Zootaxa 4861 (3): 429–443
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4861.3.9
http://zoobank.org/urn:lsid:zoobank.org:pub:57779BA3-DB7D-491D-AFB2-68A0264F0275

Morphological variation in the genus *Juliomys* (Rodentia: Cricetidae: Sigmodontinae) and taxonomic status of *Juliomys anoblepas* (Winge 1887) from the Quaternary of Southeast Brazil

CAROLINA PIRES[1*], MARCELO WEKSLER[1] & CIBELE R. BONVICINO[2]
[1]*Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Quinta da Boa Vista—São Cristóvão, 20940-040, Rio de Janeiro, Brazil.*
[2]*Programa de Genética, Instituto Nacional de Câncer, Rio de Janeiro, Brazil.*
cibele.bonvicino@gmail.com; https://orcid.org/0000-0002-1948-7643
[4] *mweksler@mn.ufrj.br; https://orcid.org/0000-0001-8111-4779*
[*]*Corresponding author. carolpiresab@hotmail.com; https://orcid.org/0000-0002-7405-4488*

Abstract

The region of Lagoa Santa, Minas Gerais, Brazil, is one of the most important karstic areas of the Brazilian Quaternary due to the faunistic diversity of living and extinct forms. Among them, some taxa remain poorly studied, as is the case of *Calomys anoblepas* Winge 1887. Despite the recent allocation of the taxon within *Juliomys*, its description and morphological analysis are condensed, based on comparative few specimens and on few informative characters. In this study, we investigate characters proposed to distinguish species of *Juliomys,* and reevaluate the taxonomic status of the fossil *Juliomys anoblepas*. We analyzed 80 cranio-dental morphological characters in 233 specimens represented by the four species currently recognized: *J. pictipes* (Osgood 1933), *J. rimofrons* Oliveira & Bonvicino 2002, *J. ossitenuis* Costa, Pavan, Leite & Fagundes 2007, and *J. ximenezi* Christoff, Vieira, Oliveira, Gonçalves, Valiati & Tomasi 2016. We also performed principal component analysis on eight craniodental measurements available for the *J. anoblepas* hypodigm. The review of morphological systems and the evaluation of the characters used in the literature revealed that there are no diagnostic characters in the anterior portion of the skull and in the molar series of *Juliomys*, being difficult to differentiate the fossil from the other living species. Only six qualitative characters were variable and applicable to the hypodigm of *J. anoblepas*. Characters are polymorphic, invariable, or the fossil is not sufficiently complete to determinate its states. The taxon could not be morphometrically differentiated from *J. pictipes* and *J. ossitenuis.* Based on the results presented herein, we consider *J. anoblepas* as a *nomen dubium* and restrict its name to the taxon's hypodigm.

Key words: taxonomy, species, morphological variation, *nomen dubium*

Introduction

Our knowledge of the mammalian diversity of late Brazilian Quaternary has increased due to several recent studies describing local faunas (Salles *et al.* 2006; Kerber *et al.* 2013; Hadler *et al.* 2016; Neves *et al.* 2017; Pires *et al.* 2018; Stutz *et al.* 2018; Boroni *et al.* 2020). One of the main karstic areas of the Brazilian Quaternary, however, still is the iconic region of Lagoa Santa, in the state of Minas Gerais, due to its great faunal and botanical diversity (Paula-Couto 1979). The extensive works of Lund (Paula-Couto 1950; Cartelle 2002) and Winge (1887), both on fossil and living forms, constitute one of the most important studies of Neotropical rodent taxonomy, and present the description of several species of sigmodontines. Many of these taxa were recognized as fossils at the time, but a few forms have been recently recognized as extant (*e.g.*, Voss & Myers 1991; Voss & Carleton 1993; Pardiñas e*t al.* 2008a).

One of these taxa is *Calomys anoblepas* Winge 1887, which had a convoluted taxonomic history. The taxon was considered by Winge (1887: 44) as closely related to *Calomys longicaudatus* (= *Oligoryzomys nigripes*); a similar view was adopted by Trouessart (1898), who moved *C. anoblepas* to the genus *Oryzomys* Baird 1857, which at that time encompassed *Oligoryzomys* species. Posteriorly, in a comparative study with other genera of sigmodontines,

Accepted by P. Teta: 7 Sept. 2020; published: 19 Oct. 2020

the connection of the *C. anoblepas* with *Oecomys* was also suggested (Pardiñas *et al.* 2002). Finally, Pardiñas & Teta (2011) proposed the allocation of *C. anoblepas* to the genus *Juliomys* González, 2000, constituting a new combination: *Juliomys anoblepas* (Winge 1887).

The genus *Juliomys* was erected by González (2000) to include the Atlantic forest endemic *Thomasomys pictipes* Osgood 1933, but a flurry of recent taxonomic work resulted in the recognition of three additional species for genus: *J. rimofrons* Oliveira & Bonvicino 2002; *J. ossitenuis* Costa, Pavan, Leite & Fagundes 2007; and *J. ximenezi* Christoff, Vieira, Oliveira, Gonçalves, Valiati & Tomasi 2016. The current known geographic distribution of the genus includes southeastern Brazil, northeastern Argentina, and eastern of Paraguay (see a synthesis in González *et al.* 2015), including several cases of sympatry between different species (Costa *et al.* 2007; Aguieiras *et al.* 2013; Grazzini *et al.* 2015; González *et al.* 2015; Christoff *et al.* 2016).

Although the taxonomic studies of *Juliomys* have provided a morphological framework for identification of the taxa (Oliveira & Bonvicino 2002; Costa *et al.* 2007; Pardiñas *et al.* 2008b; Pavan & Leite 2011; Aguieiras *et al.* 2013; González *et al.* 2015; Christoff *et al.* 2016), the recognition among species has been mainly based on karyotypes and molecular differences (Paresque *et al.* 2009; Christoff *et al.* 2016). Morphological descriptions were usually condensed and based on few specimens (Osgood 1933; González 2000; Oliveira & Bonvicino 2002; Pardiñas *et al.* 2008b; de la Sancha *et al.* 2009) and, in some cases, presented inconsistencies among them (Costa *et al.* 2007; Pardiñas *et al.* 2008b; Pavan & Leite 2011; Aguieiras *et al.* 2013; Fonseca *et al.* 2013).

The holotype and the only known specimen of *J. anoblepas* is from Lapa da Serra das Abelhas, in the municipality of Lagoa Santa, Minas Gerais State, Brazil. The hypodigm is a fragmentary skull, which presents additional difficulty for taxonomic diagnosis. Pardiñas & Teta (2011) were able to recognize the taxon as distinct from extant species of *Juliomys* based on a handful of cranial and dental characters. Nevertheless, their sampling was extremely sparse for the species of the genus, and did not include the recently described *J. ximenezi*. Therefore, the aim of the present study is to investigate diagnostic characters proposed to distinguish species of *Juliomys*, and to reevaluate the taxonomic status of *Juliomys anoblepas* based on a comprehensive sample of *Juliomys*.

Material and methods

We analyzed 233 specimens of *Juliomys* housed at the following scientific collections: Mammals Collection at Field Museum of Natural History (FMNH), Chicago, United States; Laboratório de Biologia e Parasitologia de Mamífeos Reservatórios, Instituto Oswaldo Cruz/Fiocruz (LBCE), Rio de Janeiro, Brazil; Coleção de Mamíferos do Museu de Ciências Naturais, Universidade Luterana do Brasil (MCNU), Canoas, Brazil; Coleção de Mamíferos do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN-M), Belo Horizonte, Brazil; Coleção de Mastozoologia do Museu Nacional/Universidade Federal do Rio de Janeiro (MN/UFRJ), Rio de Janeiro, Brazil; Coleção de Mamíferos do Museu de Zoologia da Universidade Estadual de Campinas (ZUEC-MAM), Campinas, Brazil; Coleção Mastozoológica do Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Coleção Científica de Mamíferos do Núcleo em Ecologia e Desenvolvimento Ambiental de Macaé/UFRJ (NPM), Macaé, Brazil; Coleção Científica de Mamíferos da Universidade Federal de Santa Maria (UFSM), Santa Maria, Brazil; Coleção de Mamíferos da Universidade Federal do Espírito Santo (UFES-MAM), Vitória, Brazil; Coleção de Mamíferos do Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais (CCT-UFMG), Belo Horizonte, Brazil; Coleção de Mamíferos do Departamento de Ecologia e Zoologia da Universidade Federal de Santa Catarina (UFSC), Florianópolis, Brazil; and Coleção Zoológica da Universidade Regional de Blumenau (FURB), Blumenau, Brazil. The holotype of *J. anoblepas* is housed at Lund collection in the Universitets Zoologisk Museum (ZMUC), Copenhagen, Denmark, and was analyzed through photographs. Examined specimens are from 75 localities (Fig. 1), and are listed in appendix 1. Specimens were identified based on comparative analysis of type material and analyses of geographic variation (Pires 2018, unpublished results).

