Short Note

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Taxonomic status of *Mus talpinus* Lund (Rodentia: Sigmodontinae) from the Quaternary deposits of Lagoa Santa, Minas Gerais, Brazil and its paleoenvironmental meaning

Abstract: *Mus talpinus*, a fossil sigmodontine rodent exhumed by P. W. Lund from Quaternary deposits in the Lagoa Santa area, Brazil, has been varyingly allocated to the genera *Oxymycterus*, *Blarinomys* or *Juscelinomys*. After our examination of the holotype, an anterior fragment of the skull from Lapa da Serra das Abelhas, Minas Gerais, Brazil, we refer the name *talpinus* to the genus *Brucepattersonius*. These mice are sylvan akodontines, widespread in the Atlantic Forest, with the nearest extant record approximately 250 km southeast of Lagoa Santa. The addition of *Brucepattersonius* to the fossil sigmodontine fauna of Lagoa Santa suggests a non-analogous assemblage of species in this area during the Late Pleistocene.

Keywords: Akodontini; *Blarinomys*; *Brucepattersonius*; Cricetidae; fossil; *Juscelinomys*; Lund; *Mus talpinus*; *Oxymycterus*; Winge.

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After nearly two centuries, the rich collection of fossil vertebrates obtained by Peter W. Lund in and around Lagoa Santa, Brazil, embraces unsuspected mammals. Cricetid rodents are the dominant members of this assemblage, both in taxon richness and number of specimens, all recovered from several cave deposits by the famous Danish naturalist (Cartelle 2002). Quaternary deposits of two caves in particular, Lapa da Escrivania Nr. 5 and Lapa da Serra das Abelhas, provided more than 15 fossil and recent taxa (Winge 1887, Voss and Myers 1991). Although several of these species have been identified as living forms, a few remain poorly understood. Winge (1887) referred to the sigmodontine genus *Oxymycterus* four taxa from the Lagoa Santa area, namely *rufus*, *breviceps*, *cosmodus* and *talpinus*. The first two have now been identified with the living akodontines *Oxymycterus dasytrichus* and *Blarinomys breviceps*, respectively (Thomas 1896, Oliveira 1998). Allocations of the other two names, *cosmodus* and *talpinus*, remain unresolved.

Lund (1839: 208) coined *Mus talpinus* (preoccupied by *Mus talpinus* Pallas, 1770, the type species of *Ellobius* Fischer, 1814) in a list of fossil forms from the Lagoa Santa caves and the das Velhas river area, Minas Gerais, Brazil. Trouessart (1898: 539) referred *talpinus* to Lund (1840: 281), although Lund first used this name in a letter published in the Annales des Sciences Naturelles in 1839. In a subsequent work, Lund (1840) gave the first data about *talpinus*, noting in particular the development of a large crest on the humerus that suggested a marked aptitude for digging. Lund coined the name *talpinus*, etimologically derived from *Talpa* Linneaus, the classical moles (Soricomorpha, Talpidae), in clear reference to the putative fossorial condition of the fossil. Winge (1887: 36) transferred *Mus talpinus* to *Oxymycterus*, under the combination *Oxymycterus talpinus* (Lund) and illustrated an anterior portion of a skull from Lapa da Serra das Abelhas (Winge 1887: Pl. II, Figure 13). This cranial fragment, the holotype of *M. talpinus* (fixed by monotypy, according to Article 73.1.2; ICZN 1999), is housed in the Natural History Museum of Denmark, Lund Collection (ZMK, Copenhagen, Denmark), under catalog number ZMK 1/1845:13257. Winge (1887) also reported the species from Lapa da Escrivania Nr. 5, another important cave excavated by Lund, based on isolated mandibles. The latter are housed unnumbered in the ZMK collection; however, this material does not represent the same species as the skull fragment from Lapa da Serra das Abelhas (U. Pardiñas, personal observation).

