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Taxonomic, biogeographic, and taphonomic reassessment of a large extinct species of paca from the Quaternary of Brazil

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The taxonomy of extinct species of *Cuniculus* (Caviomorpha, Rodentia, Mammalia) is confusing and poorly studied. Here we provide a taxonomic review of extinct cuniculids, and discuss the taxonomic, biogeographic, taphonomic and chronologic aspects of new remains of an extinct large cuniculid from Brazilian Quaternary Gruta Cuvieri cave deposits. Our taxonomic review suggests that *Cuniculus rugiceps* (Lund, 1837) is the valid taxon to include all available occurrences of extinct cuniculids. The most evident features of this taxon are its larger size and the stronger and more densely distributed rugosities on the skull external surface when compared to the extant species. At present, the distribution of *C. rugiceps* is restricted to the tropical region of Brazil. Regarding the new remains, taphonomic analysis of the specimens from Cuvieri Cave suggests our sample is represented by at least seven individuals that accumulated within the cave deposit by pitfall entrapment. The biostratinomy of the specimens was characterized by prolonged surface exposure inside the pit with fragmentation and displacement caused mostly by falling and subsequent trampling by individuals of the same and/or other species. The stratigraphically controlled excavations and chronological data allowed the establishment of a Late Pleistocene minimum age for these specimens.

Key words: Mammalia, Rodentia, Caviomorpha, Cuniculidae, cave environments, karst, Pleistocene, Lagoa Santa.

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Introduction

Cuniculus Brisson, 1762 (= *Agouti* Lacépède, 1799; *Coelogenus* Cuvier, 1807; and *Coelogenys* Illiger, 1811 [ICZN 1998: opinion 1894]; see Patton 2015) includes caviomorph rodents of the family Cuniculidae (= Agoutidae, e.g., McKenna and Bell 1997), which is nowadays represented by the extant species *Cuniculus paca* (Linnaeus, 1766) and *Cuniculus taczanowskii* (Stolzmann, 1885) (see Stolzmann 1885; Moojen 1952; Pérez 1992; Nowak 1999; Eisenberg and Redford 1999; Woods and Kilpatrick 2005; Castro et al. 2010; Patton 2015). The recently proposed extant species "*Cuniculus hernandezi*" Castro, López, and Becerra, 2010 was deemed a nomen nudum (Ramírez-Chaves and Solari

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2014), requiring further analysis. The current distribution of *Cuniculus* encompasses the tropical portion of the South and Central Americas (Pérez 1992; Queirolo et al. 2008 and references therein), but reports of *Cuniculus* fossils are restricted to the territory of Brazil.

The first description of an extinct species of this genus was made by the Danish naturalist Peter Wilhelm Lund based on fossils collected during his explorations of Lapa da Cerca Grande, Lagoa Santa, Minas Gerais, Brazil (Lund 1837: 317). Lund erected the species *Cuniculus* (= *Coelogenys*) *rugiceps* (Lund, 1837) (see Lund 1837: 331–332, pl. 3) and described it as larger than *Cuniculus paca* and presenting some morphological particularities, such as rugosities on the atlas (not observed in extant species) and stronger rugosities on the surface of the skull bones (Lund 1837: 317). During Lund's life, *Cuniculus taczanowskii* was not yet described, thus all Lund's discussions regarding extinct species were in relation to *C. paca*. However, the osteological differences between *C. paca* and *C. taczanowskii* are relatively subtle (see Pérez 1992; Ríos-Uzeda et al. 2004) and Lund's distinctions between the fossils and *C. paca* are applicable to *C. taczanowski* too. In subsequent works, Lund (1839a, b, 1841a) mentioned more fossils of cuniculids recovered from his excavations in different caves from the Lagoa Santa region. He assigned a portion of the new fossils to *Cuniculus* (= *Coelogenys*) *rugiceps* and emphasized again its larger skull proportions compared to *C. paca* (Lund 1839a: 42, 1841a: 102). Lund assigned another portion of the fossils to two new species: (i) *Cuniculus* (= *Coelogenys*) *laticeps* (Lund 1839a: 42, 1841a: 102), for which the posterior portion of the zygomatic arch was more laterally projected than in *C. paca*, giving a flattened appearance to the skull; and (ii) *Cuniculus* (= *Coelogenys*) *major* (Lund 1839a: 42, 1841a: 102), which was characterized solely by its larger dimensions relative to *Cuniculus laticeps* and *Cuniculus rugiceps*, and consequently to the extant species too.