We evaluated 80 cranial and dental characters (appendix 2) obtained from taxonomic and anatomic studies of the genus (González 2000; Oliveira & Bonvicino 2002; Costa *et al.* 2007; Pavan & Leite 2011; Aguieiras *et al.* 2013; González *et al.* 2015; Christoff *et al.* 2016) and from a compilation of Sigmodontinae characters (Weksler 2006). The anatomical nomenclature is based on Voss (1988) and Weksler (2006) for the cranial morphology and Reig (1977) and Pires *et al.* (2016) for the dentition. We inferred the levels of intra- and interspecific variation of characters using frequency graphs. We considered as polymorphic characters those where the most common character state has a frequency of less than 95%, a cutoff threshold that is historically used in the definition of polymorphism (Hartl & Clark 2007).

For morphometric analyses, we employed 12 cranial measurements taken with digital calipers to the nearest 0.01 mm. We used eight variables recorded by Pardiñas & Teta (2011) in *J. anoblepas* hypodigm: Diastema Length (DL), Incisive Foramen Breadth (IFB), Incisive Foramen Length (IFL), Interorbital Breadth (IOC), First Upper Molar Breadth (M1B), Molar Row–Crown Length (MRC), Palatal Bridge Length (PBL), and Zygomatic Plate Length (ZP); Palatal Breadth at First Molar (PB1) was excluded because of inter researcher measurement error. We only analyzed adult specimens, *i.e.*, specimens with all teeth erupted and with at least minimal wear (Oliveira *et al.* 1998), with complete set of measurements and grouped males and females due to lack of sexual dimorphism (*t*-tests, $p < 0.05$; not shown). We employed principal component analysis (Strauss 2010) to identify patterns of morphometric variation among species of *Juliomys,* and to compare *J. anoblepas* to other species of the genus; the analysis was based on the covariance matrix of logarithmic-transformed data. We also computed descriptive statistics (average, standard deviation, minimum and maximum) for each species. All statistical analyses were performed in R version 4.0.2 using RStudio (RStudio Team 2020).

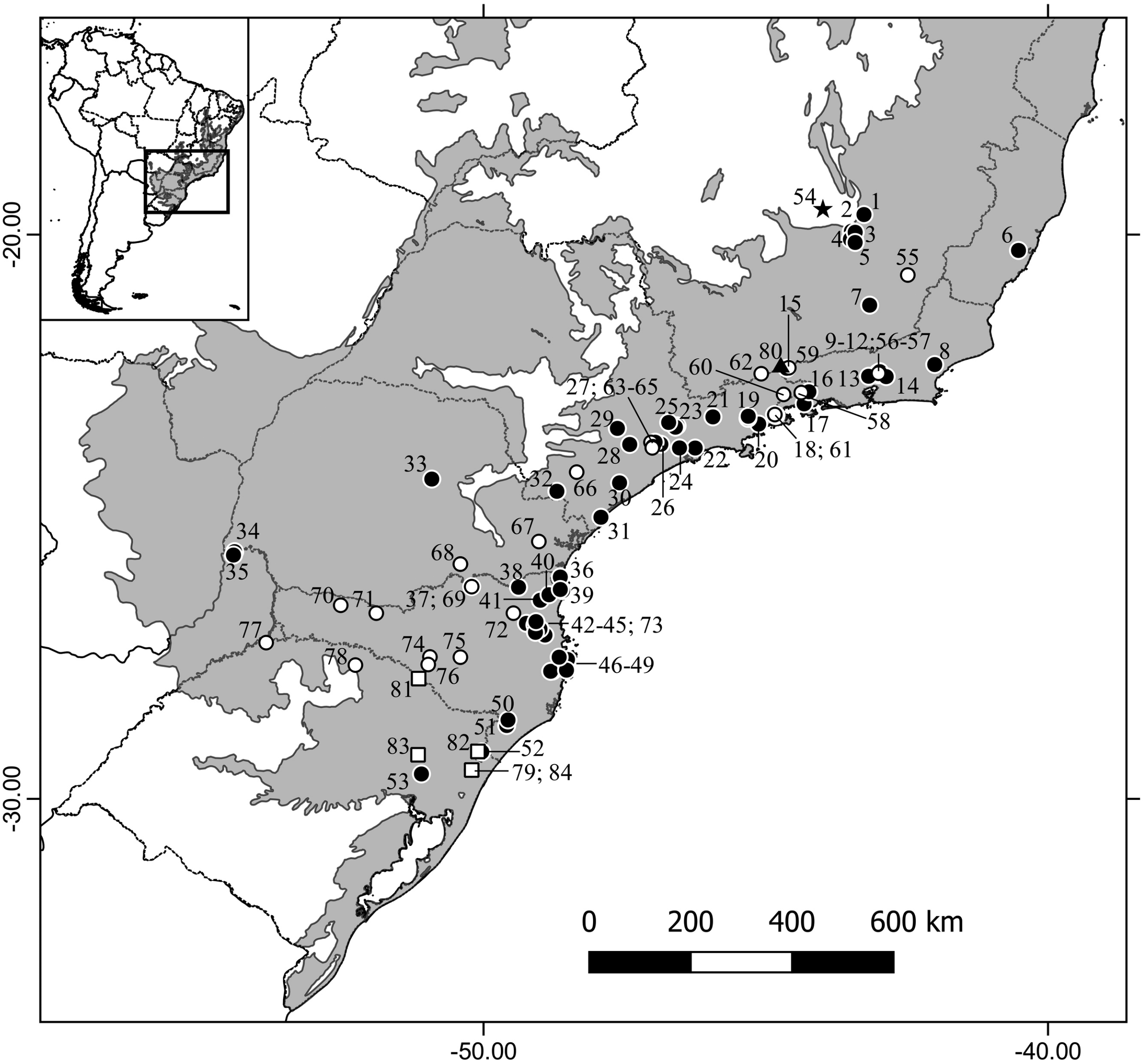


FIGURE 1. Map showing the collecting localities of specimens of *J. pictipes* (black circles), *J. anoblepas* (star), *J. ossitenuis* (white circles), *J. rimofrons* (triangles), *J. ximenezi* (squares). Atlantic Forest extension is marked in gray and numbers correspond to the localities listed in appendix 1.

Results

The specimen of *Juliomys anoblepas* consists of the anterior portion of the skull, *i.e.*, the rostrum, part of right zygomatic arch, interorbital region until to the mesopterygoid fossa, with complete toothrow. The rostrum was in a very fragile state, and was recently damaged (Fig. 2). The molar series are well preserved and, through its occlusal surface, it is possible to infer that the specimen was a young adult.

Only six characters were variable among species of *Juliomys* and applicable to the hypodigm of *J. anoblepas*: (1) posterior extension of nasals, (2) depth of zygomatic notch, (3) presence of frontal fontanella, (4) extension of incisive foramina, (5) anterior cingulum, and (6) presence of enteroloph and enterostyle on M1-M2. Below, we present the characters used in the literature to differentiate species of *Juliomys* and the new ones herein identified as being variable (*i.e.*, posterior extension of nasals, shape of the supraorbital margin, anterior cingulum, and enteroloph and enterostyle), and describe the pattern of morphological variation among and within species:

(1) Posterior extension of nasals: although the extension of nasals is a continuous trait, a distinction can be perceived among individuals when the posterior termini of the nasals are compared to the triple point suture between the lacrimal, maxillary, and frontal bones. For all *Juliomys* species, we found individuals with short nasals (*i.e.*, nasals not extending beyond the lacrimal-maxillary-frontal suture) or long nasals (*i.e.*, reaching the triple point suture plane) (Fig. 3). Even being polymorphic in all species, in *J. pictipes* the short nasals are more frequent, while in *J. rimofrons*, and *J. ossitenuis* the long nasals are more frequent. In *J. ximenezi*, the frequency of specimens with long and short nasals is basically the same (Fig. 4.1). The nasals are long in the hypodigm of *J. anoblepas*.

(2) Zygomatic notch: a deep excavation of the zygomatic notch, created by a wide zygomatic plate with a rounded anterodorsal margin (*sensu* Weksler 2006), never occurs in *Juliomys*, and variation in the degree of depth of the zygomatic notch is continuous and inapplicable for specific diagnostic. Among our sample of *Juliomys* specimens, the anterodorsal margin of the zygomatic plate is always straight, leading almost always to a little excavated zygomatic notch (Fig. 5); only few specimens were recorded with a clearly more excavated zygomatic notch (Fig. 4.2). The hypodigm of *J. anoblepas* presents a little excavated zygomatic notch.

(3) Frontal fontanelle: the frontal fontanella, also referred as frontal fontanelle (*e.g.*, Hershkovitz 1962; Steppan 1995; Gardner & Anderson 2001) is a small opening in the dorsal frontal surface, resulting from the incomplete intramembranous ossification of the embryonic frontal suture (Szabo-Rogers *et al.* 2016). It is present or absent in specimens of *J. pictipes*, *J. ossitenuis*, and *J. ximenezi* (Fig. 5), suggesting a polymorphic character. Frontal fontanella are found more frequently among *J. ossitenuis* (Fig. 4.3), and present in all three examined specimens of *J. rimofrons*. The frontal fontanelle is present in the hypodigm of *J. anoblepas*.