As usual in his work, Winge (1887: 36) described *talpinus* using for comparison a better known species, in this case a form of the genus *Oxymycterus* that he referred to *rufus* [sensu Winge 1887, a taxon now included within the *dasytrichus* group of *Oxymycterus* by Oliveira (1998)]. Winge stated that *talpinus* was smaller than *rufus* in general size, with a shorter rostrum and smaller incisive foramina but a broader interorbital region. Later, Trouessart (1898: 539) listed *Oxymycterus talpinus* as extinct. Thomas (1896) was the first to connect *talpinus* to *Brucepattersonius*, although this genus was not recognized for another century (Hershkovitz 1998). At the time, in describing *Oxymycterus iheringi*, Thomas (1896: 309) wrote "probably it [*O. iheringi*] is most nearly related to Winge's *O. talpinus*, as yet only known fossil from Lagoa Santa, but has rather a shorter head and shorter palatine foramina..." This hypothesis, astonishing evidence of Thomas' acute taxonomic eye, remained unnoticed in subsequent literature. For example, Tate (1932: 21), in summarizing the taxonomic history of several akodonts, wrote "it seems to me that *talpinus* Lund, whose humerus that author described (1841, p. 276) as distinctly fossorial in character, may belong in *Blarinomys*." Probably based on this suggestion, Paula Couto (1950: 272), as reviewer of the translation of the complete work of Lund to Portuguese, in a footnote coined the new name combination *Blarinomys talpinus*. Subsequently, Moojen (1965) proposed another generic allocation for *talpinus* when he described the akodontine genus *Juscelinomys* from Brasília, Brazil. Moojen (1965: 284) wrote "*Oxymycterus talpinus* Winge, 1888... não é, evidentemente, um *Oymycterus*. Os caracteres cranianos, especialmente o diástema menor, o bordo posterior do forame infraorbitário aquem da série molar superior, o palato e a forma da lâmina zigomática anterior – autorizam considerá-lo, provisòriamente, um *Juscelinomys*." Finally, Matson and Abravaya (1977: 74) briefly discussed the allocation of *talpinus* to *Blarinomys*, concluding that the fossil did not belong to this genus.

A new chapter in the history of *talpinus* began in the 1990s. In a clearly unintended misspelling, Musser and Carleton (1993: 706) coined a new name combination for this taxon as "*Juscelinomys vulpinus* (Winge 1887)." These authors may have followed Moojen (1965) who had referred to "*vulpinus*" (= *talpinus*) as a name created by Winge, not Lund. This issue deserves further attention (see below). In addition, Musser and Carleton treated "*vulpinus*" as a living form for the first time. Shortly thereafter, Fonseca et al. (1996: 28), although listing *talpinus* among the living mammal fauna of Brazil, cited in a footnote the opinion of Alfredo Langguth that "*J. vulpinus* is known only as a subfossil and may not be a recent species." In the most

recent edition of *Mammals of the World*, Musser and Carleton (2005) correctly listed *talpinus* under the account of *Juscelinomys* and commented on the possible availability of the name in connection with two new species of this genus erected by Emmons (1999). To close our review of the history of *talpinus*, Oliveira's (1998: 61) unpublished observation deserves special attention. This author noted that *talpinus* shared with *Oxymycterus iheringi* a ridge of bone crossing the area in front of the molar toothrow in the region between the margins of the incisive foramina and the base of the inferior zygomatic root (Figure 1), a trait not found in other species of *Oxymycterus*. In this same year, Hershkovitz (1998) included *O. iheringi* in his newly erected *Brucepatteronius*.

In summary, four generic allocations have been suggested for *Mus talpinus* Lund, including *Oxymycterus*, *Blarinomys*, *Juscelinomys* and *Brucepattersonius*. Each of these hypotheses can be tested by direct comparison with the holotype of *talpinus*. Materials used in these comparisons are listed in Appendix 1.

The holotype of *Mus talpinus* consists of the anterior portion of the skull (Figure 2) with the incisors, the entire left molar series and the right M1-2 present; the apical portion of the rostrum is broken, but the nasals are in their original position; the frontals are broken near the coronal suture; the sides of the rostrum are partially damaged, especially the nasolacrimal capsules; the zygomatic plates are almost intact, with the left better preserved although
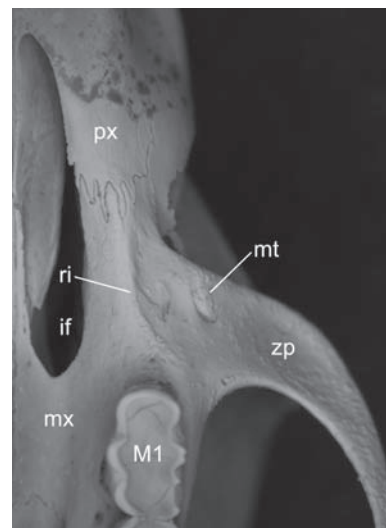
Figure 1 Detail of the skull of *Brucepattersonius* sp. (CNP 1745) in ventral view showing the anatomical traits present in the basal region of the inferior zygomatic root.
Abbreviations: if, incisive foramina; M1, first upper molar; mt, masseteric "tubercle"; mx, maxillary; na, nasal; px, premaxillary; ri, ridge of bone; zp, zygomatic plate.
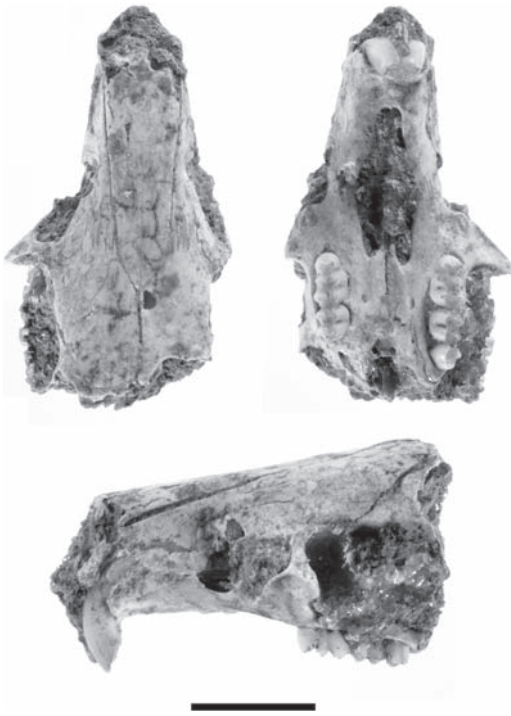
Figure 2 Holotype of *Mus talpinus* Lund (ZMK 1/1845:13257, Lagoa Santa, Brazil).
Anterior portion of skull in dorsal (top, left), ventral (top, right) and lateral (bottom) view. Graphic scale=5 mm.

