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The First Quaternary Record of the Rodent *Akodon kadiweu* Brandão, Percequillo, D'Elía, Paresque, & Carmignotto, 2021 (Rodentia: Cricetidae: Sigmodontinae)

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Rodents of the genus *Akodon* comprise 41 extant species, and are considered the most diverse genus of the tribe Akodontini. The most recently described extant species is *Akodon kadiweu*, known exclusively from Serra da Bodoquena, a karstic region located in Mato Grosso do Sul state, Brazil. Some sub-fossil and fossil specimens of *Akodon* have been reported in recent years for Brazil, but most remain unidentified at the species level. Here we examine the identity of Quaternary specimens of *Akodon* sp. from the limestone cave Nossa Senhora Aparecida, located in Serra da Bodoquena. Quantitative characters allowed the distinction of *Akodon* sp. specimens from smaller and larger congeners, and skull qualitative characters of nasal, interorbital region, supraorbital margins, zygomatic notches, zygomatic plate, incisive foramina, mesopterygoid fossa, mandible and molars allowed to identify these individuals as *A. kadiweu*. Our results revealed the first known past representatives of *Akodon* to be recorded in Mato Grosso do Sul, as well as western Brazil.

Key words: Akodontini, Cerrado, Grass mouse, Paleontology, South America.

BACKGROUND

The genus *Akodon* (Rodentia, Cricetidae, Sigmodontinae) has received considerable attention in several areas of study in the last years, including taxonomy, phylogenetics, morphology, cytogenetics and ecology, among others (Pardiñas et al. 2015 2017; Ávila et al. 2016; Jiménez and Pacheco 2016; Maestri et al. 2016; Hernandez et al. 2017; Machado et al. 2020; Jayat et al. 2020; Vilela et al. 2020; Ruelas et al. 2020; Brandão et al. 2021). *Akodon* is the most diverse genus of the tribe Akodontini, comprising 41 extant species (Pardiñas et al. 2017; Brandão et al. 2021), which are spread in a wide range of habitats in South America,

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from sea level to high Andean altitudes, and from tropical and subtropical forests to semidesert areas in Patagonia (Pardiñas et al. 2015 2017). Nevertheless, species diversity is not yet fully known and recent studies based on integrative approaches suggest a higher number of valid taxa (Pardiñas et al. 2015 2017; Jayat et al. 2020; Ruelas et al. 2020), including the recent description of a new species, *Akodon kadiweu* Brandão, Percequillo, D'Elía, Paresque and Carmignotto, 2021 from Serra da Bodoquena, Mato Grosso do Sul, in western Brazil.

Although there has been improvement in our knowledge on living forms of the genus (*e.g.*, Jiménez and Pacheco 2016; Jayat et al. 2020; Ruelas et al. 2020; Brandão et al. 2021), subfossil and fossil records of *Akodon* from Brazil, as well as from most of South America, remain poorly understood, mostly due to the lack of samples or difficulty in assigning fragmented material to valid names, either to fossil or living species. Considering that *Akodon johannis* Reig, 1987 may be related to the genus *Thaptomys* (Reig. op. cit.), at least two extinct species of *Akodon* are known from non-recent material: *A. clivigenis* (Winge, 1887) and *A. lorenzinii* Reig, 1987 (Pardiñas et al. 2002 2015). The oldest known record of the genus is *A. lorenzinii* from the Pliocene of Argentina, in Mar del Plata, Buenos Aires province (Reig 1987), but the fossil record indicates *Akodon* was more widespread during the Pleistocene and Holocene, with records found in Argentina (Pardiñas et al. 2002; Pardiñas and Teta 2012; Quintana 2016), Paraguay (Torres et al. 2015), Uruguay (Ubilla 1996), Ecuador (Fejfar et al. 1993) and Brazil (Castro and Langer 2011; Hadler et al. 2016; Stutz et al. 2017 2018; Roth 2018). Among these records, *A. clivigenis* was described based on a single specimen collected by the naturalist Peter Wilhelm Lund in the 19th century from Quaternary deposits of Lagoa Santa, Minas Gerais (Winge 1887), and became the only species of *Akodon* from Brazil known exclusively from past material.

In Brazil, at least five *Akodon* taxa were identified in different sub- and fossiliferous sites across the country, from Late Pleistocene to Holocene, all in caves and rock shelters (Table 1). Sites in the Cerrado biome include records of *A. clivigenis* and *A. cursor* from Lagoa Santa, Minas Gerais (Winge 1887); *Akodon* cf. *lindberghi* from Gruta dos Moura, Tocantins (Tobelém et al. 2013); *Akodon* sp.1 and *Akodon* sp.2 from Gruta do Urso, Tocantins (Pires et al. 2018); *Akodon* sp.1 and *Akodon* sp.2 from Caverna Carneiro, Goiás (Boroni 2019); and *Akodon* sp. from Caverna Nossa Senhora Aparecida, Serra da Bodoquena, Mato Grosso do Sul (Salles et al. 2006; Boroni et al. 2020).

Caverna Nossa Senhora Aparecida (NSA cave) is located in Serra da Bodoquena, a mountainous region in western Brazilian Cerrado, characterized by a vegetation

Table 1. *Akodon* species with fossil records at different fossiliferous sites in Brazil. Adapted from Boroni (2019). YBP = years before present

Taxon	Locality	Reference	Date interval
Akodon clivigenis	Lagoa Santa - MG	Winge (1887)	
Akodon cursor	Lagoa Santa - MG	Winge (1887)	
Akodon azarae	Sangão site - RS	Roth (2018)	Present to 6.285 YBP
	Deobaldino Marques site - RS	Roth (2018)	Present to 6.285 YBP
Akodon cf. *azarae*	Adelar Pilger site - RS	Hadler et al. (2016)	3.000 to 8.010 YBP
	Sangão site - RS	Stutz et al. (2018)	3.730 to 8.800 YBP
Akodon cf. *lindberghi*	Gruta dos Moura cave - TO	Tobelém et al. (2013)	
Akodon cf. *cursor*	Toca da Barra da Janela do Antonião cave - PI	Guérin et al. (1996)	
Akodon sp.	Igrejinha cave - GO	Salles et al. (1999)	
Akodon sp.	Carneiro cave - GO	Boroni (2019)	Present to 2.500 YBP Present to 13.300 YBP 13.300 to 121.500 YBP
Akodon sp.	Abismo Iguatemi site - SP	Castro and Langer (2011)	10.000 to 14.000 YBP
Akodon sp.	Adelar Pilger site - RS	Hadler et al. (2016)	Present to 3.000 YBP 3.000 to 6.150 YBP
Akodon sp.	Afonso Garivaldino Rodrigues site - RS	Stutz et al. (2017)	7.250 to 9.430 YBP
Akodon sp.	Sangão site - RS	Stutz et al. (2018)	3.730 to 8.800 YBP
Akodon sp.	Sangão site - RS	Roth (2018)	Present to 6.285 YBP
Akodon sp.	Deobaldino Marques site - RS	Roth (2018)	Present to 6.285 YBP
Akodon sp.	Gruta do Urso cave - TO	Pires et al. (2018)	3.800 to 22.000 YBP
Akodon sp.	Nossa Senhora Aparecida cave - MS	Boroni et al. (2020)	

mosaic, including grasslands, shrublands, marshlands, and semideciduous and deciduous forests (Eiten 1972; RADAMBRASIL 1982). Serra da Bodoquena is located in a karstic area with significant cave density, consisting of pure dolostones and limestones of the Corumbá Group (Ediacaran age) that, during the formation of Gondwana, were partially deformed in the Paraguay Mobile Belt (Alvarenga et al. 2009; Campanha et al. 2011). Due to these characteristics, the region allowed expressive fossilization of Quaternary mammals, from megafauna such as giant ground sloths, saber tooth cats, and others, to small sigmodontine rodents, including records of *Akodon* sp. (Salles et al. 2006; Perini et al. 2009 2011; Boroni et al. 2020).

The specimens of *Akodon* sp. were initially recorded by Salles et al. (2006), and later accessed by Boroni et al. (2020) in order to provide further comparisons to congeners (*A. lindberghi* and *A. montensis*), but no precise identification could be retrieved. The description of a new species of *Akodon* from Serra da Bodoquena, naturally prompted Brandão et al. (2021) to provide a few comments on the nearly topotypical *Akodon* sp., but these authors were not able to reach a conclusion of their identity without a proper evaluation of the specimens. Here, we evaluate the specimens from NSA cave and compare them with the three species of *Akodon* that currently occur in Mato Grosso do Sul, *A. kadiweu*, *A. montensis* and *A. toba* (Pardiñas et al. 2015; Brandão et al. 2021), since the Holocene and Pleistocene cave fauna from Brazil are represented by a mosaic of living and extinct species inhabiting the region. We also included comparisons with other recent congeners from nearby regions, as well as with *Akodon clivigenis*, the only extinct *Akodon* representative occurring in the Cerrado, in order to propose a hypothesis for the taxonomic identification of this material at the species level.