(4) Incisive foramina: the extension of incisive foramina shows minor variation among *Juliomys* species, suggesting that it does not represent a taxonomic diagnostic character (Fig. 4.4). We consider as long incisive foramina those that extend beyond the plane of M1 alveoli, and short foramina those that reach the alveoli of M1 or are slightly anterior to this point. The hypodigm of *J. anoblepas* displays incisive foramina that reach the alveoli of M1 (*i.e.*, short).

(5) Anterior cingulum: the anterior cingulum is a component of the procingulum, located anteriorly to the anterocone, with a lower relief than the cusp and delimited by a valley that does not open on the labial and lingual margins (see Pires *et al.* 2016). This structure is only present in few specimens of *J. pictipes* and *J. ossitenuis* (Fig. 4.5). A vestigial anterior cingulum, *i.e.*, without delimitation of the valley and present as a discrete elevation, was found in exemplars of *J. pictipes*, *J. ossitenuis*, and *J. ximenezi* (Fig. 3). The anterior cingulum is absent in specimens of *J. rimofrons* and *J. anoblepas*.

(6) Enteroloph and enterostyle: the enteroloph is a lingual loph originating as an extension of the enterostyle and connected to the median mure or to the posteromedial face of the protocone. The enterostyle is always present in specimens of *J. rimofrons*, and *J. pictipes*, whereas the enteroloph can be present or absent in specimens of the latter species (Fig. 3). The same pattern occurs in *J. ossitenuis*, except for four specimens that do not display the enterostyle. The character is polymorphic in *J. ximenezi*: both structures can be absent (50% of specimens), present (about 17%), or only the enterostyle is present (about 33%); in this case, the enterostyle is less conspicuous in relation to other species (Fig. 4.6). The enteroloph and enterostyle are both absent in the hypodigm of *J. anoblepas*.

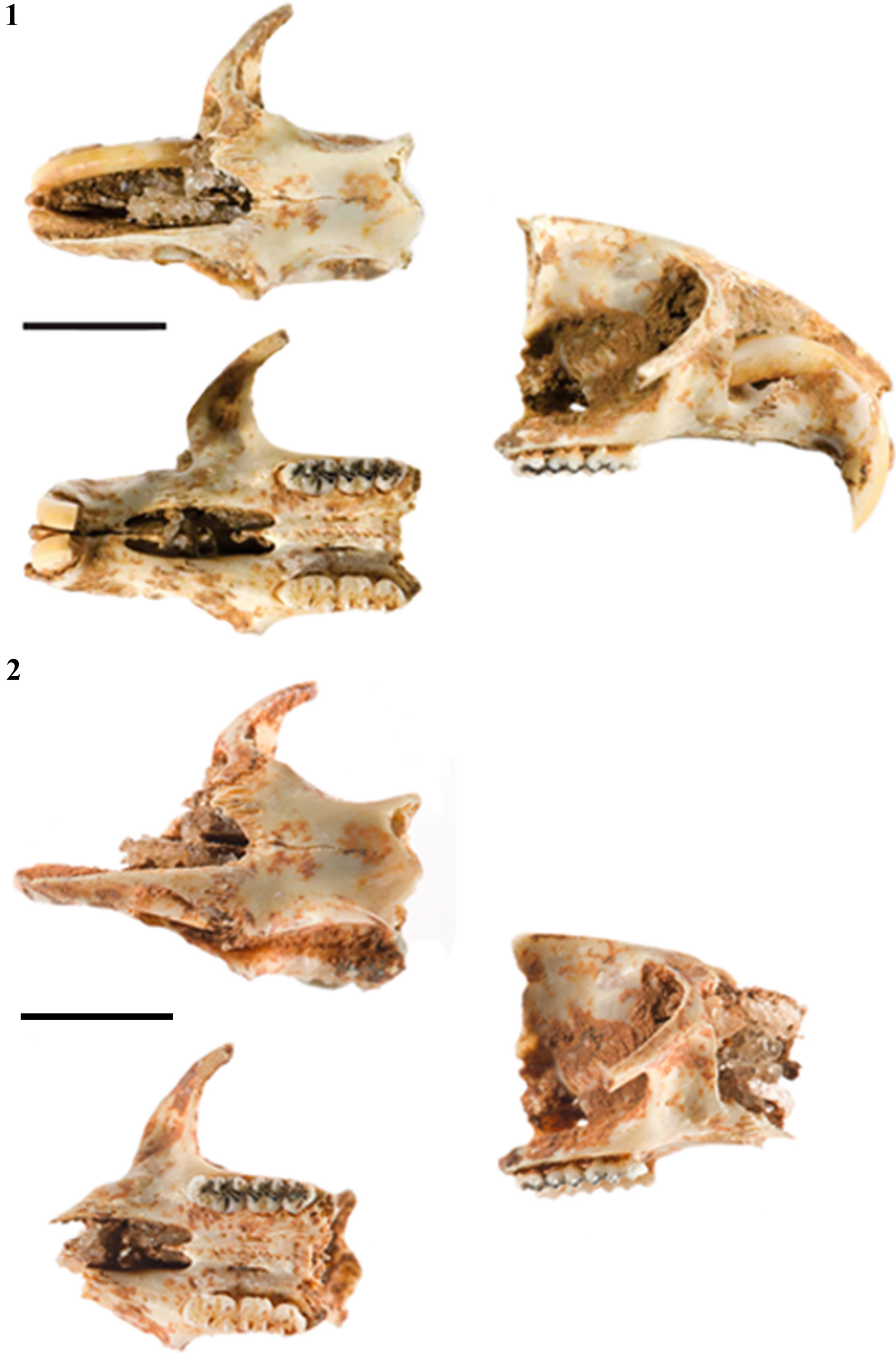


FIGURE 2. Dorsal, ventral, and lateral views of skull of *J. anoblepas*. 1—Photo modified from Pardiñas & Teta (2011); 2—Photo by Kasper Hansen, illustrating the current state of preservation of the specimen. The specimen is housed at Lund Collection (ZMUC), Copenhagen, Denmark, but it has no catalog number. Its recognition is unquestionable by Winge (1887)'s description and illustration. Scale = 5 mm.