broken at the origin of the zygomatic arch; and the palate is almost complete, with its posterior border scraped on its right side. The bone is well preserved although pitted, yellowish in coloration, with cavities filled by hard reddish calcitic material. A moderate displacement of the left hemimaxillary breaks the symmetry of the skull in the ventral view. The artist, when rendering the drawing of *talpinus* in Winge (1887), apparently "corrected" each of these "irregularities." The degree of fossilization of this specimen is comparable to other materials recovered from Lapa da Serra das Abelhas, including types of *Calomys plebejus* (cf. Voss 1993: Figure 14; allocated to *Delomys*) or *Calomys anoblepas* (cf. Pardiñas and Teta 2011: Figure 1; allocated to *Juliomys*).

This skull fragment lacks an original label, although a direct indication of its correspondence to *talpinus* is the partial word "talp" (a plausible abbreviation for *talpinus*) penciled in black on top (possibly handwritten by Lund). Regarding authorship attribution of the name, it is well known that Peter Lund briefly described new fossil sigmodontines based on humeral traits. However, several of his names were later applied and connected by Winge (1887) to cranial material also collected by Lund, such as in the case of *Habrothrix orycter* or *Scapteromys principalis*, usages that were perpetuated by subsequent authors. To

our best understanding, there is no reason to credit *talpinus* to Winge rather than to Lund.

The skull of *talpinus* has a moderately long and broad rostrum, although some degree of the apparent breadth is artificial, produced by the sedimentary matrix adhering to the sides (Figure 2). In a lateral profile, the skull is flat dorsally. Nasals are well developed, covering the rostrum partially, with straight borders gradually divergent anteriorly; the mid-nasal suture is visible as a thin line along the entire length of the bone. The nasofrontal suture is markedly V-shaped, with its posteriormost point located behind a line delineated by the premaxillary-frontal junction. The interorbital region is broad and tubular; some broadness can be attributed to the damaged right frontal border. In fact, an indication of interorbital constriction is clear on the left side of the skull. Laterally, one's eye is impressed by the height and robustness of the skull. A moderately developed gnathic process is evident, although almost covered by matrix on the anterior face of the incisors; a flake of bone anterodorsal to the left incisive indicates the degree of development of the premaxillary surpassing the frontal face of the incisor. The nasolacrimal capsule is partially eroded, but the nasolacrimal foramen seems to be oblique in orientation. The zygomatic plate is low and reclined backwards, with its posterior border located even with the anterior face of M1. The origin of the superficial masseter is marked by an osseous prominence. The upper root of the zygomatic is robust. The incisive foramina are moderately piriform in *talpinus*, although a full appreciation of size and shape is obscured by matrix; the posterior ends are rounded and reach the protocones of M1. A recessed area is present anterior to each molar row, lingually and labially flanked by a ridge of bone and the osseous protuberance mentioned above, respectively. The palate is flat, uncomplicated and short (sensu Hershkovitz 1962); the anterior border of the mesopterygoid fossa is located even with the posterior faces of M3. Although the fossa is incomplete, the short distance between its anterior corner and the maxillary process suggests that the mesopterygoid fossa is broad.