Later, Lund (1839a: 79–80, 1841a: 139–140) argued that the differences between *C. rugiceps* and *C. laticeps* might be due to sexual dimorphism, and synonymized both names under *C. laticeps*. In another work, Lund reinforced the validity of the species *C. laticeps* and the larger one, *C. major* (Lund 1839b: 228–229).

In 1840, Lund presented additional distinctive characters for *C. laticeps* in the explanation of the pl. 20 (Lund 1840: 54–55, 1841c: 270–271): (i) well-developed infraorbital foramen; (ii) narrow dorsal root of the zygomatic process of the maxilla; (iii) zygomatic arch backward projected (considered as the posterior elongation of the jugal); and (iv) a "smooth skull". In addition, the skull illustrated in pl. 20 shows that the dimensions of *C. laticeps* are very similar to *C. paca* (Lund 1840: pl. 20: 1, 2, 1841c).

After Lund, Winge (1887) in a review of the Lagoa Santa fossil rodents considered the two extinct species maintained by Lund (1939a) (*Coelogenys laticeps* and *Coelogenys major*) as subspecies of *Cuniculus* (= *Coelogenys*) *paca*. Later, Rusconi (1933) considered the validity of *Cuniculus* (= *Agouti*) *major*, assigning new material from Lapa do Caetano (= "Gaetano", Rusconi 1933), Lagoa Santa, to this taxon. Subsequently, Paula Couto (1953, 1975) and Cartelle (1999, 2002, 2012) listed *C. major* and *C. laticeps* among the extinct species identified from Lagoa Santa caves, and Vasconcelos et al. (2015) reported new material assigned to *C. major* from Prudente de Morais, Lagoa Santa. Besides Lund's (1837, 1839a, b, 1840, 1841a, c) and Winge's (1887) works, extinct cuniculids were mentioned in some publications, but few works have been devoted to thoroughly discussing extinct cuniculid taxonomy (e.g., Rusconi 1933).

Although extinct cuniculids were among the first fossil mammals studied during Lund's pioneering work in the 19th century, the little attention that has been paid to them resulted in a confusing and unresolved taxonomic arrangement. Moreover, in Lund's (1837, 1839a, b, 1840, 1841a, c) works there are no type specimens (Oliveira et al. 2010), which makes the comparison of new findings with the extinct species described by him difficult (although this issue has being partially resolved; see Hansen 2012). In general, fossils assigned to *Cuniculus* have not been described in detail, leading to scarce information about their anatomy and morphology, which hampers the critical review of taxonomic classification. Consequently, we are in need of a careful taxonomic revision of the group that will allow us to investigate basic aspects of their paleobiology and geographic distribution. Moreover, with the exception of the material reported by Vasconcelos et al. (2015), previous records did not come from excavations with stratigraphic control, and, consequently, our understanding regarding the chronological distribution of extinct cuniculids is also poor.

Within this context, we aim to clarify different aspects related to the extinct cuniculids: (i) to describe new cuniculid findings from Cuvieri Cave (Lagoa Santa, Minas Gerais, southeast Brazil; Fig. 1) and Toca de Cima dos Pilão Cave (Serra da Capivara, Piauí, northeast Brazil; Fig. 1); (ii) to provide taxonomic remarks on the extinct *Cuniculus* species; (iii) to provide a paleobiogeographic discussion of the extinct *Cuniculus* species; and (iv) to contextualize the taphonomy and chronology of *Cuniculus* fossils recovered from Cuvieri Cave. Our study suggests that there is only one extinct species, which should be *C. rugiceps*, and the distribution of this taxon, previously restricted to Lagoa Santa, southeast Brazil, should be extended up to northeastern Brazil. The taphonomic analyses suggest that the skeletons of *C. rugiceps* from Cuvieri Cave were accumulated by pitfall entrapment and represent at least seven individuals. Furthermore, the stratigraphically controlled excavations associated with U-Th chronology allow the establishment of a Late Pleistocene minimum age for *C. rugiceps* specimens from Cuvieri Cave.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; FUMDHAM, Fundação Museu do Homem Americano, São Raimundo Nonato, Piauí,

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Brazil; FZBRS, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; LEEH, Laboratório de Estudos Evolutivos Humanos da Universidade de São Paulo, São Paulo, Brazil; MCN.M, Coleção de Mastozoologia do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; MCN.P, Museu de Ciências Naturais da Universidade Federal do Paraná, Curitiba, Paraná, Brazil; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; UF, Florida Museum of Natural History, Gainesville, USA; USNM, Smithsonian National Museum of Natural History, Washington, USA; ZMK, Zoological Museum, Natural History Museum of Copenhagen, Copenhagen University, Denmark.

