Argentina; under the acronym MLP) in a collective sample composed by several dozens of fossils of small mammals, mostly isolated molars but also fragmentary mandibles and maxillaries. In order to describe anatomical features, we followed Reig (1977) for dental nomenclature; Patton et al. (2015) is used here as the general systematic treatment of the subfamily. The measurements provided are reported in mm and were obtained with a digital caliper corresponding to maximum length and width of each molar. Studied specimens, fossil and recent, are listed in Appendix 1.

The material recovered in Tarija integrates a sample collected by the French paleontologist Robert Hoffstetter; this author advanced the occurrence of the sigmodontine *Holochilus* Brandt 1835, within this Pleistocene assemblage (Hoffstetter 1963: 197). However, Reig (1972: 380) was clear connecting this record with his *Nectomys* because “*Nectomys squamipes* is the more abundant fossil in this small collection (Tarija sample) and it was undoubtedly on the basis of specimens of this species that Hoffstetter recorded the presence of *Holochilus* (as determined by F. Petter) in this faunule... I compared these specimens with the type and additional specimens of *Nectomys garleppii*... I did not find any basis to separate the fossils from the living form...” Interestingly Steppan (1996) described a fossil *Holochilus* from Tarija, *Holochilus primigenus*, although based on materials recovered by the Field Museum (FMNH, Chicago, USA) paleontological expeditions made by Elmer Riggs in 1924 and 1927 (Steppan 1996: 523). This species was recently used to erect a putative fossil genus, named *Reigomys* Machado et al. 2014, supposedly allied to several living marsh rats. In brief, the few studies made on these fossils from Tarija basin indicate a contortuous history between *Nectomys* and *Holochilus*. We examined the Tarija material housed in Paris assigned to *Holochilus* by Hoffstetter (1963) and then to *Nectomys squamipes* by Reig (1972). They are a left maxillary with M1–M3 (F-TAR 2; Supplemental Figure 1) and a left mandible with the incisor and m1–m3 (F-TAR 4). Our first conclusion is that both studied fossils belong to the same taxon, taking into account the congruence between general morphology and size. Our second conclusion is that they are conspecific with the oryzomyine

entity described and illustrated by Steppan (1996) as *Holochilus primigenus*, posteriorly used as genotype of *Reigomys* by Machado et al. (2014). Crucial dental features in order to separate these fossils from *Nectomys squamipes* and conversely, to connect with *Reigomys primigenus* are, among others (Figure 1; Supplemental Figure 1), crested coronal surfaces (vs. the typical planate condition of *Nectomys*), small mesoloph/lophids (vs. large mesoloph/lophids in *Nectomys*), anteriorly open procingulum (vs. anteriorly entire procingulum in *Nectomys*), compressed m3 (vs. large m3 in *Nectomys*). However, having said that, it is important to note that upper dentition in *Reigomys* looks more similar to *Nectomys* than to *Holochilus* or *Lundomys* (Supplemental Figure 1), casting doubts about the validity of the phylogenetic relationships of these forms advanced by Machado et al. (2014).

The material collected from a fallen block near Colonia Camet in Buenos Aires province and referred to as *Nectomys* (cf. Reig 1972, 1987) comprises four isolated molars, two upper and two lower ones (MLP 62-VII-27-95d; Figure 2 and Supplemental Figure 2). Judged by their morphology and wear degree, all belong to the same young individual. Reig (1972: Figure 7) reaches the same conclusion because he arranged the isolated teeth as composing a dental series. However, we cannot agree with this author regarding the taxonomic allocation of these fossils. Reig (1972: 106) justified the generic assignation that “there is no reasonable doubt that the fossil specimens belong to *Nectomys*, as they agree with all the characteristic states of the molar teeth of this genus... In size, they are only comparable to *N. squamipes*... The available material does not allow one to believe that the fossil specimens could belong to an extinct species different from *squamipes*”. Probably, he was confounded by the very young condition of the individual represented by the studied fossils and the inadequacy of recent materials at hand to make comparisons. MLP 62-VII-27-95d upper molars are characterized by a crested condition of the coronal surface, a dissected procingulum in the M1 and small mesoloph in both M1 and M2 (Supplemental Figure 2). These traits are very different from those displayed by young *Nectomys*, typified by a tendency to planate the surface, a complex enlarged entire procingulum and large mesoloph on both mentioned molars (cf. Hershkovitz 1944; Supplemental Figure 2). Observed differences are equally or more trenchantly judged from lower molars. To the best of our understanding, the occlusal morphology displayed by the MLP 62-VII-27-95d is impossible to reconcile with any of the living species included in *Nectomys*. However, they look very close to those of the sigmodontine genus *Scapteromys* Waterhouse 1837 (Figure 2). This akodontine



Figure 1: Comparison between F-TAR 4 (A, B and C, left lower jaw in lingual, labial and dorsal view, respectively; Middle-Late Pleistocene, Tarija, Bolivia) originally referred to *Nectomys squamipes* and PM 56940, holotype of *Reigomys primigenus* (D, right mandible in dorsal view, picture obtained from an epoxy cast, inverted; Middle-Late Pleistocene, Tarija, Bolivia). Scale=5 mm.