MATERIALS AND METHODS

We examined a total of 96 specimens of extant species of *Akodon* known to occur in Mato Grosso do Sul (*A. kadiweu*, *A. montensis* and *A. toba*) and the nearby lowlands of Chaco in Paraguay, Cerrado in central and western Brazil, and the natural grasslands in northern Argentina (*A. azarae*, *A. lindberghi*, and *A. philipmyersi*, respectively). From the cave deposit assemblage of NSA cave, a total of 33 cranial remains of *Akodon* sp. (*sensu* Boroni et al. 2020) were examined. Four NSA cave specimens were measured, photographed and then sent for radio-carbon dating (Boroni et al. 2020), so they do not have voucher numbers. We refer to the past samples from Serra da Bodoquena as NSA cave *Akodon* sp. from hereafter.

The specimens examined (Table S1) are deposited in the following mammal collections: Brazil: Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais; Museu Nacional (MN), Universidade Federal do Rio de Janeiro, Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Argentina: Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut; and U.S.A.: National Museum of Natural History (USNM), Washington, D.C; Field Museum of Natural History (FMNH), Chicago; University of Michigan Museum of Zoology (UMMZ), Ann Arbor. We examined high resolution digital pictures from the specimen of *Habrothrix clivigenis* (= *Akodon clivigenis*) deposited in the Zoological Museum, Natural History Museum of Denmark (ZMUC), Copenhagen, Denmark (also see Hansen 2012). See table S1 for the complete list of specimens and localities.

We compared the following cranial qualitative morphological characters among these species: nasal, interorbital region, supraorbital margins, zygomatic notches, zygomatic plate, incisive foramina, mesopterygoid fossa, mandible and molars. The craniodental nomenclature and descriptions follow Reig (1977), Voss (1988), Myers (1990) and Weskler (2006). We classified specimens in five age-classes based on the pattern of tooth wear established by Myers (1990).

For morphometric analyses, we used seven craniodental measurements, taken with digital calipers to the nearest 0.01 mm following the definitions of Myers (1990), Percequillo et al. (2017), Boroni et al. (2020): Least interorbital breadth (LIB), representing the least distance across the frontal bones; Length of upper molars (LM), from the anterior surface of M1 to posterior margin of M3; Breadth of zygomatic plate (BZP), measured across the central area of zygomatic plate; Breadth of first upper molar (BM1), greatest crown breadth of the M1 across the paracone-protocone; Length of lower molars (lm), from the anterior surface of m1 to posterior margin of m3; Breadth of first lower molar (bm1), greatest crown breadth of the m1 across the paracone-metacone; Greatest mandible length (GML), from the most anterior point of the mandible to the posterior point of the mandible (at the condyloid process in *Akodon*).

Descriptive univariate statistics (mean ± standard deviation, range, and sample size) are provided for all craniodental measurements of adults. As our sample of *A. kadiweu* is small, for each species we pooled specimens from all age classes (2 to 5) available for study. To explore the morphometric variation among specimens of *Akodon*, we used Principal component analysis (PCA) and Discriminant function analysis

(DFA) with extracted variance-covariance matrix of log10-transformed metric characters of skull and mandible, separately. We also use biplot and boxplot graphs using absolute values to determine size categories based on the dispersion values and to compare samples. All statistical analyses were performed in the software SPSS Statistics 19.0 (SPSS Inc. 2008).

RESULTS

Morphological variation

The best-preserved cranial remains of specimens of NSA cave *Akodon* sp. are represented by upper and lower molars, either in individual maxillae (N = 9), mandible (N = 23), or partial skull (N = 1). The morphometric comparisons of these cranial structures were useful to discriminate species of the genus *Akodon*.

The length of the upper molar series (LM; Table 2) of *A. toba* are the largest, followed by those of *A. montensis*, *A. kadiweu*, *A. azarae*, NSA cave *Akodon* sp., *A. philipmyersi*, and *A. lindberghi*, that exhibits the smallest molar series. Likewise, the length of the lower molar series (lm) decreases in size from *A. toba*, *A. montensis*, *A. kadiweu*, *A. azarae*, NSA cave *Akodon* sp., *A. philipmyersi*, to *A. lindberghi*. The same pattern of size variation is observed in relation to the breadth of first upper (BM1) and lower molars (bm1; Table 2). The biplot of dental characters (Fig. 1) reveals that specimens of *A. toba* exhibit long and wide molars,

Table 2. Descriptive statistics (mean ± SD; range and sample size - N) for craniodental measurements (in millimeters) of adults of *Akodon* sp. from Nossa Senhora Aparecida (NSA) cave, Serra da Bodoquena, Mato Grosso do Sul, Brazil, and geographically close congeners

	Akodon azarae	*Akodon kadiweu*	*Akodon lindberghi*	*Akodon montensis*	*Akodon philipmyersi*	NSA cave *Akodon* sp.	*Akodon toba*
LIB	4.29 ± 0.09 4.23–4.40 (3)	5.09 ± 0.07 5.04–5.18 (3)	4.52 ± 0.19 4.22–4.82 (10)	4.94 ± 0.18 4.68–5.47 (19)	4.52 ± 0.14 4.3–4.72 (11)	4.38 (1)	4.98 ± 0.13 4.79–5.09 (4)
BZP	2.19 ± 0.04 2.14–2.23 (3)	2.28 ± 0.28 2.00–2.56 (3)	1.83 ± 0.11 1.66–2.06 (10)	2.52 ± 0.14 2.23–2.73 (19)	2.01 ± 0.09 1.93–2.14 (11)	1.97 ± 0.13 1.75–2.22 (8)	2.95 ± 0.27 2.34–2.96 (4)
LM	4.13 ± 0.41 4.10–4.18 (3)	4.42 ± 0.07 4.33–4.47 (3)	3.74 ± 0.13 3.54–4.02 (10)	4.18 ± 0.14 3.96–4.65 (19)	3.95 ± 0.11 3.78–4.10 (11)	4.05 ± 0.20 3.91–4.20 (2)	4.80 ± 0.13 4.67–4.99 (4)
BM1	1.12 ± 0.06 1.08–1.20 (3)	1.17 ± 0.05 1.12–1.21 (3)	1.07 ± 0.03 1.03–1.17 (10)	1.23 ± 0.05 1.11–1.34 (19)	1.13 ± 0.06 1.05–1.21 (11)	1.14 ± 0.07 1.05–1.28 (10)	1.28 ± 0.03 1.25–1.34 (4)
lm	4.30 ± 0.06 4.23–4.36 (3)	4.46 ± 0.12 4.37–4.60 (3)	3.86 ± 0.13 3.62–4.06 (10)	4.39 ± 0.16 4.02–4.64 (19)	4.00 ± 0.11 3.78–4.14 (11)	4.16 ± 0.12 3.91–4.35 (9)	4.97 ± 0.23 4.76–5.28 (4)
bm1	1.03 ± 0.05 0.97–1.09 (3)	1.12 ± 0.02 1.10–1.14 (3)	0.91 ± 0.08 0.72–1.02 (10)	1.04 ± 0.06 0.90–1.15 (19)	1.10 ± 0.10 0.92–1.21 (11)	1.01 ± 0.05 0.89–1.15 (23)	1.11 ± 0.03 1.08–1.15 (4)
GML	13.37 ± 0.52 12.80–13.83 (3)	14.13 ± 1.12 13.48–15.43 (3)	11.73 ± 0.38 11.32–12.64 (10)	14.98 ± 0.55 13.79–16.15 (19)	11.57 ± 0.17 11.30–11.9 (11)	11.57 ± 1.13 9.31–12.62 (9)	15.27 ± 1.02 14.15–16.51 (4)