Wear on the maxillary teeth suggests that the holotype of *talpinus* is a subadult individual, as M3 still retains some occlusal structures, such as an open paraflexus. The incisors are robust, slightly opisthodont, with a cream enamel band. The molars are brachyodont, with a crested coronal occlusal surface and slightly alternating main cusps. The M1 has a well-marked anteromedian flexus separating two subequal conules; both the anteroloph and mesoloph + paralophule are fused to paracone and metacone, respectively, enclosing enlarged fossetes disposed on the midline of the molar; the posteroloph is short. The M2 is
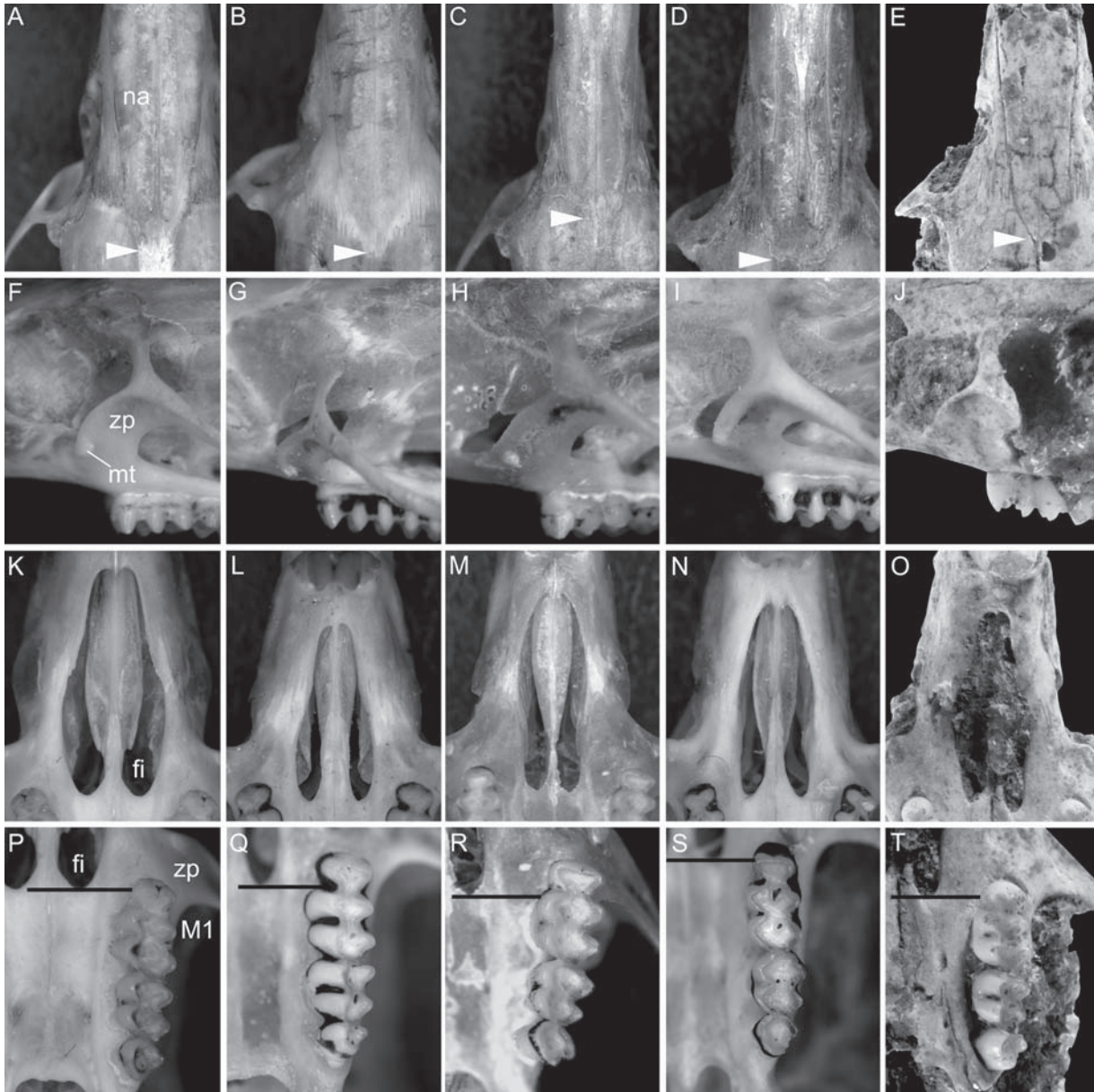
Figure 3 Comparisons involving, from left to right, *Lenoxus apicalis* (MVZ 171515), *Blarinomys breviceps* (CM 2640), *Oxymycterus hucucha* (MVZ 119948), *Brucepattersonius* sp. (CNP 3006) and *Mus talpinus* (ZMK 1/1845:13257).
(A–E) Posterior end of nasals (indicated by the white arrow); (F–J) zygomatic plate; (K–O) incisive foramina; and (P–T) upper molar toothrow and palate (black line highlights the posterior extension of the incisive foramina). Abbreviations: fi, incisive foramina; M1, first upper molar; mt, masseteric "tubercle"; na, nasal; zp, zygomatic plate. Not scaled.

similar to the comparable portion of the M1, with a well-developed anteroloph. The M3, although reduced with respect to the M2, is complex, with an interior enamel ring in the central position and an open paraflexus.