Other abbreviations.—MNI, minimum number of individuals; NISP, number of identifiable skeletal parts.

Material and methods

Studied sites.—*Lagoa Santa karst*: The fossils recovered from Cuvieri Cave, Minas Gerais, Brazil (coordinates: UTM 7.846.105N and 603.756E; fuse 23K; Córrego Alegre datum; Fig. 1) are housed in the LEEH. This small cave has a main horizontal passage with three pits. The remains discussed here were excavated between 2002 and 2008 from Locus 3, which is characterized by a vertical shaft with an abrupt pit about 8 m deep (Fig. 1B). The excavation techniques adopted systematically recorded the spatial distribution of the remains and the stratigraphic sequence of the deposit (see Hubbe et al. 2011 for details).

Serra da Capivara karst: The fossils recovered from Toca de Cima dos Pilão (coordinates: UTM 9.019.281N and 768.738E; fuse 23L; South American datum; Fig. 1) are housed in FUMDHAM. This cave consists of two open chambers partially separated by detached blocks (Guérin et al. 1996; Fig. 1C). The fossils reported here were excavated from Salão Terezinha between 1986 and 1990 (Guérin et al. 1996).

Descriptive and comparative procedures for new fossil material.—To describe and compare the cuniculid material excavated from Cuvieri Cave and Toca de Cima dos Pilão we performed both qualitative and quantitative analyses.

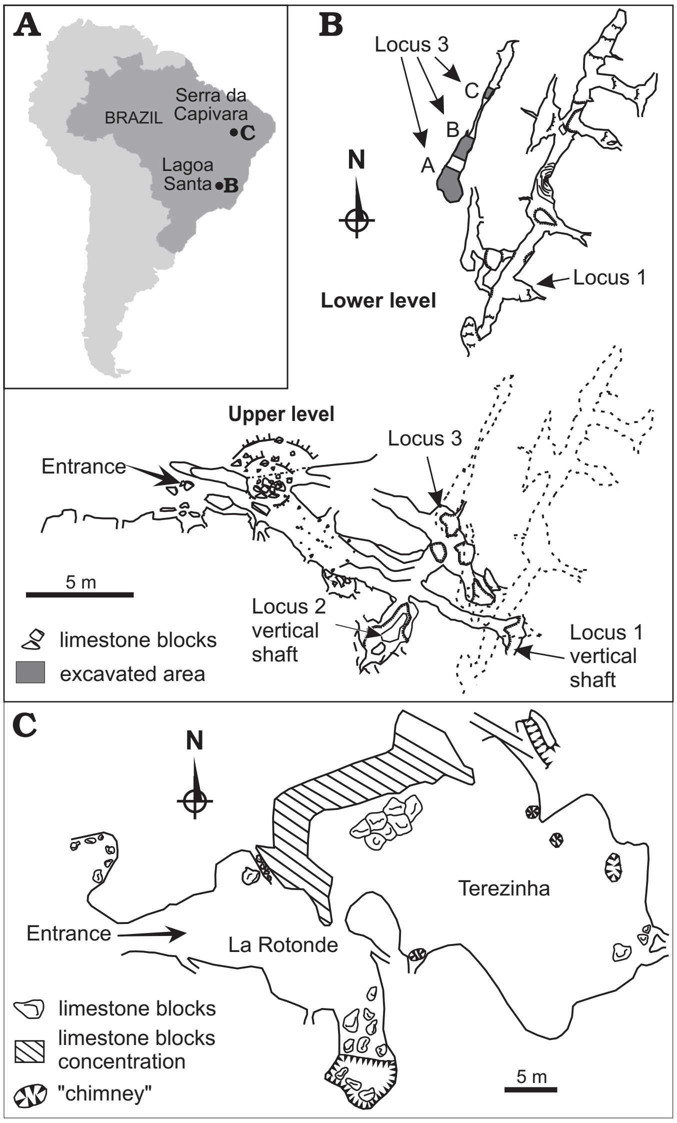

Fig. 1. Map showing the location of the Brazilian studied areas (**A**), and maps of Cuvieri Cave (Lagoa Santa, Minas Gerais) (**B**), and Toca de Cima dos Pilão Cave (Serra da Capivara, Piauí) (**C**). In Cuvieri Cave, fossils were excavated from Locus 3, and in Toca de Cima dos Pilão, fossils were excavated from Salão Terezinha. Map in B courtesy of Laboratório de Estudos Evolutivos Humanos and Grupo Bambuí de Pesquisas Espeleológicas, map in C adapted from Acervo da Fundação Museu do Homem Americano.