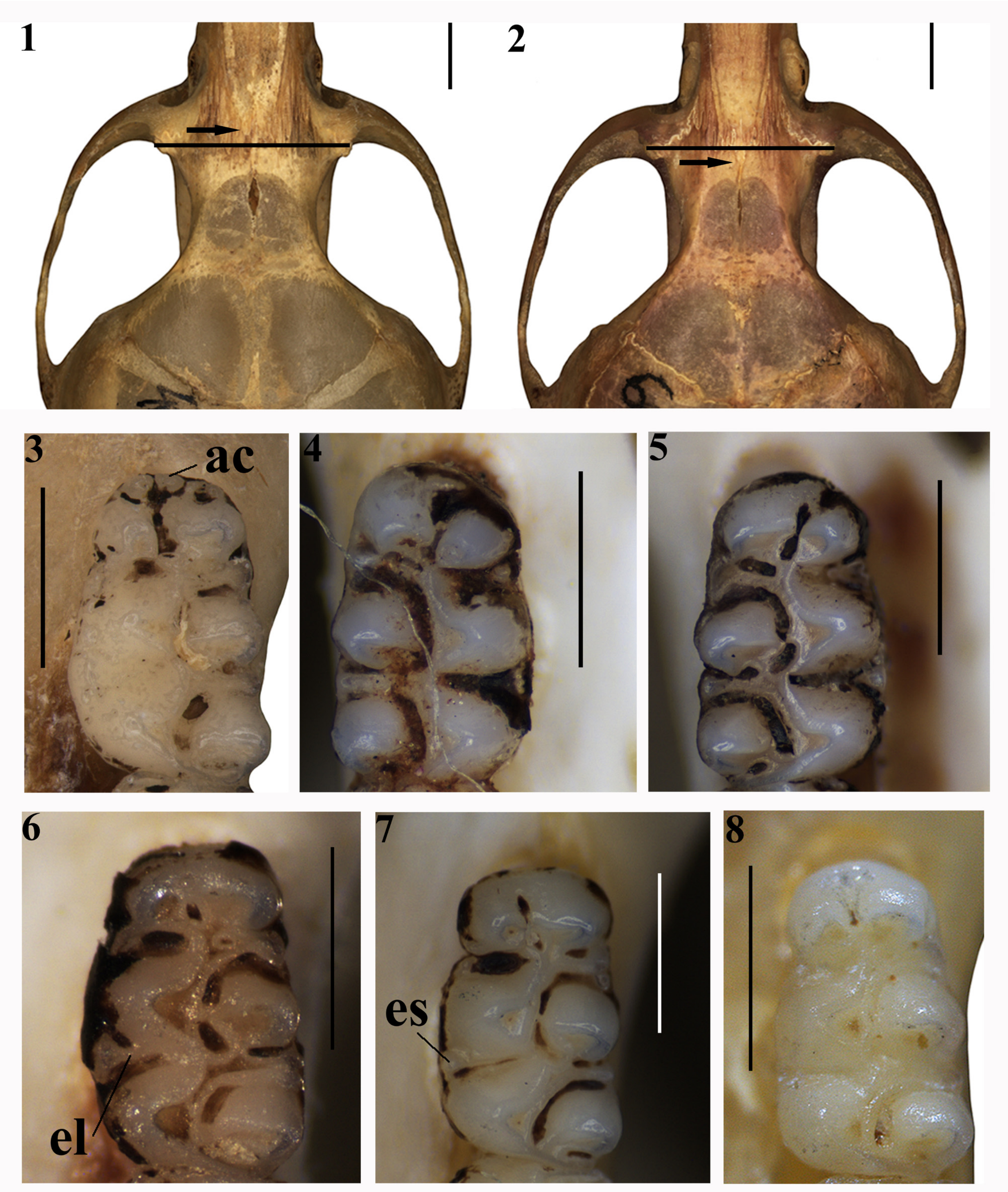


FIGURE 3. Characters proposed herein and identified as polymorphic in *Juliomys* species. 1—Short nasal in the paratype of *J. rimofrons* (MN46703); 2—Long nasal in the paratype of *J. rimofrons* (MN61646); 3—Anterior cingulum in *J. pictipes* (UFES2269); 4—Vestigial anterior cingulum in *J. ossitenuis* (UFSM599); 5—Anterior cingulum absent in *J. ossitenuis* (MN81912); 6—Enteroloph and enterostyle, both present in *J. pictipes* (MN77793); 7—Only enterostyle present in *J. pictipes* (UFSM517); 8—Both absent in the holotype of *J. ximenezi* (MCNU868). Line = triple point lacrimal-maxillary-frontal suture; arrow = extension of nasal; ac = anterior cingulum; el = enteroloph; es = enterostyle. Scale = 2 mm in images 1–2 and 1 mm in images 3–8.

(7) Interorbital region: the interorbital region of *Juliomys* is always hourglass shaped, and the supraorbital crests are absent. Differences in the region are found in relation to the supraorbital margin, which is squared in specimens of *J. pictipes*, and rounded in *J. rimofrons* and *J. ossitenuis* (Fig. 5). *J. ximenezi* specimens commonly have slightly squared supraorbital margins, and are here defined as an intermediate state, *i.e.*, they are not strictly squared margin as in *J. pictipes* nor completely rounded with the lateral margin of the frontal visible in dorsal view. The shape of the supraorbital margin is a diagnostic character, but it cannot be evaluated in *J. anoblepas* due to its fragmentary condition.

(8) Posterolateral palatal pits: no variation was found in relation to the size of the posterolateral palatal pits in *J. pictipes*, *J. rimofrons, J. ossitenuis*, and *J. ximenezi* (Fig. 5). This structure cannot be evaluated in *J. anoblepas*.

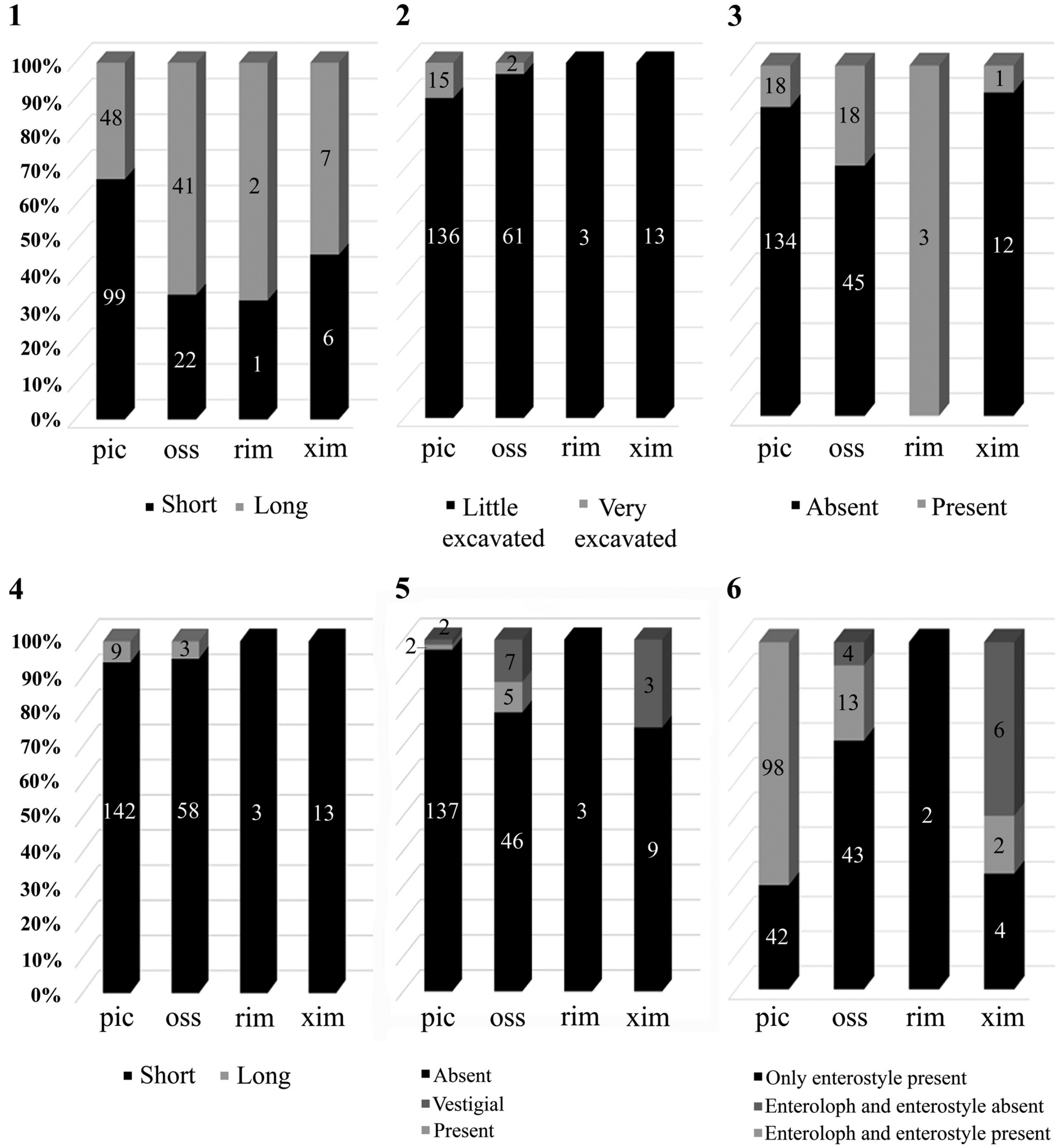


FIGURE 4. Frequency of states related to characters that can be applied to *J. anoblepas*. 1—Extension of the nasal; 2—Depth of the zygomatic notch; 3—Frontal fontanelle; 4—Extension of the incisive foramen; 5—Anterior cingulum; 6—Enteroloph and enterostyle. Numbers in bars correspond to number of specimens that have each state. Abbreviations: pic = *J. pictipes*, oss = *J. ossitenuis*, rim = *J. rimofrons*, and xim = *J. ximenezi*.