In general terms, the craniodental anatomy of *talpinus* resembles that of several akodont rodents, including *Blarinomys*, *Brucepattersonius*, *Juscelinomys*, *Lenoxus*, "*Microxus*," *Oxymycterus* and *Podoxymys*; roughly the "oxymycterine" group sensu Hinojosa et al. (1987). The remainder of living or extinct members of this Akodontini, particularly those genera most similar to *talpinus* (*Akodon*, *Necromys*, *Scapteromys* and *Thaptomys*) can be ruled out as plausible linkages to Lund's taxon by trenchant differences in their rostral and zygomatic plate morphologies. Furthermore, a combination of both cranial and dental traits provides useful evidence that *talpinus* cannot be easily allocated to most of the "oxymycterines" group of genera (Figure 3). For example, the moderately shorter

rostra of *Blarinomys*, *Juscelinomys* and *Podoxymys* contrast with the condition in *talpinus*. In addition, *Blarinomys* has a unique set of traits, including hypsodont teeth, very reduced zygomatic plates well exposed when viewed from below and very conspicuous masseteric "tubercles" (the quotation marks indicate that the true masseteric tubercle condition is that of some ichthyomyines; cf. Voss 1988). In turn, *Juscelinomys* has moderately well-developed zygomatic plates, more similar to those of *Oxymycterus*, with an upper free border clearly evident when viewed from above, penetrating incisive foramina that reach the protocones of M1 and nasal bones that end anterior to the lacrimal plane (cf. Moojen 1965, Emmons 1999). Finally, *Podoxymys* also displays large incisive foramina and a differential configuration of the zygomatic plate (cf. Pérez-Zapata et al. 1992). These comparisons generally falsify prior allocations of *talpinus* to either *Blarinomys* or *Juscelinomys*, although, to be fair, the putative connection to *Blarinomys* was based on similarities in their humeri, not craniodental features. The general cranial morphology of *Lenoxus* is very similar to that of *talpinus*, although the former is larger in both the cranium and molars. Furthermore, the teeth of *Lenoxus* are strongly crested and have a persistent anteromedian cusp on M1, and the osseous swelling located at the origin of the superficial masseter is displaced laterally on the zygomatic plate (Figure 3). "*Microxus*," restricted here to *mimus*, the type species of the genus, is slightly smaller than *talpinus* and has a different zygomatic plate morphology, characterized by a straighter anterior border, less conspicuous masseteric swelling and less oblique nasolacrimal fissure, features consistent with its shorter rostrum.

In contrast to the above comparisons, the majority of similarities of *talpinus* lie with both *Brucepattersonius* and *Oxymycterus*, resurrecting the original perceptions of both Winge (1887) and Thomas (1896). With respect to the morphological diversity among species of *Oxymycterus* (e.g., Hershkovitz 1994, Oliveira 1998), we concentrated on comparisons between *talpinus* and similar-sized species of *Oxymycterus*, namely *Oxymycterus hiska* and *Oxymycterus hucucha*. Both of the latter contrast with *talpinus* in having large incisive foramina, elliptical in outline, that extend posteriorly to the protocones of M1. In addition, the molars of *Oxymycterus* are mesodont and simplified, the interorbital region is hourglass in shape and the nasofrontal suture is U-shaped and positioned forward of the lacrimal plane (Figure 3). As Oliveira (1998) highlighted, an important difference between *talpinus* and *Oxymycterus* is the more attenuate condition in the latter of the ridge of bone located in the area in front of the molar toothrow.