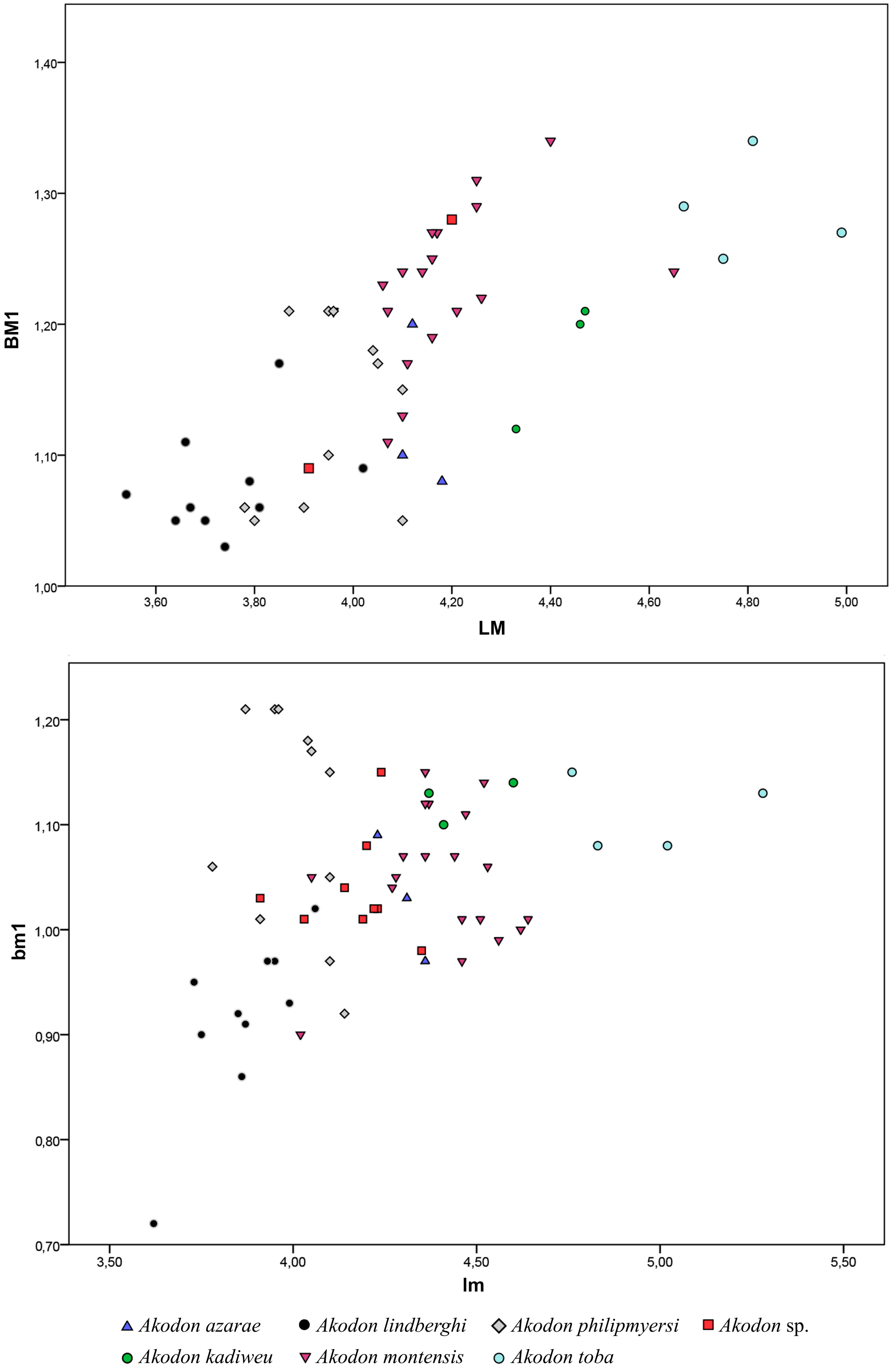

Fig. 1. Biplot graph displaying the length of upper molars (LM) versus the breadth (BM1) of M1, and length of lower molars (lm) versus breadth (bm1) of m1 of seven species of *Akodon* showing the different size categories.

versus small and narrow molars of most specimens of *A. lindberghi*. The remaining specimens exhibit an intermediate condition, with most specimens of *A. montensis* and *A. kadiweu* presenting larger molars than *A. philipmyersi*, *A. azarae* and NSA cave *Akodon* sp., with the latter slightly overlapping with these intermediate-size species.

The cranial measurements based on the skull and mandible fragments of NSA cave *Akodon* sp., such as the breadth of zygomatic plate and least interorbital constriction, and length of mandible, also follow a similar size pattern among the species studied (Table 2). The breadth of zygomatic plate (BZP) is smallest in *A. lindberghi*, followed by *A. philipmyersi*, NSA cave *Akodon* sp., *A. azarae*, *A. kadiweu*, *A. montensis* and *A. toba*, with the last two referring to the largests species. The least interorbital breadth (LIB) is narrower in *A. azarae*, followed by NSA cave *Akodon* sp., *A. lindberghi*, *A. philipmyersi*, *A. kadiweu*, *A. montensis* and *A. toba*. Although the range of variation in the length of mandible is higher in NSA cave *Akodon* sp. (9.31–12.62 mm), its mean is equal to *A. philipmyersi* (11.57 mm) and only slightly smaller than *A. lindberghi* (11.73 mm). Thus, the length of mandible is smaller in *A. philipmyersi*, *A. lindberghi* and NSA cave *Akodon* sp., followed by *A. azarae*, *A. kadiweu*, *A. montensis* and *A. toba* (Table 2).

The boxplot of cranial (Fig. 2) and mandible (Fig. 3) characters reveals the pattern of variation among specimens, with specimens of *A. toba* and *A. lindberghi* being the largest and smallest species, respectively, while other species are intermediate in size. We found some variables that distinguish some species from the others: low values of LIB for *A. azarae*; high values of LM and lm for *A. toba*; and low values of GML for *A. lindberghi*, *A. philipmyersi*, and NSA cave *Akodon* sp.

The first two principal components together summarized 94.9% and 93.47% of the total variation in the PCA of the skull and mandible, respectively (Fig. 4). All morphometric characters are positively correlated

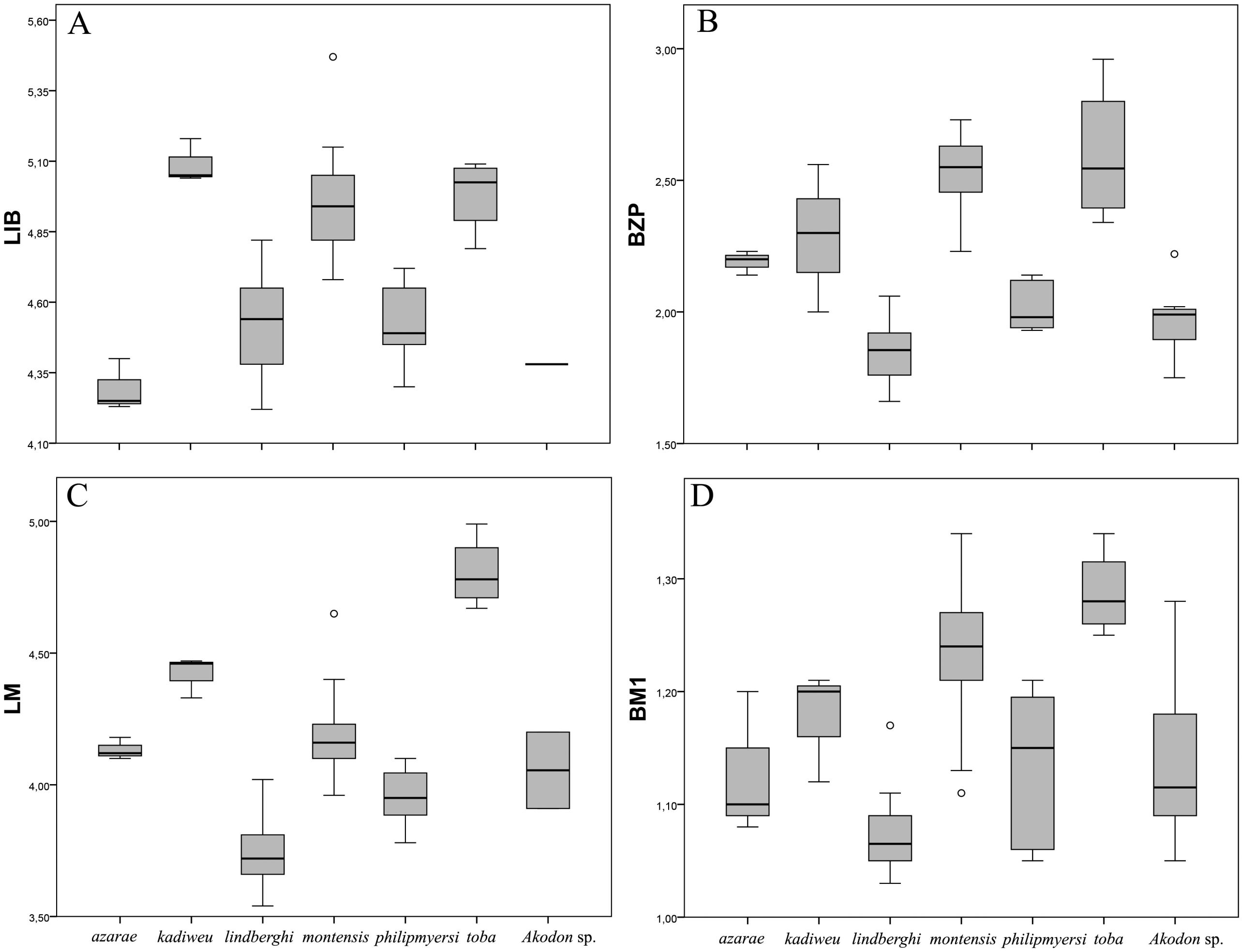

Fig. 2. Boxplots of the ratio of cranial measurements of seven species of *Akodon*. Outliers are represented by dots. Variables are defined in the text.

with PC1, which reflects size (Voss and Marcus 1992) and accounted for 86.51 and 68.72% of the variation of the skull and mandible, respectively. The scatterplots between PC1 versus PC2 show partial segregation among samples, with two species almost entirely isolated from the others: *A. lindberghi* and *A. toba*, the smallest and largest species. The remaining taxa are intermediate in size, with NSA cave *Akodon* sp. slightly overlapping with all species, except *A. montensis*. PC2, which accounted for 8.39 and 24.75% of the variation of the skull and mandible, respectively, revealed a similar pattern of separation among groups. *Akodon lindberghi* and *A. toba* are the most distinctive species in size and shape of the skull as shown by the results of PC1 and PC2, respectively (Fig. 4). The dispersal of individual scores of principal components is quite similar to the dispersion of specimens on the univariate scatterplots, with *A. lindberghi* and *A. toba* representing the extremes of variation.