In the qualitative analysis, we described the morphology of the skull portions, dentaries (anatomic terms following Woods and Howland 1979 and Pérez 2010) and lower cheek teeth from Cuvieri Cave, and isolated molars from Toca de Cima dos Pilão. Furthermore, we compared the fossils from both caves with the extinct cuniculid fossils excavated by Lund, *C. paca*, *C. taczanowskii* (for details see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Mayer_etal_SOM.pdf) and "*Cuniculus hernandezi*". Note that although "*Cuniculus hernandezi*" (Castro, López, and Becerra, 2010) is a nomen nudum (Ramírez-Chaves and Solari 2014) we decided to incorporate "*C. hernandezi*" in our analyses for morphological comparisons and biogeographic purposes.

All analyses were based on comparisons with material deposited in museum collections, with the exception of the comparisons with *C. taczanowskii* that were based on Ríos-Uzeda et al. (2004: fig. 2) and "*C. hernandezi*" that were based on Castro et al. (2010: fig. 6). Among the material collected by Lund (from 1837 to 1845), we selected the most complete specimens that maintain the original assignation to "*C. paca* forma *laticeps*" and "*C. paca* forma *major*" by Winge (1887; for details see Appendix 1 and SOM 2). The morphological descriptions prioritize comparisons with *C. paca* because it has the widest geographic distribution

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within Cuniculidae and is represented in many collections, which makes *C. paca* a good extant reference for comparisons with future cuniculid fossil discoveries. Comments regarding *C. taczanowskii* and “*C. hernandezi*” are presented only when *C. taczanowskii* and/or “*C. hernandezi*” present conspicuous morphological differences to *C. paca.*

In the quantitative analyses, we used digital callipers (accurate to 0.01 mm) to measure six linear distances on dentaries (following Driesch 1976; SOM 1: fig. 1A), the mesio-distal length and linguo-labial width of teeth, and six linear distances on skull bones (SOM 1: fig. 1B). Regarding the dentary analysis, measurements were taken from specimens from Cuvieri Cave, Lund’s collection and the extant *C. paca* and *C. taczanowskii* (for details see SOM 2: table 1). A principal component analysis was performed to compare these sets of materials using the pooled-within species covariance matrix based on the six dentary linear distances. For the extant species (*C. paca* and *C. taczanowskii*) and the extinct *C. paca laticeps*, specimens with missing data were excluded from the analysis. We were unable to include *C. paca major* in our analysis, because three linear distances were missing from all specimens. For the material from Cuvieri Cave we averaged the information available for all specimens and used these averages in our analysis since no single specimen allowed the measurement of all distances. Regarding the tooth analysis, we measured the lower cheek teeth from Cuvieri Cave and isolated molars from Toca de Cima dos Pilão and then compared the measurements between both sites. Concerning the skull measurements, we measured skulls from fossils found in Cuvieri Cave with the goal of preliminarily characterizing this material, and to serve as a metric reference for future attempts to recognize extinct cuniculids.

Lastly, we need to make a methodological clarification. The fossil material recovered from Cuvieri Cave excavations, either plotted on site or retrieved later from sieving, received an individual number (for details regarding the excavation procedure see Hubbe et al. 2011). For the sake of brevity, wherever such fossil fragments have been refitted together, the new repaired specimens are simply referred to as Fossil 1, Fossil 2, ... etc., throughout the text, and the original specimen numbers are presented within parenthesis when they first appear in the text. The same terminology is adopted when a single fossil is represented by a nearly complete bone element.

Taxonomic and paleobiogeographic procedures.—Our taxonomic and paleobiogeographic considerations were based on: (i) Lund’s (1837, 1839a, b, 1840, 1841a, c) works on extinct cuniculids; and (ii) anatomical data from our descriptions and comparisons of findings from Cuvieri Cave, and Toca de Cima dos Pilão with Lund’s fossil collection. The taxonomic remarks take into consideration the principles of the International Commission of Zoological Nomenclature (ICZN). The paleobiogeographic notes are based on records from the literature and the identification of material from northern (Acre) and southern (Paraná) regions of Brazil (SOM 1: fig. 2).