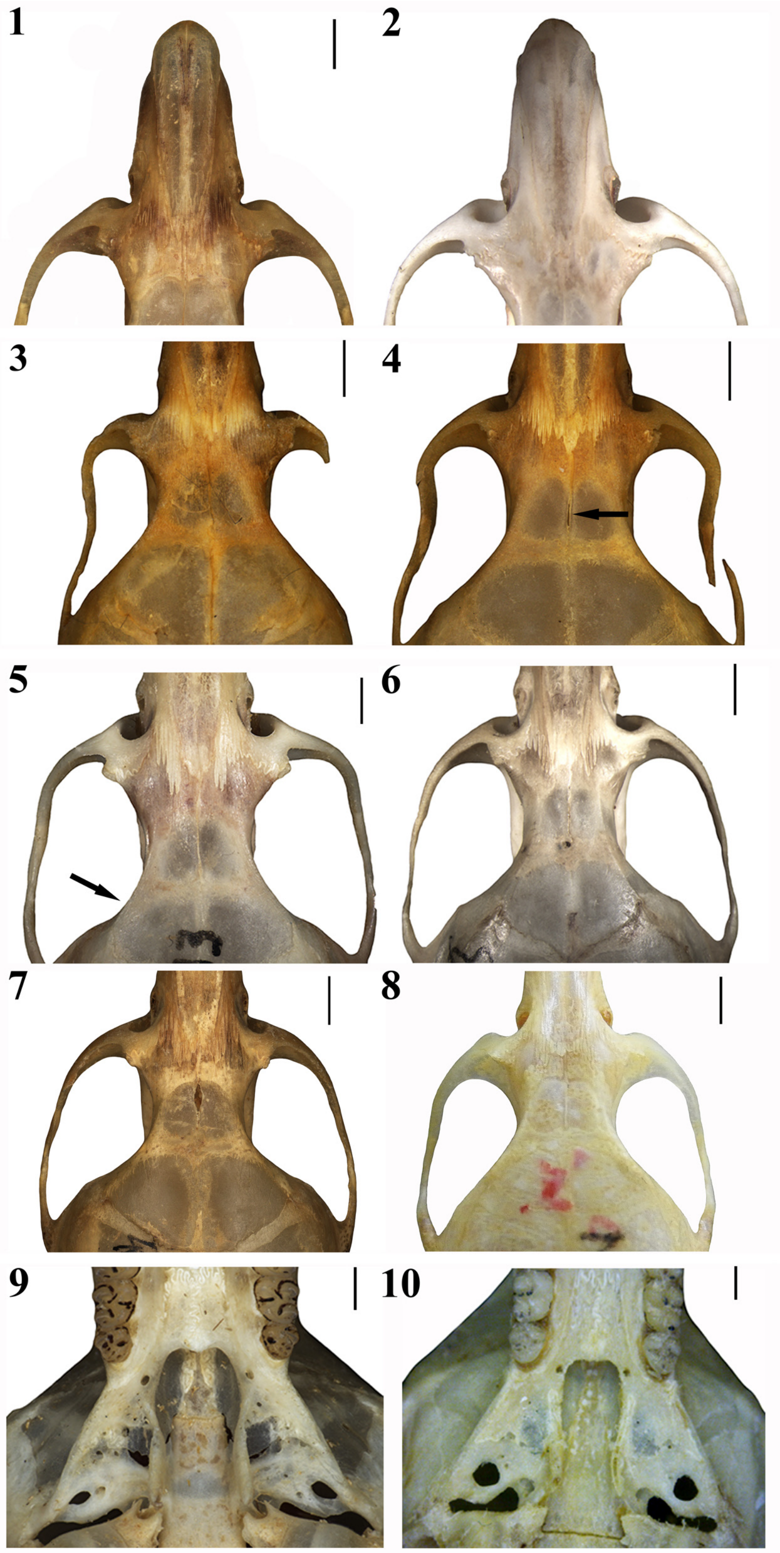


FIGURE 5. Characters previously proposed as diagnostic, and herein identified as polymorphic or invariable. 1—Little excavated zygomatic notch in *J. pictipes* (MN81096); 2—Zygomatic notch more excavated in *J. pictipes* (MN69764); 3—Frontal fontanelle absent in *J. pictipes* (UFES2421); 4—Frontal fontanelle present in *J. pictipes* (UFES2432); 5–8—Interorbital region is hourglass shaped in all specimens of *Juliomys*: note differences in the shape of supraorbital margin, which is squared in *J. pictipes* (Fig. 5.5, MN77793), rounded in *J. ossitenuis* (Fig. 5.6, MN81085), rounded in *J. rimofrons* (Fig. 5.7, MN46703), and slightly squared in *J. ximenezi* (Fig. 5.8, MCNU868); 9–10—Posterolateral pits with same size in *J. ossitenuis* (Fig. 5.9, MN81852), and in *J. pictipes* (Fig. 5.10, MZUSP32666). Horizontal arrow = frontal fontanelle; inclined arrow = supraorbital margin. Scale = 2 mm in images 1–8 and 1 mm in images 9–10.

All eight measurements of *J. anoblepas* holotype fall within the minimum-maximum range observed for *J. pictipes* (Table 1), while six measurements are within the range of *J. ossitenuis.* In turn, only DL was within the range of *J. rimofrons,* and IFB and MRC within the range of *J. ximenezi*, but the two latter taxa have small sample size (n = 3 and 12, respectively). Principal component analysis produced a similar result. The biplots of the first 3 principal components (Fig. 6), which account for 76.8% of the total variance, reveal an overall juxtaposition of the species scores in the multivariate space. *J. pictipes* is slightly separated from *J. ossitenuis, J. rimofrons,* and *J. ximenezi* in the second component, but the scores of remaining species overlap in all components. The PCA score for *J. anoblepas* is within the range for *J. pictipes* and *J. ossitenuis* for the first 3 components.

TABLE 1. Skull measurements (in mm) of the type specimen of *J. anoblepas* and descriptive statistics for all other *Juliomys* species. Values are given as average (standard deviation) minimum–maximum. See Material and Methods for measurements acronyms.

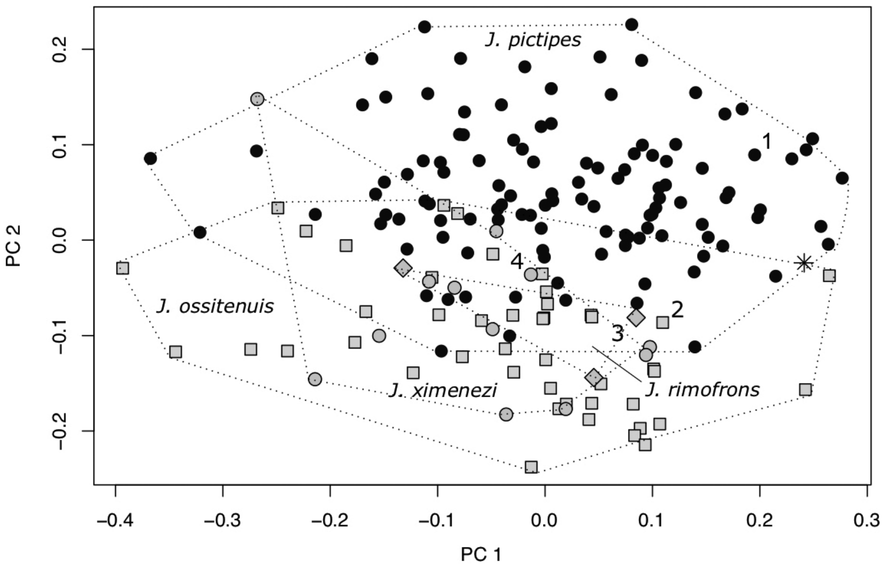
Taxon	***J. anoblepas*** (n=1)	***J. pictipes*** (n=114)	***J. rimofrons*** (n=3)	***J. ossitenuis*** (n=45)	***J. ximenezi*** (n=12)
PBL	4.29	3.88 (0.25) 3.27–4.49	3.69 (0.16) 3.52–3.83	3.56 (0.27) 2.91–4.67	3.66 (0.20) 3.34–3.97
ZP	2.38	2.24 (0.20) 1.71–2.67	2.08 (0.15) 1.92–2.21	2.08 (0.18) 1.60–2.53	2.05 (0.13) 1.85–2.23
IOC	4.14	4.02 (0.19) 3.56–4.97	3.69 (0.11) 3.58–3.79	3.73 (0.12) 3.51–3.98	3.81 (0.13) 3.64–4.02
DL	6.39	5.91 (0.44) 4.76–6.90	6.02 (0.61) 5.33–6.45	6.09 (0.42) 4.95–6.99	5.65 (0.44) 4.69–6.27
IFL	5.25	4.40 (0.36) 3.60–5.52	4.93 (0.27) 4.67–5.21	4.69 (0.45) 3.34–5.50	4.70 (0.39) 3.96–5.23
IFB	1.77	1.63 (0.14) 1.24–1.96	1.63 (0.06) 1.58–1.70	1.71 (0.13) 1.43–1.98	1.71 (0.14) 1.49–2.01
MRC	4.13	3.89 (0.14) 3.61–4.72	3.83 (0.11) 3.70–3.91	3.75 (0.12) 3.37–4.02	3.81 (0.21) 3.45–4.23
M1B	1.19	1.06 (0.05) 0.96–1.21	1.11 (0.03) 1.09–1.15	1.02 (0.04) 0.90–1.15	1.01 (0.06) 0.91–1.15