Traits listed by Hershkovitz (1998: 227–228) when he diagnosed *Brucepattersonius* and useful in our discussion about of the generic allocation of *talpinus* include "rostrum long," "rostral width less than that of interorbital region," "molars tetralophodont, quadritubercular, hypsodont," "first molar with anterior median fold, mesoloph present to absent," "upper incisors short, narrow, orthodont" and "cuspids more or less subprismatic." It is important to note that this diagnosis was constructed based mainly on populations of *Brucepattersonius* from São Paulo and Rio de Janeiro states in Brazil. Furthermore, two species established by Hershkovitz (1998) as strongly different, namely *griserufescens* and *albinasus*, are now regarded as conspecific (Vilela et al. 2006). At the generic level, *Brucepattersonius* and *talpinus* share several general traits, including long rostra, developed gnathic processes, flat skull profiles, tubular interorbits, well-developed but tending to piriform incisive foramina not reaching posteriorly to M1 protocones, short palates and broad mesopterygoid fossae (Figure 3). More specific similarities are evident by comparing the zygomatic plates and molar series. Species of *Brucepattersonius* and *talpinus* have comparable recessed areas anterior to each molar row, labially flanked by osseous prominences at the origin of the superficial masseter. In addition, these two taxa exhibit low, backwardly reclining zygomatic plates, with their posterior borders located even with the anterior faces of M1. Despite Hershkovitz's (1998) use of terms such as hypsodont and subprismatic to describe the molars of *Brucepattersonius*, clearly the dentition of this genus is closer to brachyodont or mesodont and with a degree of occlusal complexity in accordance with this condition. Similarities between the molars of *Brucepattersonius* and *talpinus* are not restricted to the height of the crown, as both taxa share well-developed anteromedian flexi, laterally expanded procingula, mesolophs + paralophules fused to metacones, the particular pattern of closure of labial flexi described earlier for *talpinus* and complex M3s with internal enamel rings.

Based on available morphological evidence that can be surmised from the holotype of *Mus talpinus*, we allocate with some confidence this taxon to *Brucepattersonius* Hershkovitz. A separate matter, however, is the possible connection of *talpinus* to any of the eight extant forms of this genus in the current literature, namely *soricinus* (the type species), *igniventris*, *griserufescens* (including *albinasus*), *ihering* [populations from Misiones, Argentina, referred to *iheringi* by Massoia (1963)], *paradisus*, *guarani* and *misionensis*. Several of these "species" are known from few specimens, with the latter three described from their holotypes alone (Mares and Braun

2000). Moreover, the only reasonably comprehensive analysis of the systematics of the genus, which regrettably remains unpublished (Vilela 2005), suggests an even more complex alpha-taxonomy composed of several distinct evolutionary lineages. A detailed comparison of *talpinus* to each of the described forms of *Brucepattersonius* is thus not possible at this time. However, gross comparisons of the available material at hand, including representatives of Argentinean populations as well as the holotype of *albinasus*, suggest that *talpinus* is different from each of these at the specific level. In general terms, *talpinus* seems to be one of the larger species in the genus (Table 1), with robust incisors, a broad rostrum and a particularly acute and posteriorly directed nasofrontal suture. This latter feature is also evident in the holotype of *igniventris*, a species restricted to Parque Nacional Iporanga National in southwestern São Paulo state (cf. Hershkovitz 1998: Figure 22). Future reviewers of the genus are encouraged to test the hypothesis that *talpinus* is a senior synonym of *igniventris*.

Thanks to the revisionary efforts of several researchers today, it is now possible to update the sigmodontine assemblage from Lapa da Serra das Abelhas, at least preliminarily (Table 2) and thus to consider the paleoenvironmental meaning of this cohort of taxa. Three major concerns, however, are important to highlight in any attempt to base environmental reconstruction on Winge (1887). First, the exact location of Lapa da Serra das Abelhas is not known, and Lund worked many caves across an area approximately 70 km long, from the Rio das Velhas near Lagoa Santa to Maquiné cave (Cartelle 2002). Second, absences in cave assemblages are difficult to interpret as real because Winge (1887) focused primarily on cranial fragments; the Lund collection at ZMK includes many unstudied mandibles. And, third, the cave assemblages lack the requisite stratigraphy, so that synchrony among the recorded species is a weak presumption at best. For example, Auler et al. (2006) demonstrated a variety of taphonomic biases and different ages involved in the formation of of the cave deposits in the vicinity of Lagoa Santa. U-series dating obtained or listed by these authors indicates that these fossil cave faunas cover the entire Late Pleistocene and part of the Middle Pleistocene.