is characterized by medium-sized molars with crested coronal surfaces, dissected procingulum and moderately well-developed mesoloph/phids. These latter traits,

unusual in akodontines, promoted to Pardiñas (1996) to typify scapteromyines as “complex tetralophodont” sigmodontines. In particular, MLP 62-VII-27-95d lower molars show a somewhat amplified condition in mesolophid development, probably related to aging. In any case, the fossil material from Camet is almost indistinguishable from living examples of *Scateromys* spp. with the same degree of wear (Figure 2). Hence, we can discard this record from the fossil history of *Nectomys* and add it to the past evidence of *Scapteromys*. The latter has a biochron that coarsely involves the last millions of years. The MLP 62-VII-27-95d was found in a fallen block and therefore, its attribution to the Miramar Formation (Middle Pleistocene) promoted by Reig (1987: 382) is unconfirmed. We have worked many times in the Atlantic cliffs near Colonia Camet where the studied material came from, a sector called Félix U. Camet (37.90° S, 57.52° W). There, sedimentary outcrops are about 10 m high and fossils are small mammal assemblages, which are not infrequent (see the heavy review in Tassara and Cenizo 2014). Many stratigraphical units integrate these cliffs and the assignation to a fallen block is largely problematic.

A summary of our findings related to the Quaternary record attributed to *Nectomys* is given in Appendix 2. In brief, *Nectomys* does not have Pleistocene occurrences, neither in Bolivia, nor in Argentina. Those reported for the Brazilian Quaternary, materials extracted from cave deposits of undetermined age, are pending for confirmation. The record for Toca da Boa Vista, a famous cave in Bahia, seems erroneous; at least the material attributed to *Nectomys* and figured (Parisi Dutra 2012: Figure 7) belongs to *Holochilus*. In this context, the only confident record appears to be those described by Winge (1887) for Lapa da Escrivania Nr. 3, 5 and 11, in Minas Gerais. *Nectomys* is consistently absent in the several Holocene assemblages studied from Rio Grande do Sul and São Paulo (Hadler et al. 2016 and the references therein), an issue that deserves a further scrutiny keeping in mind that today is broadly distributed there (Chiquito 2015).

The findings reported in this note reflect unexpected connections. As a corollary, it is probably worthwhile to briefly address the rationality behind these misidentifications. The certainty displayed by Reig (1972) connecting the fossils of Tarija with the holotype of *Nectomys squamipes* is so strong that our conclusion about the *Reigomys primigenus* classification of these materials is necessarily shocking. During the 70s, Reig worked, as did several other morphologists devoted to sigmodontines (e.g. P. Hershkovitz, O. Pearson), under the evolutionary paradigm of genera capable of containing an important degree of morphological variation. In fact, Hershkovitz’s

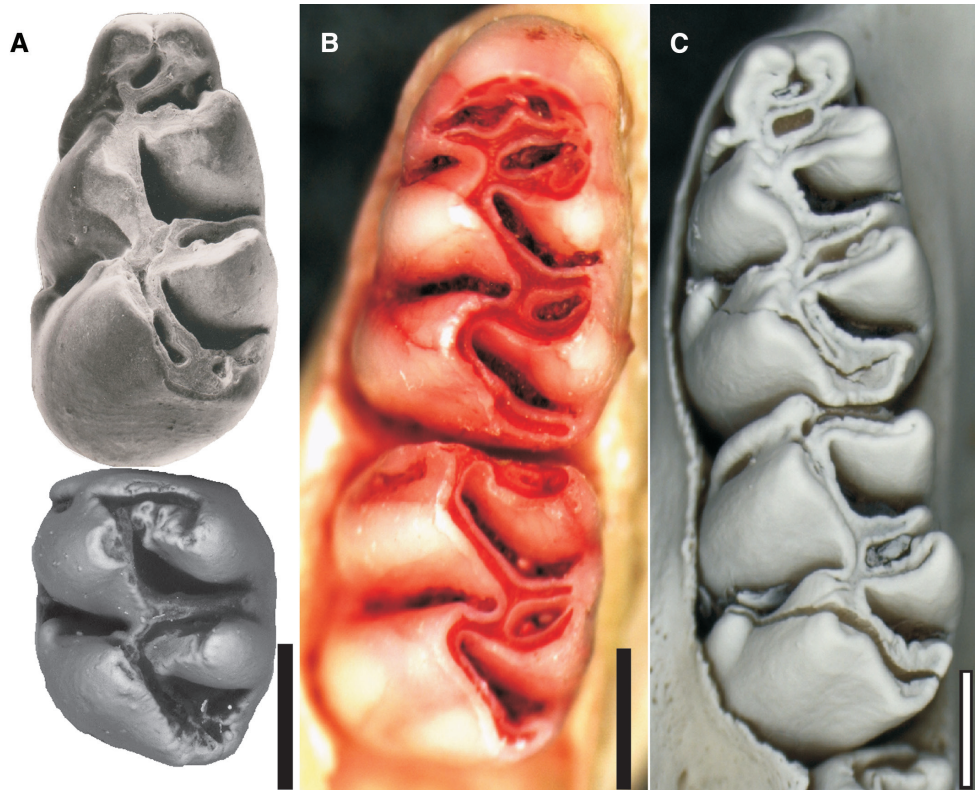


Figure 2: Occlusal views of left m1 and m2: (A) MLP 62-VII-27-95d (Parque Camet, Buenos Aires, Argentina; Middle Pleistocene?) originally referred to *Nectomys squamipes*; (B) MACN 49.468 (Misiones, Argentina; Recent), *N. squamipes*; (C) CNP-E 882-1 (Selvas del río de Oro, Chaco, Argentina; Recent), *Scapteromys aquaticus*. Scale=1 mm.