Taphonomic and chronologic contextualization of material from Cuvieri Cave.—To identify the bone accumulation processes and characterize the biostratinomic history of the sample, we analysed the mode of fossil occurrence (articulated/scattered), the horizontal and vertical spatial distribution of specimens, the main bone surface modifications (i.e., fragmentation, tooth marks, and weathering stages) and stratigraphic data. Fragmentation was estimated for each specimen as percentage intervals relative to the respective whole skeletal element that it represents. Specimens comprising at least 90% of the respective skeletal element were noted as almost complete; specimens encompassing less than 50% were noted as fragments; and specimens of intermediary condition were noted as incomplete. Observations of tooth marks produced by carnivores and rodents followed Lyman (1994) and weathering stages followed Behrensmeyer (1978).

To characterize the materials from Cuvieri Cave quantitatively regarding individual representation, we adopted the Number of Identifiable Skeletal Parts (NISP) and the Minimum Number of Individuals (MNI). NISP values were obtained from the total number of specimens identified taxonomically and MNI values were calculated from the most abundant skeletal element identified taxonomically, taking into consideration the symmetry of the mammalian body (Lyman 1994). To avoid ambiguity in the quantitative units used in the taphonomic analysis, the terms specimen and element refer to “a bone or tooth, or fragment thereof” and “a single complete bone or tooth in the skeleton of an animal”, respectively (Shotwell 1955, 1958; see Lyman 1994 for discussion). Since extinct cuniculids were described mainly based on cranial characters, we are in need of a full description of the postcranial skeleton of extinct cuniculids. In spite of this, we preliminarily assigned taxonomically the postcranial elements from Cuvieri Cave to extinct cuniculids based on their morphological similarity to *C. paca* and their larger size compared to *C. paca* before calculating MNI and NISP. The description of the postcranial skeleton of *C. rugiceps* will be presented in a forthcoming publication.

To provide a chronological contextualization for the Cuvieri Cave remains we considered the fossils’ stratigraphic positions relative to the chronological information available.

Taxonomic remarks

In this section we will review the description of all erected extinct cuniculid species (*Cuniculus rugiceps* Lund, 1837, *Cuniculus laticeps* Lund, 1839, and *Cuniculus major* Lund, 1839), and make the point that *C. laticeps* and *C. major* were poorly characterized, while *C. rugiceps* (Lund, 1837) should be the only extinct species of *Cuniculus.* Moreover, we consider the synonymy between *C. rugiceps* and *C.*

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laticeps proposed by Lund (1839a) inadequate, because, as shown below, we consider that *C. laticeps* is not a well-established species for several reasons. First, two out of four morphological characters described by Lund for *C. laticeps* (i.e., well-developed infraorbital foramen and narrow dorsal root of the zygomatic process of the maxilla; Lund 1840: 54–55, pl. 20: 1, 1841c: 270–271) can be observed in recent specimens of *C. paca* (e.g., MCN.M 1052 and specimens figured by Mendes-Oliveira et al. 2012: fig. 4A, B) and *C. taczanowskii* (figured by Ríos-Uzeda et al. 2004: fig. 3). There are also examples of variation in these structures during the ontogeny of *C. paca* (Mendes-Oliveira et al. 2012: fig. 4A–D). The other two characters, related to the zygomatic arch (zygomatic arch laterally projected and jugal posteriorly elongated), are not clear on Lund's figured material of *C. laticeps* (Lund 1840: 54–55, pl. 20: 1, 1841c: 270–271) and in the material assigned to *C. paca laticeps* housed in ZMK (Appendix 1; SOM 2). Second, there is not a well-marked distinction between *C. laticeps* and the other extinct and extant species regarding size. The plate that illustrated both *C. laticeps* and *C. paca* skulls (Lund 1840: 54–55, pl. 20: 1, 2, 1841c: 270–271) shows they have very similar dimensions. Note, however, that our quantitative analysis of the dentaries shows that *C. laticeps* may be slightly larger than extant species, but without a more representative sample size, few solid conclusions can be drawn. Third, it seems that specimens assigned to *C. laticeps* have different characteristics. For example, there are specimens housed in ZMK assigned to *C. paca laticeps* that present morphological and size similar to *C. paca*, while others are more robust, resembling more the first taxon described by Lund (1837)—*C. rugiceps*