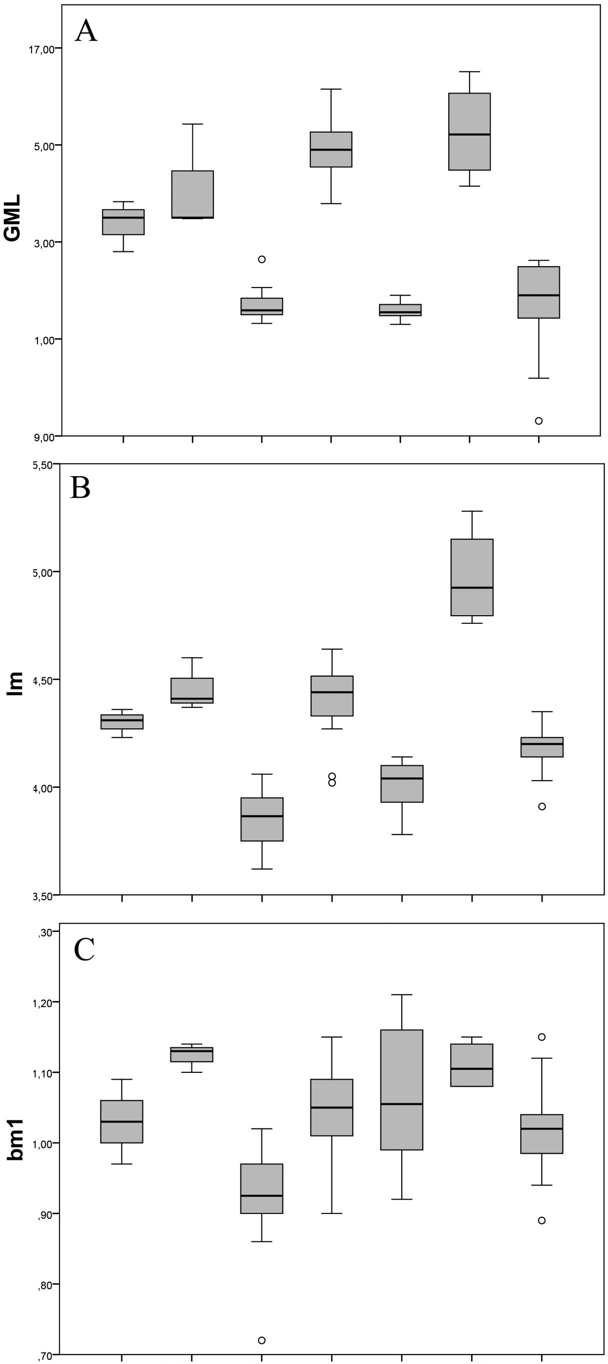

Fig. 3. Boxplots of the ratio of mandible measurements of seven species of *Akodon*. Outliers are represented by dots. Variables are defined in the text.

The DFA indicates that the first two canonical variables (DF1 and DF2) from the cranial variation were responsible for 78.54% and 13.55% of the total variance, respectively, which together compose 92.09% of the total variation (Fig. 5). The canonical correlation showed moderate association between DF1 and the pre-defined groups of the analysis, revealing that this function discriminated the groups in a similar way as depicted by the PCA analysis and the univariate scatterplots: the smallest and largest species (*A. lindberghi* and *A. toba*, respectively) segregated in relation to the remaining taxa of intermediate size. One interesting piece of data of the DFA concerns the predicted classification, which reveals that a total of 66.1% of the specimens were correctly classified and 33.9% were not, including NSA cave *Akodon* sp. identified as *A. kadiweu*, *A. philipmyersi* or *A. azarae* (11%, 22% and 11%, respectively) but never as *A. lindberghi*, *A. montensis* or *A. toba* (Table 3).

Qualitative cranial characters can also be used to distinguish species. The dorsal view of the skull reveals differences in three characters: nasal, zygomatic notches and interorbital region (Fig. 6). The nasals of *A. kadiweu*, *A. lindberghi* and *A. philipmyersi* present notably curved margins that acuminate posteriorly (U-shaped in *A. philipmyersi* and V-shaped in the other species), when compared to sub-parallel straighter margins of *A. montensis* (V-shaped posteriorly) and *A. toba* (V-shaped or squared posteriorly), and the slightly curved margins of *A. azarae* (somewhat squared posteriorly). Moreover, the nasals of *A. philipmyersi* are moderate in length, as well as the ones from *A. azarae* and *A. toba* (extending slightly beyond premaxillae-frontal suture), when compared to the longer nasals of *A. kadiweu*, *A. montensis*, and *A. lindberghi* (extending well beyond premaxillae-frontal suture). Although the anterior portion of rostrum and the nasals are broken in NSA cave *Akodon* sp. specimen (MN 58086), the shape and extension of the suture between nasals and premaxillae-frontal are similar to those found in *A. kadiweu* and *A. lindberghi*. The zygomatic notch is notably deep in *A. toba* and shallow in *A. kadiweu* and *A. lindberghi*, while *A. azarae*, *A. philipmyersi* and *A. montensis* exhibit an intermediate condition (*i.e.*, neither deep or shallow). Although the zygomatic notches of the NSA cave *Akodon* sp. specimen (MN 58086) are filled with sediment, it is possible to see that they are as shallow as in *A. kadiweu* and *A. lindberghi*. Although the interorbital region is hourglass shaped in all species, including those of NSA cave *Akodon* sp., the interorbital constriction is more pronounced in *A. montensis* and *A. toba* when compared to the other species, in which lateral margins of the supraorbital region are much less curved, and the interorbital constriction is less evident. Moreover, only the supraorbital margins of *A. toba* are distinctly sharp, contrary to the smoother margins of the other taxa.

In the ventral view of the skull some important diagnostic features can also be observed (Fig. 7). The posterior margins of incisive foramina reach the protoflexus or anterior portion of protocone level of M1 in *A. kadiweu*, and the mid or posterior portion of the protocone in *A. montensis* and *A. toba*, while in *A. azarae*, *A. philipmyersi* and *A. lindberghi* they reach the hypoflexus level (or, in a few specimens, slightly anterior in *A. philipmyersi*, or slightly posterior in *A. lindberghi*). The incisive foramina and the majority of

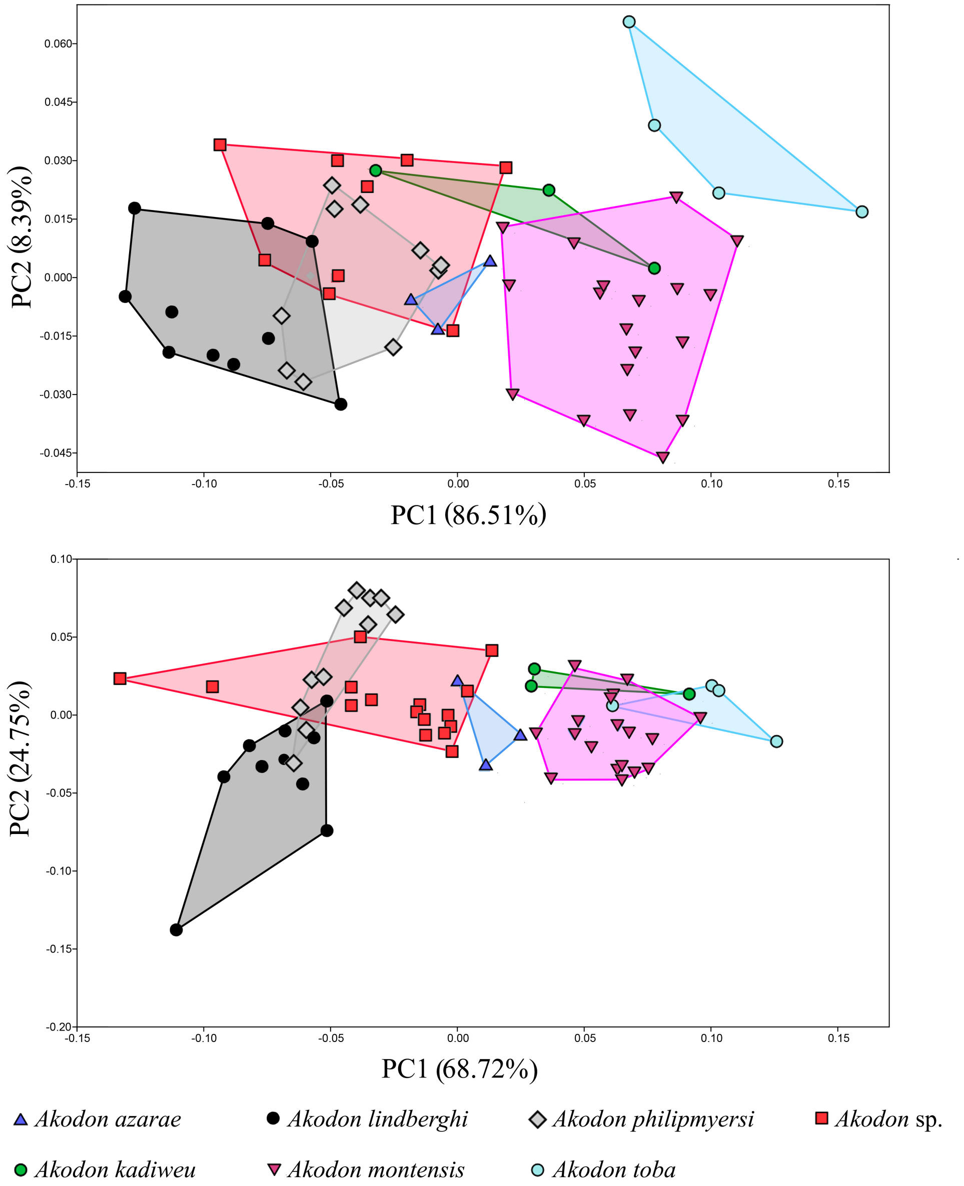

Fig. 4. Distribution of the factorial scores in the first (PC1) and second principal (PC2) components of log-transformed craniometric variables of skull (above) and mandible (below) of adult specimens of *Akodon*.