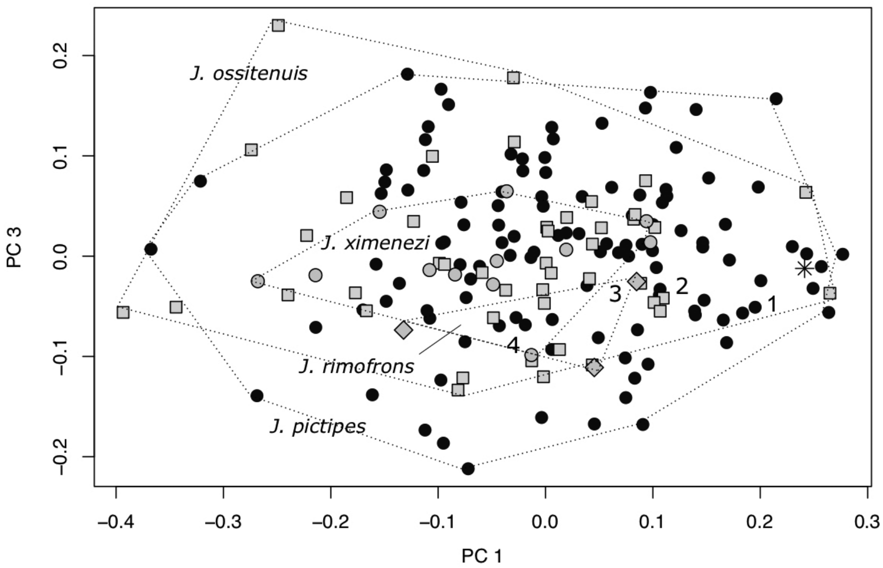
Discussion

Based on the cranial and dental morphology of the hypodigm of *C. anoblepas* and the variation observed on current species of *Juliomys*, we corroborate the results of Pardiñas & Teta (2011) and confirm the allocation of the taxon as a member of *Juliomys*. However, the specific identification of the fossil is hampered by its fragmentary nature. The detailed review of cranial and dental systems of *Juliomys* and the evaluation of characters used in the literature (Oliveira & Bonvicino 2002; Costa *et al.* 2007; Pardiñas *et al.* 2008b; Pardiñas & Teta 2011; Pavan & Leite 2011; Aguieiras *et al.* 2013; Fonseca *et al.* 2013; González *et al.* 2015; Christoff *et al.* 2016) revealed that there are no characters for specific identification, at least in the available portion of the *Juliomys anoblepas* hypodigm. The specific identification is also obstructed by high level of morphological polymorphism. The number of characters for *Juliomys* species in the anterior portion of skull and molar series is very reduced, and we discuss them below.

The degree of depth of the zygomatic notch has been used as a taxonomic feature, being considered deep in *J. pictipes* and shallow in other species (Costa *et al.* 2007; Pardiñas & Teta 2011; González *et al.* 2015; Christoff *et al.* 2016), or shallow in all *Juliomys* species (Pavan & Leite 2011). Our analysis showed that this trait is continuous, with little intraspecific variation only observed in *J. pictipes*, and *J. ossitenuis*. We conclude that the genus have intermediate (*sensu* Weksler 2006) degree of depth of the zygomatic notch.

The frontal fontanella is described as a diagnostic feature, being consistently present in *J. rimofrons* and *J. anoblepas* (Oliveira & Bonvicino 2002; Costa *et al.* 2007; Pardiñas & Teta 2011; Christoff *et al.* 2016). However, as both taxa are represented by few specimens in collections, and considering that this character is polymorphic in





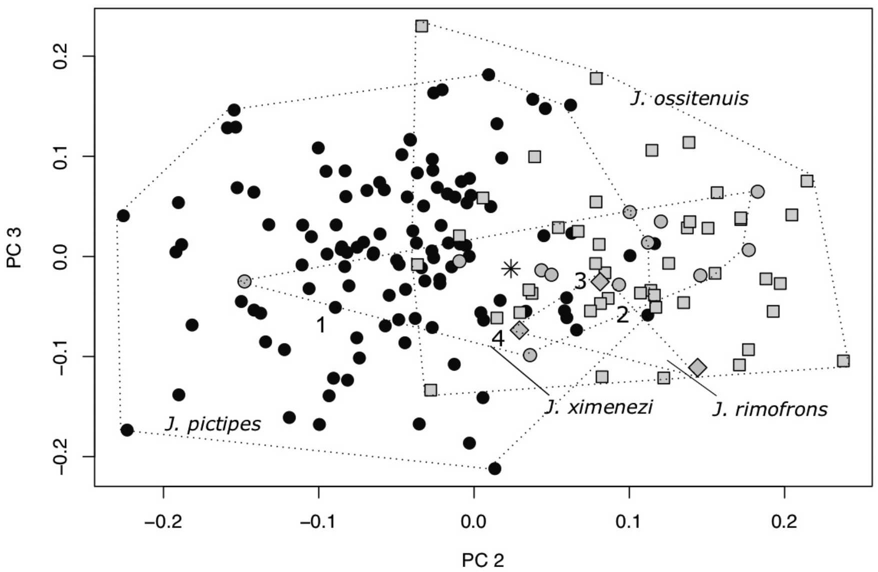


FIGURE 6. Scatterplot results of principal component analysis of log-transformed cranial measurements. *Juliomys anoblepas* hypodigm is indicated by an asterisk (*). Numbers indicate holotypes: 1, *J. pictipes* (FMNH26814); 2, *J. ossitenuis* (MN69752); 3, *J. rimofrons* (MN61647); and 4, *J. ximenezi* (MCNU868).

other species of *Juliomys* (see Fig. 4; see also Costa *et al.* 2007; Pardiñas *et al.* 2008b; Christoff *et al.* 2016), additional samples are required to establish if this feature could be used diagnostically.

The extension of the incisive foramina shows little variation among the species, being a polymorphic character. Other authors considered the incisive foramina as long in *J. rimofrons* (reaching slightly beyond anterior plane of first molars), intermediate in *J. ossitenuis*, and short in *J. pictipes* (Oliveira & Bonvicino 2002; Costa *et al.* 2007; Pardiñas & Teta 2011). *J. anoblepas* hypodigm has incisive foramina reaching the alveoli of M1 (short), which is a condition within the variation range of all species.

The enteroloph and enterostyle were herein described for the first time as a character for *Juliomys* species. The enterostyle is apparently absent in the hypodigm of *J. anoblepas* (see Fig. 2). This structure is found in the majority of the *Juliomys* species, except in four specimens of *J. ossitenuis*, and in *J. ximenezi*, which display some intraspecific variation. Thus, the absence of enterostyle in *J. anoblepas* can represent: (1) a feature that in combination with another diagnostic character could lead to identification of *J. anoblepas* as a valid species, or (2) an evidence that *J. anoblepas* is the same species of *J. ossitenuis* or *J. ximenezi*. As many characters cannot be applied to *J. anoblepas* due to its fragmentary condition, we do not know if the absence of the enterostyle is a feature that in combination with other allow its specific recognition. Besides that, the presence of a single fossil specimen precludes discussions about frequency of variation. We consider that establishing a specific identification of a fossil based on absence of enterostyle is a fragile decision.

The interorbital regions of all analyzed specimens of *Juliomys* were here considered as hourglass shaped, representing an invariable feature of the genus. This finding is at odds with previous studies, in which the shape of the interorbital region was considered as wide and anteriorly convergent in *J. pictipes*, and narrow and hourglass shaped in the remaining species (Costa *et al.* 2007; Pardiñas *et al.* 2008b; Pardiñas & Teta 2011; González *et al.* 2015; Christoff *et al.* 2016). The variation found in relation to the shape of supraorbital margin, however, may be considered as a diagnostic character (see results), but it cannot be evaluated in *J. anoblepas*.

No variation was found among *Juliomys* species in relation to the size of the posterolateral palatal pits. This structure was considered large in *J. pictipes* and *J. rimofrons*, and small in *J. ossitenuis* and *J. ximenezi* (Costa *et al.* 2007; Pardiñas & Teta 2011; Aguieiras *et al.* 2013; González *et al.* 2015; Christoff *et al.* 2016). The size of the posterolateral palatal pits could not be evaluated in *J. anoblepas* due to its fragmentary condition.

Taxonomic status of *J. anoblepas*

Pardiñas & Teta (2011) proposed the allocation of *C. anoblepas* within *Juliomys* and mentioned that comparisons between *J. anoblepas* and other living species of *Juliomys* are difficult to make due to the fragmentary nature of the fossil, the incomplete knowledge, the scarce number of specimens deposited in collections, and its dispersion across several museums. The authors also provided a summary of the skull characters among species of *Juliomy*s, highlighting the set of states that differentiated *J. anoblepa*s from the other species. Moreover, authors also pointed craniodental measurements as a factor that corroborated the proposition of the new nomenclatural combination. For these reasons, Pardiñas & Teta (2011) decided to keep the fossil as a putative extinct form of the *Juliomys* under the combination of *J. anoblepas* (Winge 1887).