The Lapa da Serra das Abelhas sigmodontine assemblage (Table 2) includes at least eight taxa without recent records of occurrence within the Lagoa Santa area. Most of these sigmodontines are widespread in the mountain ranges of southeastern Brazil covered by the Atlantic Forest biome (Gonçalves 2006), especially *Thaptomys*, *Juliomys*, *Delomys*, *Sooretamys* and *Euryoryzomys*. Recent nearest records for some of these taxa are in the Serra do Caraça, a mountain system approximately 50 km SE of Lagoa Santa, or the Serra do Cipo, about 70 km NNE of Lagoa Santa (cf. Ávila-Pires 1960). In particular, *Brucepattersonius* are widespread sylvan mice, although only limitedly represented in collections, with records from Minas Gerais (about 20°22'S) in Brazil to Misiones (27°S) in Argentina (Massoia 1963, Hershkovitz 1998, Vilela 2005). Occurrences of *Brucepattersonius* in the northern

Table 1 Craniodental measurements of the holotype of *Mus talpinus* and several species of *Brucepattersonius*.

	B. talpinus (lectotype)	B. igniventris[a]	B. iheringi[b]	B. griserufescens (+ albinasus)[c]	B. soricinus[a]	Brucepattersonius sp.[d]
Interorbital breadth	5.8	6.0–6.3	6.0	6.2 (5.9–6.6)	6.0 (5.8–6.2)	5.8 (5.5–6.2)
Width of rostrum	4.4	4.8	–	4.4 (4.0–4.8)	4.7 (4.6–4.9)	4.8 (4.7–5.1)
Width of nasals	3.1	–	–	–	–	–
Width of zygomatyc plate (at base)	2.2	1.6–2	–	1.6 (1.5–1.9)	1.7 (1.5–2.0)	1.8 (1.6–1.9)
Length of upper diastema	7.1	7.0–7.2	6.8	7.5 (7.1–8.4)	6.6 (6.2–7.0)	6.9 (5.8–7.8)
Palatal bridge	4.0	4.1–4.2	–	4.4 (4.1–4.9)	4.1 (3.7–4.3)	–
Palatal width between protocones	3.3	–	–	–	–	–
Length of incisive foramina	6.1	6.3–6.5	5.2	6.4 (6.0–6.6)	6.0 (5.9–6.1)	5.5 (5.0–5.9)
Length of maxillary tootrow (alveolar)	4.7	4.5–4.7	4.2	4.6 (4.4–4.9)	4.3 (4.2–4.6)	4.6 (4.1–4.9)
Length of M1	2.1	–	–	–	–	–
Width of M1	1.2	–	–	–	–	1.3 (1.2–1.3)
Incisor deep	1.3	–	–	–	–	–

[a]Data from Hershkovitz (1998).
[b]Data from Thomas (1896).
[c]Data from Vilela et al. (2006).
[d]Argentinean populations (n=17), this work.

Table 2 Sigmodontine assemblage of Lapa da Serra das Abelhas as recorded by Winge (1887: 8), an updated taxonomy and recent occurrences in the Lagoa Santa area, Minas Gerais, Brazil.

Original name	Current taxonomy	Recent occurrence
Hesperomys simplex	*Pseudoryzomys simplex*[a]	Yes
Hesperomys molitor	*Gyldenstolpia fronto*[b]	No
Hesperomys expulsus	*Calomys expulsus*	Yes
Sigmodon vulpinus	*Holochilus brasiliensis*	Yes
Habrothrix orycter	*Thaptomys nigrita*[c]	No
Habrothrix angustidens	"*Akodon*" *serrensis*[d]	No
Oxymycterus talpinus	*Brucepattersonius talpinus*	No
Oxymycterus rufus	*Oxymycterus dasytrichus*	Yes
Oxymycterus cosmodus	Not revised yet[e]	–
Calomys anoblepas	*Juliomys anoblepas*[f]	No
Calomys longicaudatus	*Oligoryzomys nigripes*	Yes
Calomys plebejus	*Delomys plebejus*[g]	No
Calomys rex	*Sooretamys angouya*[h]	No
Calomys coronatus	*Euryoryzomys russatus*[i]	No
Rhipidomys mastacalis?	*Rhipidomys mastacalis*?[j]	Yes

[a] After Ávila-Pires (1960) and Voss and Myers (1991).
[b] Mandible illustrated by Winge (1887); after Pardiñas et al. (2008).
[c] After Ávila-Pires (1960).
[d] Robert Voss (personal communication).
[e] Probably, a large species of *Oxymycterus*.
[f] After Pardiñas and Teta (2011).
[g] After Voss (1993).
[h] After Ávila-Pires (1960) and Musser et al. (1998).
[i] After Musser et al. (1998).
[j] Based on a mandible dubiously assigned to this species (Winge 1887).

portion of its range are restricted to forested habitats in the mountain systems of Serra do Caparaó, about 250 km SE of Lagoa Santa (Hershkovitz 1998).