(1966) hesitations when he coined *Kunsia* clearly reflect this base concept, “The non-technical term scapteromyine is employed here in the sense of a super-genus or generic group coordinate with oryzomyine, phyllotine... With fuller knowledge... one or another of these natural aggrupations of closely related and nominal genera may be consolidated into a single well defined genus” (Hershkovitz 1966: 82). It is evident that the general perception of the morphological distinctiveness must have been in the eyes of these scholars, the guidance to interpret as conspecific individual variation features that today are taken as trenchant differences, enough to separate genera. The gradual spread that is now called “integrative taxonomy”, an approach reported in several seminal works with muroids sometimes under the term “byosystematics” (see Patton and Hafner 1983), radically changed our baseline to interpret differences. The “generic unit” handled by Hershkovitz (1966) capable of containing the entire “evolutionary line” hypothesized from *Scapteromys* to *Kunsia* disappeared in favor of smaller and more cohesive atomized groups. The current tendency in sigmodontine taxonomy is toward a growing recognition of full genera (Patton et al. 2015). Recent numbers indicate that

the subfamily generic content (93 genera including historical extinctions) is threefold Cabrera (1961) listed; less than 30% of this increment derived from new field-based taxa. Taking into account that there are still large polytypic genera, such as *Akodon* or *Thomasomys*, the proposition of new genera among sigmodontines will be a common fact in the following years. A horizon of generic numbers to equal murines by 2050 is not disparate.

Appendix 1: Specimens studied

Specimens studied in this contribution belong to the following collections:

Colección de Mamíferos and Colección de Material de Egagrópilas y Afines del Centro Nacional Patagónico (CNP and CNP-E, respectively; Puerto Madryn, Chubut, Argentina), Colección Nacional de Mastozoología, Museo Argentino de Cs. Naturales (MACN; Buenos Aires, Argentina), Field Museum of Natural History (FMNH, PM; Chicago, USA), Museo de La Plata (MLP; La Plata, Buenos Aires, Argentina), and Muséum National d’histoire Naturelle (F-TAR; Paris, France).

Reigomys primigenus Steppan 1996.– PM 56940, right dentary with m1–3 (epoxy cast of holotype; Pleistocene, Tarija, Bolivia).

Nectomys squamipes: Reig 1972.– MLP 62-VII-27-95d, left M1 (length=3.36, width=2.12), left M2 (length=2.16, width=2.08), left m1 (length=2.80, width=1.80), left m2 (length=2.12, width=1.72); 5 km Parque Camet, Buenos Aires, Argentina; Middle Pleistocene? F-TAR 2, left maxillary with M1–M3, and F-TAR 4, left mandible with the incisor and m1–m3; Tarija, Bolivia; Middle-Late Pleistocene.

Nectomys squamipes Brants 1827.– MACN 49-468, MACN 52.13, Misiones, Argentina; CNP 2525, 2527, Refugio Moconá, Misiones, Argentina; CNP 2528, Reserva de Usos Múltiples Guaraní, Misiones, Argentina.

Scapteromys aquaticus Thos.– CNP 14, Muelle Madre-selva, Delta del Paraná, Buenos Aires, Argentina; CNP 710, 711, 17 km W Cnia. M. Villafañe, Formosa, Argentina; CNP 717–721, Club de Pesca La Terraza, La Balandra, Buenos Aires, Argentina; CNP-E 882–1, Selvas del río de Oro, Chaco, Argentina.

Appendix 2: Taxonomic summary for the species discussed in this contribution

Subfamily: Sigmodontinae

Tribe: Akodontini

Scapteromys sp.

Nectomys cf. *squamipes*: Reig 1972: 103

Nectomys: Marshall et al. 1984: 19

Nectomys squamipes: Reig 1987: 381.

Tribe: Oryzomyini

Reigomys primigenus (Steppan 1996)

Holochilus: Hoffstetter 1963: 197

Nectomys squamipes: Reig 1972: 380

Nectomys: Marshall et al. 1984: 32.

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with us photographs derived from her heavy revision of *Nectomys*. P. Hadler kindly assisted in feedback on *Nectomys* records in Brazil. Funds for this research were derived from PICT (Agencia) 2014-1039 (to UFJP). We deeply appreciate the help received from the above-mentioned persons and institutions.

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Supplemental Material: The online version of this article (DOI: 10.1515/mammalia-2017-0020) offers supplementary material, available to authorized users.