Our results diverge from that of Pardiñas & Teta (2011) because features presented by them as diagnostic for *J. anoblepas* are polymorphic, continuous or invariable, and the available material is incomplete to determinate the states of the characters (Table 2; see also Figs. 3-5). The holotype, the only known specimen of *J. anoblepas*, consists of an anterior portion of the skull and molar series, in which no taxonomic character allow its differentiation from the other species. In addition, Pardiñas & Teta (2011) used a small sample size that did not cover all the *Juliomys* geographic distribution, and the recently described *J. ximenezi* was not included in their studied. Finally, our analyses show that *J. anoblepas* cannot be morphometrically differentiated from other species, in particular from *J. pictipes* and *J. ossitenuis.*

Our results point to three taxonomic possibilities that can be applied to *J. anoblepas*: (1) consider one of the living species of the genus as its junior synonym; (2) keep the current nomenclatural combination; or (3) consider *J. anoblepas* as a *nomen dubium*. Each possibility is discussed below:

TABLE 2. Morphological comparisons among currently recognized *Juliomys* species, showing the codification of Pardiñas & Teta (2011) after slash. WI = without information

Characters	***J. anoblepas***	***J. pictipes***	***J. rimofrons***	***J. ossitenuis***	***J. ximenezi***
Nasal extension	Long/WI	Polymorphic (short 67%)/WI	Polymorphic (long 66%)/WI	Polymorphic (long 65%)/WI	Polymorphic (long 53%)/WI
Zygomatic notch	Little excavated/Deep	Polymorphic (little excavated 90%)/Deep	Little excavated/Shallow	Little excavated/Shallow	Little excavated/WI
Frontal fontanella	Present/Present	Polymorphic (absent 88%)/Absent	Present/Present	Polymorphic (absent 71%)/ Usually absent	Polymorphic (absent 92%)/ WI
Interorbital region	Narrow, hourglass shaped/ Narrow, hourglass shaped	Narrow, hourglass shaped/ Broad, convergent anteriorly	Narrow, hourglass shaped/ Narrow, hourglass shaped	Narrow, hourglass shaped/ Narrow, hourglass shaped	Narrow, hourglass shaped/ WI
Incisive foramen	Short/Long	Short (94%)/Short	Short/Long	Short (93%)/Intermediate	Short/WI
Posterior palatine pits	Small/Large?	Small/Large	Small/Large	Small/Small	Small/WI
Anterior cingulum	Absent/WI	Polymorphic (absent 97%)/WI	Absent (100%)/WI	Polymorphic (absent 79%)/ WI	Polymorphic (absent 75%)/ WI
Enteroloph	Absent/WI	Present (70%)/WI	Absent (100%)/WI	Absent (78%)/WI	Absent (83%)/WI
Enterostyle	Absent/WI	Present (100%)/WI	Present (100%)/WI	Present (93%)/WI	Absent (50%)/WI

(1) To associate any living species to *J. anoblepas* would be a random decision due to the absence of taxonomic diagnostic features in the anterior portion of skull and in molar series of *Juliomys*. Because *J. anoblepas* was described before the other species of the genus, the name has priority (ICZN 1999). If we designate the hypodigm as the type of any living species, we will lose several diagnostic features (external, skull, postcranial, cytogenetic, and molecular) that cannot be recuperated for *J. anoblepas*. Thus, we will be replacing a type specimen with many taxonomic characters by another with none. We therefore consider this decision as arbitrary and detrimental to our taxonomic understanding of the genus, and reject this possibility.

(2) To consider *J. anoblepas* as a valid species, it is necessary morphological evidence. Our results demonstrate that this fossil, in a fragile state of preservation, has only available the anterior part of skull and the molar series. Variable characters in this region are polymorphic and, therefore, it is within the variation range that can correspond to any of the living species. The single feature that could be diagnostic, the absence of enterostyle and enteroloph, is also found in some specimens of *J. ossitenuis* and *J. ximenezi*. Therefore, no conclusion can be reached about the differentiation of this taxon from the others.

(3) A *Nomen dubium* is a term that refers to a name of unknown or dubious application, as defined by the International Code of Zoological Nomenclature (ICZN 1999: article 75.5). A *nomen dubium* means that the available evidence for the type bearing a name is insufficient to allow the recognition of the zoological species for which it is applied. Examples of *nomina dubia* are common in vertebrate paleontology (Mones 1989), and have already been recorded for the fauna of Lagoa Santa, *e.g*., in *Calomys plebejus* Winge 1887 (= *Delomys plebejus*) (Voss 1993), and *Lonchophorus fossilis* Lund 1840 (= *Phyllomys fossilis*) (Emmons *et al.* 2002). Because there are no characters that clearly distinguish *J. anoblepas* from the other *Juliomys* species, we consider the identification of *J. anoblepas* as questionable. Without additional fossil material that can provide morphological information to complement and clarify its true taxonomic identity, we propose *J. anoblepas* as a *nomen dubium* and restrict its name to the taxon's hypodigm.

Acknowledgments

We are thankful for the curators and collection support staff: Bruce Patterson (FMNH), Paulo D'Andrea (LABPMR, IOC/Fiocruz), Alexandre Christoff and Preta (MCNU), Claudia Costa (MCN-M), João Oliveira (MN/UFRJ), Ivan Sazima (ZUEC-MAM), Mario de Vivo and Juliana Gualda (MZUSP), Pablo Gonçalves (Nupem/UFRJ), Milton Cáceres (UFSM), Yuri Leite e Monique Nascimento (UFES), Fernando Perini (UFMG), Maurício Graipel and Jorge Cherem (UFSC), Sérgio Althoff and Elizabeth (FURB) for allowing the access of the mammal collection. We also thank managers of the collections of Herpetology section of Museu Nacional (MN/UFRJ), Pedro Pinna, Manoela Cardoso, and José Pombal Jr. for allowing us to use the photo equipment, Aldo Caccavo for providing photos and measurements of the holotype of *J. pictipes*, and Kasper Lykke Hansen and Alexandre R. Percequillo, for kindly providing photos of the fossil specimen. We are grateful to CAPES, CNPq, and FAPERJ for financial support, and would like to thank Pablo Teta, and an anonymous reviewer for suggestions to improve the manuscript.

References

Aguieiras, M., Santos, B.D.A., Azamor, L., Barbosa, J.L., Bezerra, A.C., Cristina, K. & Geise, L. (2013) Primeiro registro de *Juliomys ossitenuis* Costa, Pavan, Leite & Fagundes, 2007 e simpatria com *Juliomys pictipes* (Osgood, 1933) (Rodentia, Cricetidae, Sigmodontinae) na Serra dos Órgãos, Rio de Janeiro. *Boletim da Sociedade Brasileira de Mastozoologia*, 68, 57–64.

Baird, S. (1857) *Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. Vol. 8.* Bekerly Tucker, Washington, 757 pp.

Boroni, N., Perini, F., Boggiani, P., Almeida, L.H., Toledo, P. & Salles, L. (2020) Quaternary sigmodontines (Mammalia, Rodentia) from Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Historical Biology*, 1–26. https://doi.org/10.1080/08912963.2020.1722659

Cademartori, C.V., Marques, R.V. & Pacheco, S.M. (2008) Estratificação vertical no uso do espaço por pequenos mamíferos (Rodentia, Sigmodontinae) em área de Floresta Ombrófila Mista, RS, Brasil. *Revista Brasileira de Zoociências*, 10, 189–196.

Cartelle, C. (2002) Peter W. Lund, a naturalist of several sciences. *Lundiana*, 3, 83–85.

Christoff, A.U., Vieira, E.M., Oliveira, L.R., Gonçalves, J.W., Valiati, V.H. & Tomasi, P.S. (2016) A new species of *Juliomys* (Rodentia, Cricetidae, Sigmodontinae) from the Atlantic Forest of Southern Brazil. *Journal of Mammalogy*, 97, 1469–1482.
https://doi.org/10.1093/jmammal/gyw082

Costa, L.P., Pavan, S.E., Leite, Y.L.R. & Fagundes, V. (2007) A new species of *Juliomys* (Mammalia: Rodentia: Cricetidae) from the Atlantic forest of southeastern Brazil. *Zootaxa*, 1463 (1), 21–37.
https://doi.org/10.11646/zootaxa.1463.1.3

de la Sancha, N., D'Elía, G., Netto, F., Pérez, P. & Salazar-Bravo, J. (2009) Discovery of *Juliomys* (Rodentia, Sigmodontinae) in Paraguay, a new genus of Sigmodontinae for the country's Atlantic Forest. *Mammalia*, 73, 162–167.
https://doi.org/10.1515/MAMM.2009.026

Emmons, L.H., Leite, Y.L.R., Kock, D. & Costa, L.P. (2002) A review of the named forms of *Phyllomys* (Rodentia: Echimyidae) with the description of a new species from coastal Brazil. *American Museum Novitates*, 3380, 1–40.
https://doi.org/10.1206/0003-0082(2002)380<0001:arotnf>2.0.co;2

Fonseca, R., Bergallo, H.G., Delciellos, A.C., Rocha-Barbosa, O. & Geise, L. (2013) *Juliomys rimofrons* Oliveira and Bonvicino, 2002 (Rodentia: Cricetidae): distribution extension. *Check List*, 9, 684–685.
https://doi.org/10.15560/9.3.684

Gardner, S. & Anderson, S. (2001) Persistent fontanelles in rodent skulls. *American Museum Novitates*, 3327, 1–16.
https://doi.org/10.1206/0003-0082(2001)327<0001:pfirs>2.0.co;2

González, E.M. (2000) Un nuevo género de roedor sigmodontino de Argentina y Brasil (Mammalia: Rodentia: Sigmodontinae). *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo*, 12, 1–12.

González, E.M., Oliveira, J.A. de & Teta, P. (2015) Genus *Juliomys* E. M. González, 2000. *In*: Patton, J.L., Pardiñas, U.F.J. & D'Elía, G. (Eds.), *Mammals of South America. Vol. 2. Rodents*. The University of Chicago Press, Chicago, Illinois, pp. 92–96.