Recent sigmodontine assemblages in the Lagoa Santa area are comprised mainly of *Calomys* (at least two species, *Calomys expulsus* and *Calomys tener*) and *Necromys lasiurus*, with species of *Akodon*, *Cerradomys*, *Holochilus*, *Nectomys*, *Oligoryzomys*, *Pseudoryzomys*, *Rhipidomys* and *Thalpomys* considerably less common (Boroni Martins 2012). Major human disturbance, such as wood extraction, extensive cattle grazing and large-scale agriculture, can explain part of these trenchant differences in the faunal composition of extant and fossil assemblages in the Lagoa Santa region (Boroni Martins 2012). For example, a dramatic increase in *Calomys* and

virtual extirpation of some micromammal species verified during the Late Holocene in Argentina are apparently linked to human impact on regional environments (Pardiñas et al. 2000, 2012, Pardiñas and Teta 2012). However, the taxonomic structure of the Lapa da Serra das Abelhas sigmodontine assemblage, which is characterized by the extensive presence of Atlantic Forest elements mixed with Cerrado species, suggests also a different regional environment during the Late Pleistocene. In this context, the cooling episodes could have generated a depression of vegetation belts and an expansion of the Atlantic Forest, promoting at its ecotonal contact with the Cerrado the formation of a non-analogue fauna in comparison to that of today. In this context, we follow Barnosky (1993) in his view of a non-analogous assemblage, the sympatric occurrence of species that today are allopatric or vice-versa. Periods of increased rainfall and wetter events during the Late Pleistocene have been extensively documented from semi-arid northeastern Brazil favoring both forest expansion and the existence of rich faunal assemblages (Cartelle 1999, Auler et al. 2004).

Appendix

Appendix 1

Specimens used in comparisons are housed at the following mammal collections: Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina); Colección Elio Massoia (CEM; acquired by the Fundación de Historia Natural Félix de Azara, Buenos Aires, Argentina); Museu de Zoologia "João Moojen de Oliveira," Universidade Federal de Viçosa (CM; Viçosa, Minas Gerais, Brazil); Museu Nacional (MN, Rio de Janeiro, Brazil); Museum of Vertebrate Zoology (MVZ, Berkeley, USA). These are: *Blarinomys breviceps* (3): Brazil, Minas Girais, Mata do Paraiso (CM 2640), Brazil, Espiritu Santo, two specimens, a juvenile and an adult collected by Yuri Leite studied at the MVZ (MAS 17, RM 46). *Brucepattersonius albinasus* (1): Brasil, Minas Gerais, Pico da Bandeira (MN 32017). *Brucepattersonius soricinus* (2): Brasil, São Paulo, Salesópolis, Estação Biológica de Boracéia (MVZ 183036, MVZ 183037). *Brucepattersonius* sp. (17): Argentina, Misiones, Reserva de Uso Múltiple E. E. A. Anexo Cuartel río Victoria (CEM 4978, CEM 4979, CEM 7543), Dos de Mayo (CEM 4570, CEM 4571, CEM 2401), locality unknown (CEM 6101), Tobunas, Ruta 14, 352 km (CEM 279), Aristóbulo del Valle, Balneario arroyo Cuña Pirú (CNP 1745, CNP 1747, CNP 1787, CNP 1834, CNP 1843, CNP 3006, CNP 3007), Salta El Paraíso (CNP 1932; topotype of B. paradisus), RP 2, 6 km NE arroyo El Paraíso (CNP 1933; topotype of *B. guarani*). *Juscelinomys candango* (3): Brazil, Brasília (MN 22800, MN 22805, MN 22807). *Lenoxus apicalis* (2): Peru, Puno, 14 km W Yanahuaya (MVZ 171512, MVZ 171515). "*Microxus*" *mimus* (2): Peru, Puno, Agualani (MVZ 171745, 171746). *Oxymycterus hiska* (1): Peru, Puno, 14 km W Yanahuaya (MVZ 172659). *Oxymycterus hucucha* (1): Bolivia, Cochabamba, 20 mi E Totora (MVZ 119948). *Oxymycterus misionalis* (4): Argentina, Aristóbulo del Valle, Balneario arroyo Cuña Pirú (CNP 851, CNP 1856, CNP 1965, CNP 2369). *Oxymycterus rufus* (7): Argentina, Buenos Aires, Punta Lara (CNP 1900, CNP 1901, CNP 1902, CNP 1903, CNP 1904, CNP 1905, CNP 1906). Data about *Juscelinomys huanchacae* and *Podoxymys roraimae* were retrieved from literature (Pérez-Zapata et al. 1992, Emmons 1999, Emmons and Patton 2012).

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Q2: Please update Ref. Pardiñas and Teta 2011