the palatal region of the preserved skull of the NSA cave *Akodon* sp. specimen (MN 58086) is encrusted with sediment. However, a partially clean (without sediment) portion of the palate of this specimen is aligned with the anterior portion of protocone of M1, with no trace of the incisive foramina. Thus, the posterior margins of the incisive foramina of the preserved skull of NSA cave *Akodon* sp. (MN 58086) is probably located anteriorly

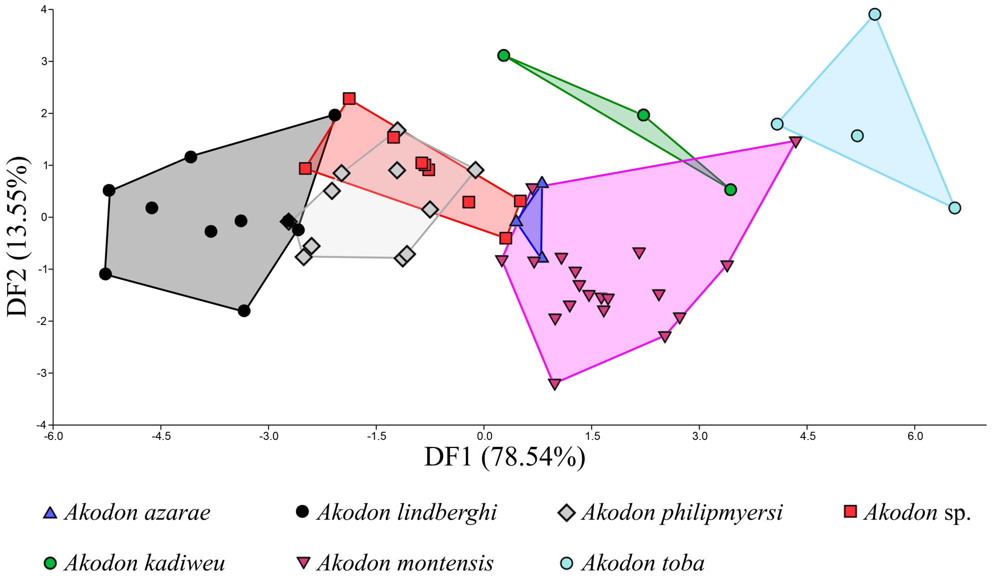

Fig. 5. Distribution of the factorial scores in the first (DF1) and second (DF2) canonical variates of the discriminant function analysis (DFA) of log-transformed craniometric variables of the skull of adult specimens of *Akodon*. The DFA could not be performed using the data of mandibles separately due to the low number of measurements.

Table 3. Classification matrix for *Akodon* spp. obtained by discriminant function analysis concerning the probabilities of classifying each species correctly into one of the seven species

	Predicted classification results (%) *							
Species	*A. azarae*	*A. kadiweu*	*A. lindberghi*	*A. montensis*	*A. philipmyersi*	*Akodon* sp.	*A. toba*	Total
A. azarae	100%							100%
A. kadiweu		33%		33%		33%		100%
A. lindberghi			70%		20%	10%		100%
A. montensis				89%		5%	5%	100%
A. philipmyersi		9%	27%		18%	45%		100%
Akodon sp.	11%	11%			22%	56%		100%
A. toba							100%	100%

* A total of 66.1% of the specimens were correctly classified.

to the protocone of M1. Moreover, in three maxillae fragments it is possible to observe that the posterior margins of the incisive foramina reach the level of the protocone of M1. Therefore, the incisive foramina of the NSA cave *Akodon* sp. specimens is not as long as found in most congeners studied herein, being most similar to the one of *A. kadiweu.* It is also noteworthy that in one maxilla of NSA cave *Akodon* sp. specimens the incisive foramina posterior margin reaches the hypocone. Most taxa, including NSA cave *Akodon* sp., exhibit mesopterygoid fossa with a median posterior palatine process (margins M-shaped), except for *A. montensis*, in which this process is absent (margins U-shaped). The presence of a median palatine process in *A. azarae* is polymorphic within the specimens analyzed here (present in 3 out of 7 specimens), and Pardiñas et al. (2005) considered this character as generally absent in a much larger sample (N = 67). Although M3 is missing in all remnants of NSA cave *Akodon* sp. specimens, it is possible to see the markings of its margins when it was present. Thus, the anterior margin of mesopterygoid fossa is likely even with posterior margin of M3 in NSA cave *Akodon* sp., as well as in *A. kadiweu*, *A. lindberghi* and *A. montensis* (or only slightly anterior or posterior in a few specimens of the latter two species), while the anterior margin of mesopterygoid fossa is notably posterior to M3 in *A. azarae*, *A. philipmyersi* and *A. toba*.

The lateral view of the skull also reveals that the development and shape of the zygomatic plate is markedly different among taxa (Fig. 8). The zygomatic plate is notably broad in *A. toba*, and moderate in *A. montensis* and *A. azarae* (larger in the former, as pointed in Table 2), with these three species exhibiting

Fig. 6. Dorsal view of the skull of past (A) and extant (B-G) species of *Akodon*. A: *Akodon* sp. (MN 58086). B: *A. azarae* (CNP 3154). C: *A. philipmyersi* (CNP 3029). D: *A. lindberghi* (MN 33501). E: *A. kadiweu* (MZUSP 35994). F: *A. montensis* (UFMG 2695). G: *A. toba* (FMNH 164129). Legends: Nasal (Na), supraorbital margins (spm), zygomatic notch (zn). The dotted white and red lines show the different shapes of the interorbital and nasal region, respectively.

a distinct dorsal free margin, with a markedly concave anterior surface, especially in *A. toba*. In *A. lindberghi*, NSA cave *Akodon* sp. and *A. kadiweu*, the plate is narrow and only slightly concave (slopes gently backward from bottom to top), with free dorsal margin distinctly reduced. *Akodon philipmyersi* also presents a narrow zygomatic plate, but the dorsal free margin is more evident than in other narrow-plate congeners *A. lindberghi*, NSA cave *Akodon* sp. and *A. kadiweu*. It is noteworthy that *A. lindberghi* and *A. philipmyersi* present a variation on the anterior margin of the zygomatic plate, varying from nearly straight to somewhat S-shaped margins.

As most fragments of NSA cave *Akodon* sp. are mandibles (N = 23), we also provide detailed comparisons of this structure (Fig. 8). Apart from the difference in length described above (Table 2), the mandible of *A. toba* is more robust than in all other species examined herein. The capsular projection of the lower incisor and the masseteric ridges are more conspicuous in *A. montensis* and *A. toba*. *Akodon philipmyersi* exhibit the most inconspicuous capsular projection and masseteric ridges, and the other four species present intermediate conditions between the latter species and *A. montensis* and *A. toba*. NSA cave *Akodon* sp. and *A. kadiweu* show more delicate coronoid and condylar processes and a shallower and flatter sigmoid notch excavation, making the two species very similar in shape; all other species exhibit stronger coronoid and condylar processes, especially *A. montensis* and *A. toba*, as well as more excavated sigmoid notches.

The general morphology of upper and lower molar toothrows of species of *Akodon* are similar (Reig 1987; Myers 1990), including the taxa studied here (Fig. 8). Nonetheless, although the mesoloph is reduced in most species of the genus (D'Elía and Pardiñas 2015), this structure is generally more developed in *A. montensis*