Grazzini, G., Mochi-Junior, C.M., de Oliveira, H., Pontes, J. dos S., de Almeida, F.G., Sbalqueiro, I.J., Hass, I. & Tiepolo, L.M. (2015) First record of *Juliomys ossitenuis* Costa, Pavan, Leite & Fagundes, 2007 (Rodentia, Sigmodontinae) in Paraná state, southern Brazil. *Check List*, 11, 1–5.
https://doi.org/10.15560/11.2.1561

Hadler, P., Cherem, J.J., Turbay, R., Alberti, A. & Pardiñas, U.F.J. (2016) Diversidade de pequenos mamíferos (Didelphimorphia e Rodentia) do Holoceno do Nordeste do estado do Rio Grande do Sul, Brasil: implicações taxonômicas e paleoambientais. *Revista Brasileira de Paleontologia*, 19, 127–144.
https://doi.org/10.4072/rbp.2016.1.10

Hartl, D. & Clark, A. (2007) *Principles of population genetics*. Sinauer Associates, Massachusetts, 545 pp.

Hershkovitz, P. (1962) Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Fieldiana: Zoology*, 46, 1–524.
https://doi.org/10.5962/bhl.title.2781

ICZN (International Code of Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature. 4th Edition*. The International Trust for Zoological Nomenclature, London, 117 pp.

Kerber, L., Ribeiro, A.M., Lessa, G. & Cartelle, C. (2013) Late Quaternary fossil record of *Myocastor* Kerr, 1792 (Rodentia: Hystricognathi: Caviomorpha) from Brazil with taxonomical and environmental remarks. *Quaternary International*, 352, 147–158.
https://doi.org/10.1016/j.quaint.2013.11.022

Lund, P.W. (1840) Tillaeg til de to Sidste Afhandlinger over Brasiliens Dryeverden för sidste Jordomvaeltning. *Det Konigelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger*, 8, 273–296.

Mones, A. (1989) Nomen dubium vs. nomen vanum. *Journal of Vertebrate Paleontology*, 9, 232–234.
https://doi.org/10.1080/02724634.1989.10011757

Neves, S.B. das, Mayer, E.L., Hadler, P. & Ribeiro, A.M. (2017) Sigmodontine rodents (Rodentia, Cricetidae) from Quaternary cave deposits of Serra da Capivara, Northeastern Brazil. *Revista Brasileira de Paleontologia*, 20, 163–178.
https://doi.org/10.4072/rbp.2017.2.02

Oliveira, J.A. de & Bonvicino, C.R. (2002) A new species of sigmodontine rodent from the Atlantic forest of eastern Brazil. *Acta Theriologica*, 47, 307–322.
https://doi.org/10.1007/BF03194149

Oliveira, J.A. de, Strauss, R.E. & Reis, S.F. (1998) Assessing relative age and age structure in natural populations of *Bolomys lasiurus* (Rodentia: Sigmodontinae) in Northeastern Brazil. *Journal of Mammalogy*, 79, 1170–1183.
https://doi.org/10.2307/1383008

Osgood, W.H. (1933) Two new rodents from Argentina. *Zoological Series of Field Museum of Natural History*, 20, 11–14.
https://doi.org/10.1192/bjp.112.483.211-a

Pardiñas, U.F.J., D'Elía, G. & Ortiz, P.E. (2002) Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: estado actual de su conocimiento y prospectiva. *Mastozoología Neotropical*, 9, 209–252.

PardinÞas, U.F.J., D'Eliìa, G. & Teta, P. (2008a) Una introducción a los mayores sigmodontinos vivientes: revisión de *Kunsia* Hershkovitz, 1966 y descripción de un nuevo género (Rodentia: Cricetidae). *Arquivos do Museu Nacional, Rio de Janeiro*, 66, 509–594.

Pardiñas, U.F.J. & Teta, P. (2011) On the taxonomic status of the Brazilian mouse *Calomys anoblepas* Winge, 1887 (Mammalia, Rodentia, Cricetidae). *Zootaxa*, 2788 (1), 38–44.
https://doi.org/10.11646/zootaxa.2788.1.2
Pardiñas, U.F.J., Teta, P., D'Elía, G. & Galliari, C. (2008b) Rediscovery of *Juliomys pictipes* (Rodentia: Cricetidae) in Argentina: emended diagnosis, geographic distribution, and insights on genetic structure. *Zootaxa*, 1758 (1), 29–44.
https://doi.org/10.11646/zootaxa.1758.1.2
Paresque, R., Christoff, A.U. & Fagundes, V. (2009) Karyology of the Atlantic forest rodent *Juliomys* (Cricetidae): a new karyotype from southern Brazil. *Genetics and Molecular Biology* 32, 301–305.
https://doi.org/10.1590/S1415-47572009005000031
Paula-Couto, C. de (1950) *Peter Wilhelm Lund: memórias sobre a paleontologia brasileira*. Instituto Nacional do Livro, Rio de Janeiro, 590 pp., 56 pls.
Paula-Couto, C. de (1979) *Tratado de paleomastozoologia*. Academia Brasileira de Ciências, Rio de Janeiro, 590 pp.
Pavan, S.E. & Leite, Y.L.R (2011) Morphological diagnosis and geographic distribution of Atlantic red-rumped mice of the genus *Juliomys* (Rodentia: Sigmodontinae). *Zoologia*, 28 (5), 663–672.
https://doi.org/10.1590/S1984-46702011000500015
Pires, C. (2018) *Revisão taxonômica do gênero Juliomys González, 2000 (Rodentia: Sigmodontinae)*. Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, 207 pp.
Pires, C., Avilla, L. & Weksler, M. (2018) Fossil cricetid rodents from the Quaternary of Northern Brazil and their paleoenvironmental significance. *Ameghiniana* 55, 162–178.
https://doi.org/10.5710/AMGH.14.11.2017.3094
Pires, C., Gudinho, F. & Weksler, M. (2016) Morfologia dentária de gêneros de Sigmodontinae (Rodentia: Cricetidae) com ocorrência no Cerrado brasileiro. *Boletim da Sociedade Brasileira de Mastozoologia*, 75, 1–32.
Reig, O.A. (1977) A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *Journal of Zoology*, 181, 227–241.
https://doi.org/10.1111/j.1469-7998.1977.tb03238.x
RStudio Team (2020) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, Massachusetts. Available from: http://www.rstudio.com/ (accessed 27 July 2020)
Salles, L.O., Cartelle, C., Guedes, P.G., Boggiani, P.C., Janoo, A. & Russo, C.A.M. (2006) Quaternary mammals from Serra da Bodoquena, Mato Grosso do Sul, Brazil. *Boletim do Museu Nacional*, 521, 1–12.
Steppan, S. (1995) Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. *Fieldiana: Zoology*, 80 (1464), 1–112.
https://doi.org/10.5962/bhl.title.3336
Strauss, R.E. (2010) Discriminating groups of organisms. *In*: Elewa, A.M.T. (Ed.), *Morphometrics for nonmorphometricians*. Springer-Verlag, Berlin, pp. 73–91.
Stutz, N.S., Hadler, P., Cherem, J.J., Fernández, F.J., Pardiñas, U.F.J. & Ribeiro, A.M. (2018) Noteworthy sigmodontine (Rodentia: Cricetidae) diversity in southern Brazil as an indication of environmental change during the Holocene. *Historical Biology*, 32 (5), 649–670.
https://doi.org/10.1080/08912963.2018.1524470
Szabo-Rogers, H., Yakob, W. & Liu, K. (2016) Frontal bone insufficiency in *Gsk3β* mutant mice. *PLOS ONE*, 11 (2), 1–14.
https://doi.org/10.1371/journal.pone.0149604
Trouessart, E.-L. (1898) *Catalogus mammalium tam viventium quam fossilium a doctore E.-L. Trouessart. Vol. 2*. R. Friedländer & Sohn, Berlin, 1469 pp.
https://doi.org/10.5962/bhl.title.61437
Voss, R.S. (1988) Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History*, 188, 259–493.
Voss, R.S. (1993) A revision of the Brazilian muroid rodent genus *Delomys* with remarks on "Thomasomyine" characters. *American Museum Novitates*, 44 pp.
Voss, R.S. & Carleton, M.D. (1993) A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. *American Museum Novitates*, 3085, 1–39.
Voss, R.S. & Myers, P. (1991) *Pseudoryzomys simplex* (Rodentia: Muridae) and the significance of Lund's collections from the caves of Lagoa Santa, Brazil. *American Museum of Natural History*, 206, 414–432.
Weksler, M. (2006) Phylogenetic relationships of oryzomine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. *Bulletin of the American Museum of Natural History*, 296, 1–149.
https://doi.org/10.7934/p657
Winge, H. (1887) Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. *E Museo Lundii*, 1, 1–178, 18 pls.
https://doi.org/10.5962/bhl.title.14696