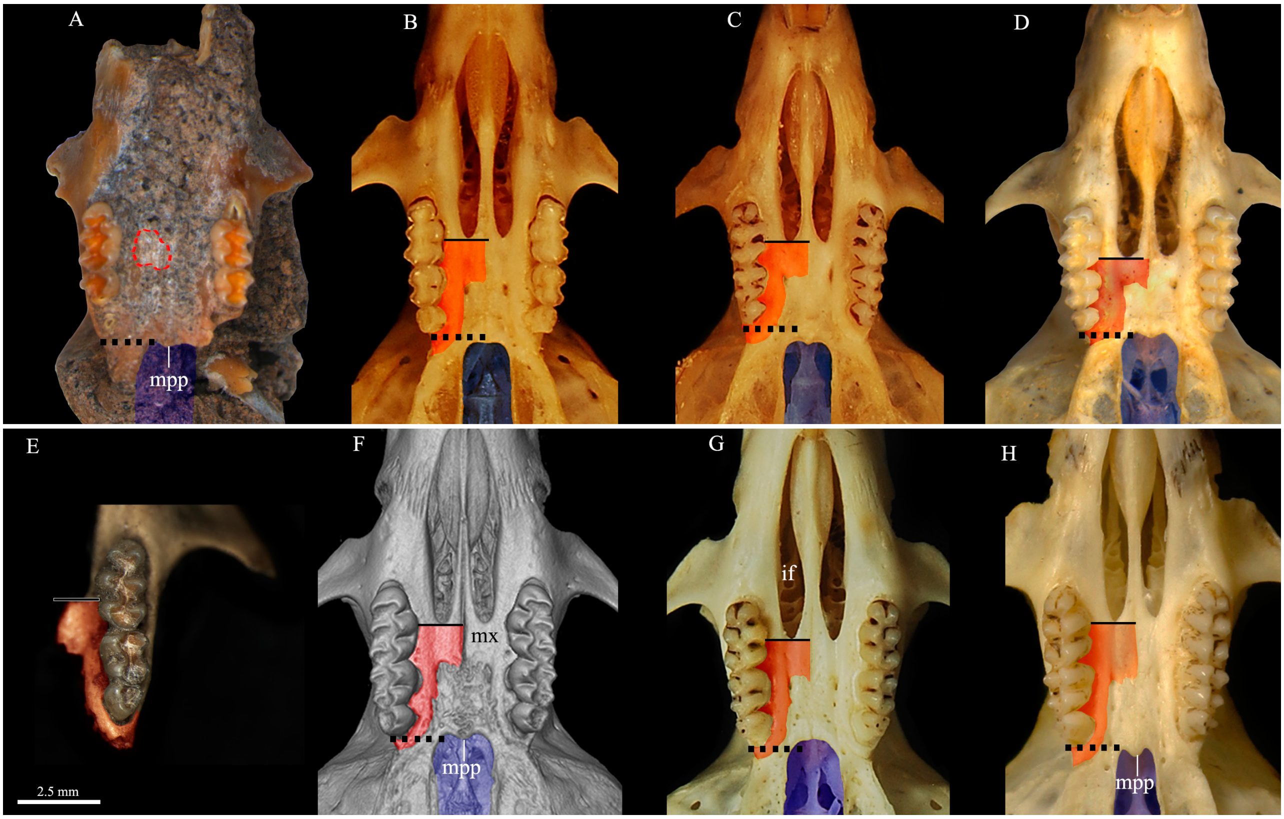

Fig. 7. Ventral view of the skull of past (A, E) and extant (B-D, and F-H) species of *Akodon*. A: *Akodon* sp. (MN 58086). B: *A. azarae* (CNP 3154). C: *A. philipmyersi* (CNP 3029). D: *A. lindberghi* (MN 33683). E: *Akodon* sp. (MN 57635). F: *A. kadiweu* (MZUSP 35994). G: *A. montensis* (UFMG 2695). H: *A. toba* (FMNH 164136). Legends: incisive foramen (if), maxillary (mx), median palatine process (mpp). The bluish and reddish markings evidence, respectively, the mesopterygoid fossa region and right portion of maxillary located posteriorly to the posterior margin of the incisive foramen (black bars). The black bars are level with hypoflexus (B, C, D – see text for variation), and anterior (E, F, H) or posterior (B, G) portion of protocone of M1. Note that in *Akodon* sp. (A) the clean part of the palate (dotted reddish markings) is aligned with the mid portion of protocone of M1, with no trace of the incisive foramen (encrusted with sediments). The dotted black bars show the level between the posterior margin of molars and anterior margin of mesopterygoid fossa.

and *A. toba* than other species examined here. The most distinctive character in the molars of *A. kadiweu* is the presence of the ectostylid in m1, m2 and m3, which forms conspicuous structures in m1 and m2, but is less developed in m3. Ectolophids are also present in m1, m2 and m3 as a narrow and slender structure, or partially coalesced to the hypoconid due to wear. Both these dental structures are also present in congeners, but never as developed as in *A. kadiweu*, and more commonly distinct only in m1. Moreover, we observed that some specimens of *A. montensis* do not present both structures in one or on both sides of lower molars; when present, the ectolophids are not connected to the ectostylid, or only the ectostylid is present. Just as in *A. kadiweu*, ectostylids and ectolophids are present in NSA cave *Akodon* sp. specimens. However, *Akodon* sp. exhibits a morphological variation in these characters: from the 20 specimens examined, some exhibit less developed ectostylids in m1 (n = 10) and m2 (n = 12). Ectolophids in m1 are present in ten specimens with different ages, while in m2 they are present in just two specimens. The presence of ectostylids was not observed in the seven specimens analyzed with the presence of m3 (Fig. 9). Nonetheless, these molars present moderate occlusal surface wear, which could hamper the visualization of this stylid. Despite these minor differences, the morphological resemblance between molars of *A. kadiweu* and NSA cave *Akodon* sp. specimens is noteworthy.

All morphological characters described above are summarized in table 4, which along with morphometric data (Table 2) and multivariate analyses (Figs. 1–5), provide evidence for the identity of NSA cave *Akodon* sp. specimens.

Name attribution

The sample of *Akodon* sp. (*sensu* Salles et al. 2006) from NSA cave was collected about 50 km from Fazenda Califórnia, Parque Nacional da Serra da Bodoquena, the single known locality of *A. kadiweu*. Despite considerable sampling efforts in Serra da

Fig. 8. Lateral view of the skull and mandible of past (A) and extant (B-G) species of *Akodon*. A: *Akodon* sp. (MN 58086, 57649). B: *A. azarae* (CNP 5639). C: *A. philipmyersi* (CNP 3029). D: *A. lindberghi* (MN 33683, 33682). E: *A. kadiweu* (MZUSP 35994). F: *A. montensis* (UFMG 2719, 2723). G: *A. toba* (FMNH 164169). Legends: angular notch (an), angular process (ap), condyloid process (cp), capsular projection (cap), coronoid process (crp), sigmoid notch (sn), zygomatic plate (zp). The dotted white bars show the different shapes of the zygomatic plate, and the arrow points to two broken portions of the mandible of *Akodon* sp.

Bodoquena (Salles et al. 2006; Cáceres et al. 2007; Carmingotto et al. 2022), the only *Akodon* species known from the region is *A. kadiweu.* Additionally, only *A. montensis* and *A. toba* are also known from Mato Grosso do Sul (Brandão et al. 2021). Other species are known from adjacent tropical and subtropical lowlands in Brazilian states, like *A. cursor* in eastern São Paulo state, and *A. lindberghi* in Cerrado of Federal District and Minas Gerais, as well as from other adjacent countries, like *A. philipmyersi* from southern Misiones in Argentina, and *A. azarae* and *A. paranaensis* from eastern Paraguay (Pardiñas et al. 2015). Thus, the identity of *Akodon* sp. from NSA cave likely refers to one of these species as hypothesized here.

Akodon cursor and *A. paranaensis* belong to the *Akodon cursor* species group, along with *A. montensis*, which are all similar in morphological characters (Gonçalves et al. 2007; Pardiñas et al. 2015), such as the long nasals with straight margins, moderate to broad zygomatic plate, and U-shaped margin of mesopterygoid fossa, as described here for *A. montensis*. Moreover, most specimens of *A. cursor* and *A. paranaensis* are

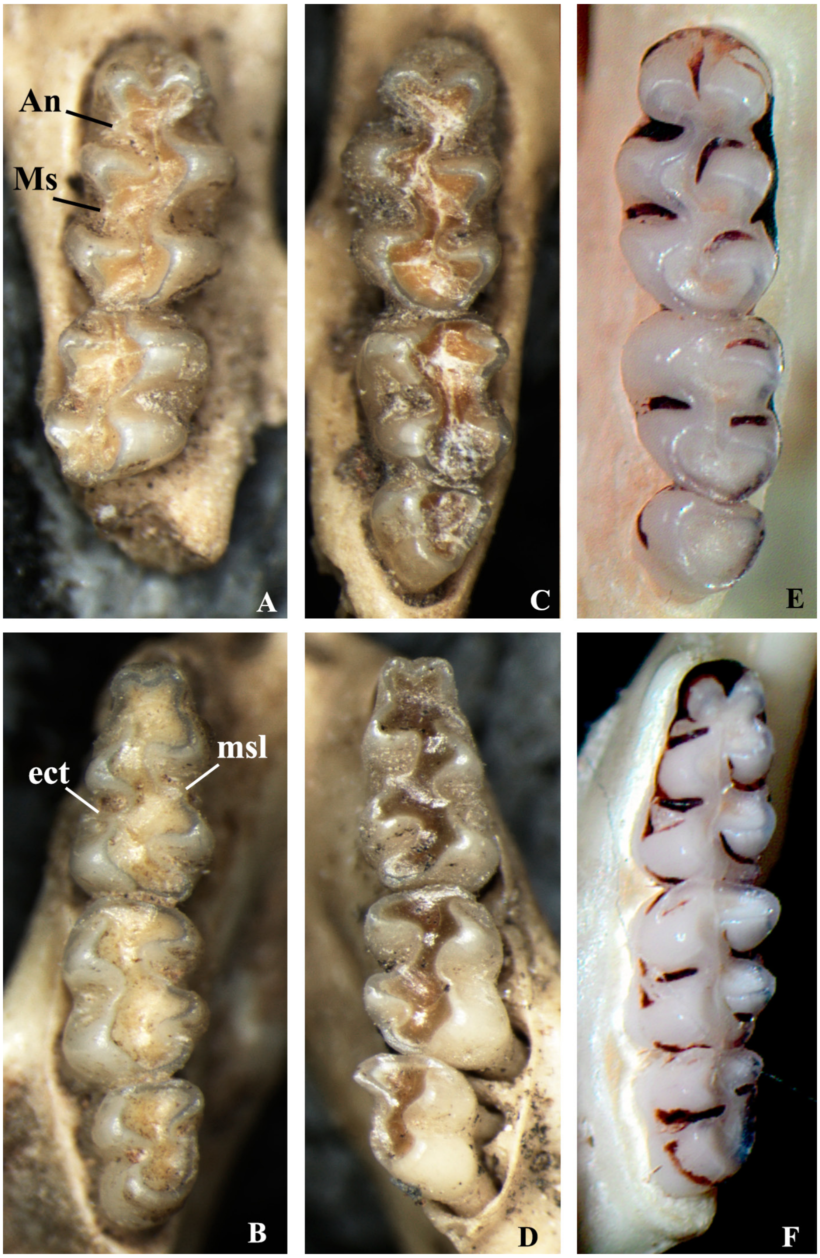

Fig. 9. Occlusal views of the upper and lower molar toothrows of *Akodon* sp. (A–D) and *Akodon kadiweu* (E–F). Legends: anteroloph (An); ectolophid (ect); mesoloph (Ms), mesolophid (msl). Vouchers: MN 57650 (A), MN 57631 (B), MN 57635 (C), MN 57642 (D), MZUSP 35767 (E, F).

slightly larger than *A. montensis* (Gonçalves et al. 2007), and therefore markedly larger than the NSA cave *Akodon* sp. specimens. According to our analyses, these NSA cave fragments overlap morphometrically with smaller congeners. A similar conclusion can be made comparing the large *A. toba* and the smaller NSA cave *Akodon* sp., with the former presenting a comparatively shorter nasal, deeper zygomatic notches, broader zygomatic plate, sharper interorbital margins, and anterior margin of mesopterygoid fossa posterior to M3. All these characters are absent in NSA cave *Akodon* sp., making it very unlikely that this fossil material refers to a member of the *Akodon cursor* species group or to *A. toba*.

It is also worthwhile to provide comparisons to other congeners from the Cerrado domain, *A. clivigenis* (Winge, 1887) from the Quartenary deposits of Lagoa Santa, Minas Gerais. Nowadays, only members of the *A. cursor* species group are present in this region, more precisely *A. cursor* (type locality) and probably *A. montensis*. Pardiñas et al. (2015) mention that *A. clivigenis* is very similar to another member of this species group, *A. paranaensis*, a species currently known from southern Brazil. The single known specimen of *A. clivigenis* is heavily broken and only the anterior portion of the skull remains somewhat preserved. Although broken, it seems that the specimen presents an interorbital region, supraorbital margins,

Table 4. Morphological comparisons of selected qualitative traits of *Akodon* sp. from Nossa Senhora Aparecida (NSA) cave, Serra da Bodoquena, Mato Grosso do Sul, Brazil, with geographically close congeners

	Akodon azarae	*Akodon kadiweu*	*Akodon lindberghi*	*Akodon montensis*	*Akodon philipmyersi*	*Akodon* sp.	*Akodon toba*
Nasal	Moderate, with slightly curved margins	Long, with curved margins	Long, with curved margins	Long, with straight margins	Moderate, with curved margins	Long[1], with curved margins	Moderate, with straight margins
Interorbital region	Narrow, with smooth margins and constriction not marked	Wide, with smooth margins and constriction not marked	Wide, with smooth margins and constriction not marked	Wide, with smooth margins and moderate constriction	Wide, with smooth margins and constriction not marked	Wide, with smooth margins and constriction not marked	Wide, with sharp margins and marked constriction
Zygomatic notches	Moderate	Shallow	Shallow	Moderate	Moderate	Shallow	Deep
Zygomatic plate	Moderate, with dorsal free margin patent	Narrow, with dorsal free margin not patent	Narrow, with dorsal free margin not patent	Moderate to broad, with dorsal free margin patent	Narrow, with dorsal free margin patent	Narrow, with dorsal free margin not patent	Broad, with dorsal free margin distinctly patent
Median palatine process	Present or absent[2]	Present	Present	Absent	Present	Present	Present
Anterior margin of mesopterygoid fossa	Posterior to M3	Even to M3	Usually even to M3	Usually even to M3	Posterior to M3	Even to M3	Posterior to M3
Incisive foramen posterior margin	Usually level with hypoflexus of M1	Level with protoflexus or anterior portion of protocone of M1	Usually level with hypoflexus of M1	Level with mid or posterior portion of protocone of M1	Level with hypoflexus of M1	Level with anterior or mid portion of protocone of M1[3]	Level with mid or posterior portion of protocone of M1
Capsular projection of mandible	Moderate	Moderate	Moderate	Developed	Inconspicuous	Moderate	Developed
Masseteric ridges	Moderate	Moderate	Moderate or indistinct	Moderate or developed	Inconspicuous	Moderate	Developed
Sigmoid notch	Shallow and flat	Moderate deep and curved	Moderate deep and curved	Moderate deep and curved	Moderate deep and curved	Shallow and flat	Moderate deep and curved

[1] Anterior portion of rostrum is broken – see text for details. [2] Present study and Pardiñas et al. (2005). [3] In one specimen (MN 57650) the incisive foramen reaches the hypoflexus of M1. It may be an individual of *A. lindberghi* (see text).

and mesopterygoid fossa similar to members of the *A. cursor* species group. Other characters also call for attention, like the shape and size of the zygomatic plate and incisive foramina. The zygomatic plate exhibits a distinct dorsal free margin, with a concave anterior surface, and the incisive foramina reaches the posterior portion of protocone of M1. Winge (1887) indicates that the closest species to *A. clivigenis* is *A. cursor*, with the former presenting smaller dimensions. These differences are probably related to ontogeny since *A. clivigenis* refers to a relatively young specimen with poor wear on the upper molars. Based on the characters just described, although we can not reach a conclusion about the identity of *A. clivigenis*, the evidence shows that this taxon most likely refers to one of the species under the *Akodon cursor* species group mentioned here, rather than the same taxa as NSA cave *Akodon* sp.

As for comparisons with the smaller sized congeners, NSA cave *Akodon* sp. differs from *A. lindberghi* morphometrically, but there is considerable overlap in craniodental dimensions with other species as shown by the PCA and DFA. Nonetheless, qualitative characters allow the distinction of NSA cave *Akodon* sp. from *A. azarae* and *A. philipmyersi*, since both species present anterior margin of mesopterygoid fossa posterior to M3, posterior margins of incisive foramen near the hypoflexus of M1 level, and moderately deep zygomatic notches. In turn, besides the smaller size, *A. lindberghi* also exhibit a long incisive foramen that reaches the hypoflexus of M1 in most specimens, or is even longer in a few specimens, reaching the hypocone. Thus, we hypothesized that NSA cave *Akodon* sp. specimens are not attributable to any of those smaller species of *Akodon*. Nonetheless, one adult specimen of NSA cave *Akodon* sp. (MN 57650), represented by a maxillae fragment with moderate molar surface wear, has similarities with *A. lindberghi*: the incisive foramina reaches the hypoflexus of M1, and the molar is smaller in size (length of M1 = 1.73 mm, WM1 = 1.07 mm). As this specimen is based only in a single fragment of the maxilla, we refrain from providing a more definitive identification, although it could represent an individual of *A. lindberghi.*

Finally, the NSA cave *Akodon* sp. has very similar qualitative characters to *A. kadiweu*. The only differences between these two taxa are: i) the development of ectostylids, which are more developed in *A. kadiweu* than in any other species examined herein, and ii) the slightly larger size of *A. kadiweu* specimens. Despite these few differences, the extension of the variation in dental characters observed in NSA cave *Akodon* sp. is comparable to those observed in other taxa with larger sample sizes, such as *A. montensis* and, to a lesser extent, *A. lindberghi* and *A. philipmyersi*. Moreover, the morphological variation of *A. kadiweu* is poorly known, since only four specimens of this species are known to date (Brandão et al. 2021), all with considerable molar wear (including one with heavy wear), in contrast to the larger sample of NSA cave *Akodon* sp. that includes a larger range of age classes and sizes that are not yet known for *A. kadiweu*.

The quantitative data presented here allow for the distinction of NSA cave *Akodon* sp. to the smallest (*A. lindberghi*) to the largest congeners (*A. toba*), but it could not be morphometrically distinguished so clearly from other taxa. However, the qualitative morphological characteristics of skull and mandible provide unambiguous evidence that specimens of *Akodon* sp. (*sensu* Salles et al. 2006) from the Serra da Bodoquena deposits are members of the recently described species *A. kadiweu*, extending its temporal range throughout the Quaternary.

DISCUSSION

Akodon kadiweu from the NSA cave is the first known past representative of this genus to be recorded in Mato Grosso do Sul, as well as western Brazil (Fig. 10). *Akodon* subfossils and fossils from Holocene to Late Pleistocene have been found in fossiliferous sites in Brazil, revealing a geographic distribution broader than the currently known range for living species of the genus (Fig. 10), due to past records in Serra da Mesa, Goiás (Boroni 2019), Gruta dos Moura and Gruta do Urso, Tocantins (Tobelém et al. 2013; Pires et al. 2018), and Serra da Capivara, Piauí (Guérin et al. 1996).

Interestingly, if our attribution is correct, we can infer size difference through time in *A. kadiweu*, as it was documented in other rodent species such as *Wiedomys pyrrhorhinus* (Cricetidae) and *Kerodon rupestris* (Caviidae), of which subfossil individuals present some craniodental measurements larger than living specimens (Lessa et al. 2005; Lins et al. 2017). Also, shape difference over time is frequently observed in rodent molars, associated with climate change (*e.g.*, Piras et al. 2009; Kimura et al. 2013; Roth 2018; Boroni 2019). Therefore, the variation observed herein within *A. kadiweu* based on extant and past specimens could be a reflection of the climatic and environmental changes that had occurred in Serra da Bodoquena over thousands of years. This would be an interesting topic to investigate, but there are only three skins and skulls and one fluid extant specimens of *A. kadiweu* currently available in collections; in addition, there are only small fragments of 33 past specimens. These limited samples, both extant and extinct, would not allow a proper analysis of the variation through time and space.

Thus, effort should be made in the future to investigate this issue after larger series of specimens of past and recent series of *A. kadiweu* are available in scientific collections.

In NSA cave, specimens of *Akodon kadiweu* were found from the stratigraphic units (S.U.) 2, 4 and 7, but no date estimates are available for these stratigraphic profiles (see Boroni et al. 2020). The specimens from S.U. 7 are from the surface of the cave floor and suggest a recent presence of the genus in NSA area, along with typical Sigmodontinae of the Cerrado biome, as *Necromys lasiurus*, *Thalpomys lasiotis*, *Calomys tener*,

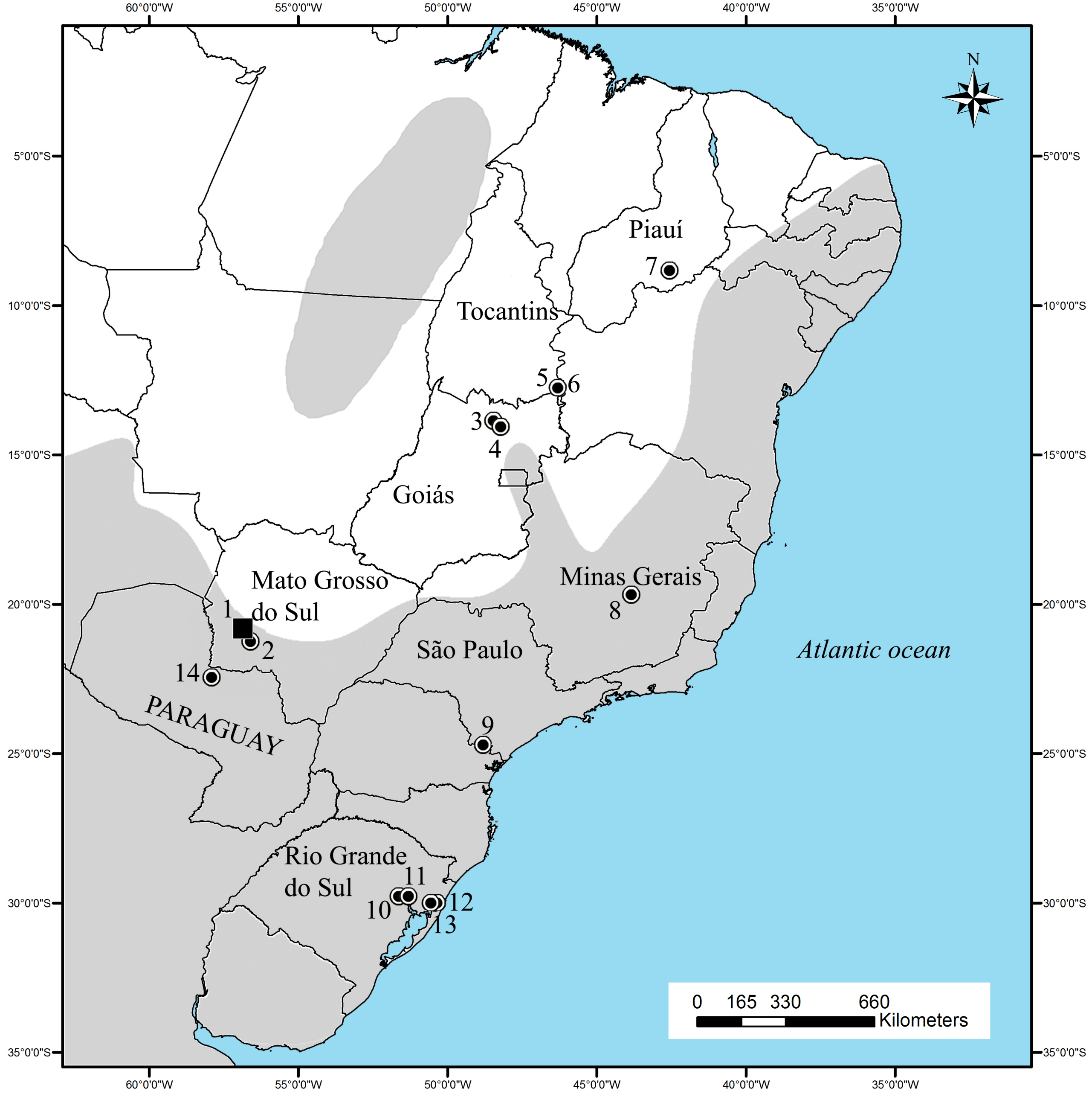

Fig. 10. Range distribution of extant and fossil species of *Akodon* in Brazil and Paraguay. Localities: 1 – Fazenda Califórnia, Parque Nacional da Serra da Bodoquena (Brandão et al. 2021); 2 – Nossa Senhora Aparecida cave, Serra da Bodoquena (Boroni et al. 2020); 3 – Carneiro cave (Boroni 2019); 4 – Igrejinha cave (Salles et al. 1999); 5 – Gruta dos Moura cave (Tobelém et al. 2013); 6 – Gruta do Urso cave (Pires et al. 2018); 7 – Toca da Barra da Janela do Antonião cave (Guérin et al. 1996); 8 – Lagoa Santa (Winge 1887); 9 – Abismo Iguatemi site (Castro and Langer 2011); 10 – Garivaldino site (Stutz et al. 2017); 11 – Adelar Pilger site (Hadler et al. 2016); 12 – Deobaldino Marques site (Roth 2018); 13 – Sangão site (Stutz et al. 2018); 14 – Risso Cave, Paraguay (Torres et al. 2015). Also see table 1. Gray area was based on the geographic range of the extant species of genus *Akodon* according to Pardiñas et al. (2015).

Cerradomys and *Pseudoryzomys simplex*. Along with *A. kadiweu*, other open-habitat sigmodontines were also recorded in deeper strata S.U. 4 and 2, such as *Kunsia tomentosus*, *Wiedomys* sp. and *Graomys* cf. *chacoensis*.

Studies on past assemblages of Sigmodontinae rodents show high diversity during the Holocene and Late Pleistocene, followed by pronounced changes in abundance and geographic range, with extinction occurring well into recent times (*e.g.*, Winge 1887; Voss and Myers 1991; Pardiñas et al. 2002; Pardiñas and Teta 2011 2013; Pires et al. 2018; Boroni 2019; Neves et al. 2020). These community shifts are associated with the environmental alterations especially during glacial and interglacial periods, leading to retraction and expansion of forested and open areas during the Pleistocene and Holocene epochs (Cartelle 1999; Bueno et al. 2016). For instance, the Quaternary mammalian fauna recorded in Serra da Bodoquena suggests different conditions in the past than nowadays, characterized by open vegetation formations with flooded areas (Salles et al. 2006; Boroni et al. 2020). In Risso Cave, Paraguay, the fossiliferous site closest to our sample, approximately 180 km southwest of NSA cave, Quaternary remains also corroborate this paleoenvironmental scenario, including remains of species of Sigmodontinae, such as *Akodon* cf. *toba* and *Holochilus chacarius*, species typical of open and flooded vegetation (Torres et al. 2015). The genera recovered in the deeper stratigraphic layers (*i.e.*, *Kunsia*, *Wiedomys* and *Graomys*) do not currently occur in Serra da Bodoquena, suggesting regional extinctions for some species over the Quaternary in this region, as their preferred habitat become unavailable with landscape changes over time.

CONCLUSION

A few past records of *Akodon* from Brazil have been identified to species level, such as *A. clivigenis* and *A. cursor* from Lagoa Santa (Winge 1887; Paula-Couto 1950). Here, we provided the taxonomic identity of *A. kadiweu*, a past representative of *Akodon* from Serra da Bodoquena, which helps us understand the evolutionary history of this genus in South America, and at the same time increase our knowledge of this recently described and poorly known taxon, currently restricted to a limited portion of western Brazil.

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Supplementary Materials

Table S1. List of specimens examined in the present study through morphological analyses. Abbreviations: CNP, Colección de Mamíferos del Centro Nacional Patagónico; MN, Museu Nacional, Universidade Federal do Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo; UFMG, Universidade Federal de Minas Gerais; UMMZ, University of Michigan Museum of Zoology; USNM, National Museum of Natural History; FMNH, Field Museum of Natural History. (download)