On the other hand, we consider there is solid evidence to support the validity of *C. rugiceps*. Regarding the morphology of the material originally assigned to *C. rugiceps* prior to its synonymy with *C. laticeps*, based on the original drawings in Lund's (1837) works we can specify that *C. rugiceps* had a more posteriorly elongated jugal than *C. paca* (relative to the position of the squamosal/jugal contact in lateral view; Fig. 2). Note that although this character was described by Lund (1840) only in *C. laticeps* after to the synonymy, a more posteriorly elongated jugal is not observable in the respective figured specimen of *C. laticeps* in Lund's (1840: 54–55, 1841c: 270–271) work, as mentioned above. This contradiction reinforces our position about the mistaken character of the synonymy of *C. rugiceps* and *C. laticeps*.

In relation to size, the jugal fragment of the zygomatic arch assigned to *C. rugiceps* before its synonymy (Fig. 2) is clearly larger than the corresponding portion of the *C. laticeps*' skull figured in Lund's (Lund 1837: 331–332, pl. 3: 1, 1840: 54, pl 20: 1, 1841c: 270) work. Although the *C. rugiceps* and *C. laticeps* specimens figured were represented at different scales, both skulls of *C. laticeps* and the jugal of *C. rugiceps* were illustrated along with comparative specimens of *C. paca* (Lund 1837: pl. 3, 1840: pl. 20: 1–4, 1841c), allowing us to indirectly compare the sizes of *C. rugiceps* and *C. laticeps*. The differences in size between *C. rugiceps* and *C. laticeps* are most probably not associated with ontogenetic variation. This is because Lund specified that the jugal of *C. paca* compared to *C. rugiceps* (Lund 1837: 331–332, pl. 3) and the skull of *C. paca* compared to *C. laticeps* (Lund 1840: 55, pl 20: 2, 1841c: 271) represent senile individuals, and the differences observed in the size of the *C. rugiceps* and *C. laticeps* specimens exceed the measured sexual variations observed in extant *C. paca* (see Richard-Hansen et al. 1999).

Based on this evidence, we consider that the first extinct cuniculid species erected by Lund, *C. rugiceps*, originally described as presenting a larger size and stronger rugosities than *C. paca* (Lund 1837: 331–332), should be revalidated and maintained as distinct from *C. laticeps*. In turn, we suggest that *C. laticeps* or *C. paca laticeps* (*Coelogenys laticeps*, Lund 1839b: 228; *Coelogenys laticeps*, Lund 1839a: 42 [Lund 1841a: 102]; "*Cuniculus paca* forma *laticeps*", Winge 1887: 64–66; *Cuniculus paca laticeps*, Paula Couto 1950: 43, footnote 4; *Coelogenys paca laticeps*, Paula Couto 1950: 169, footnote 146; *Agouti laticeps*, Cartelle 1999: 32) is a species inquirenda. We consider the possibility that this taxonomic unit could be based on a mix of materials of *C. rugiceps* and *C. paca*. A wide-ranging review of the material assigned to *C. laticeps* is required to clarify this issue.

Finally, the last extinct cuniculid species erected by Lund, *C. major*, was designated solely based on a statement mentioning the larger size of this species when compared to *C. rugiceps* and *C. laticeps* (Lund 1839b: 228–229). No illustration of this taxon was provided. However, the jugal that comprises the posterior portion of the zygomatic arch assigned to *C. major* (i.e., ZMK 1/1845: 2200) presents a size and morphology equivalent to the jugal of *C. rugiceps* figured prior to its synonymy with *C. laticeps* (Fig. 2). In this sense, in our opinion, there are no characters to validly maintain more than one extinct cuniculid species, and following the Principle of Priority (ICZN 1999: article 23), *C. major* is considered here as a synonym of *C. rugiceps* (Fig. 2).

Furthermore, we would like to clarify that based on the discussion above and our analyses, we assigned the material excavated from Cuvieri Cave and Toca de Cima dos Pilão to the large extinct species *C. rugiceps*. In the following sections we provide an in-depth description of the new material as well as biogeographic, taphonomic and chronologic remarks regarding the remains found in Cuvieri Cave.

Systematic palaeontology

Mammalia Linnaeus, 1758

Euarchontoglires Murphy, Eizirik, O'Brien, Madsen, Scally, Douady, Teeling, Ryder, Stanhope, de Jong, and Springer, 2001

Rodentia Bowdich, 1821

Ctenohystrica Huchon, Catzeflis, and Douzery, 2000

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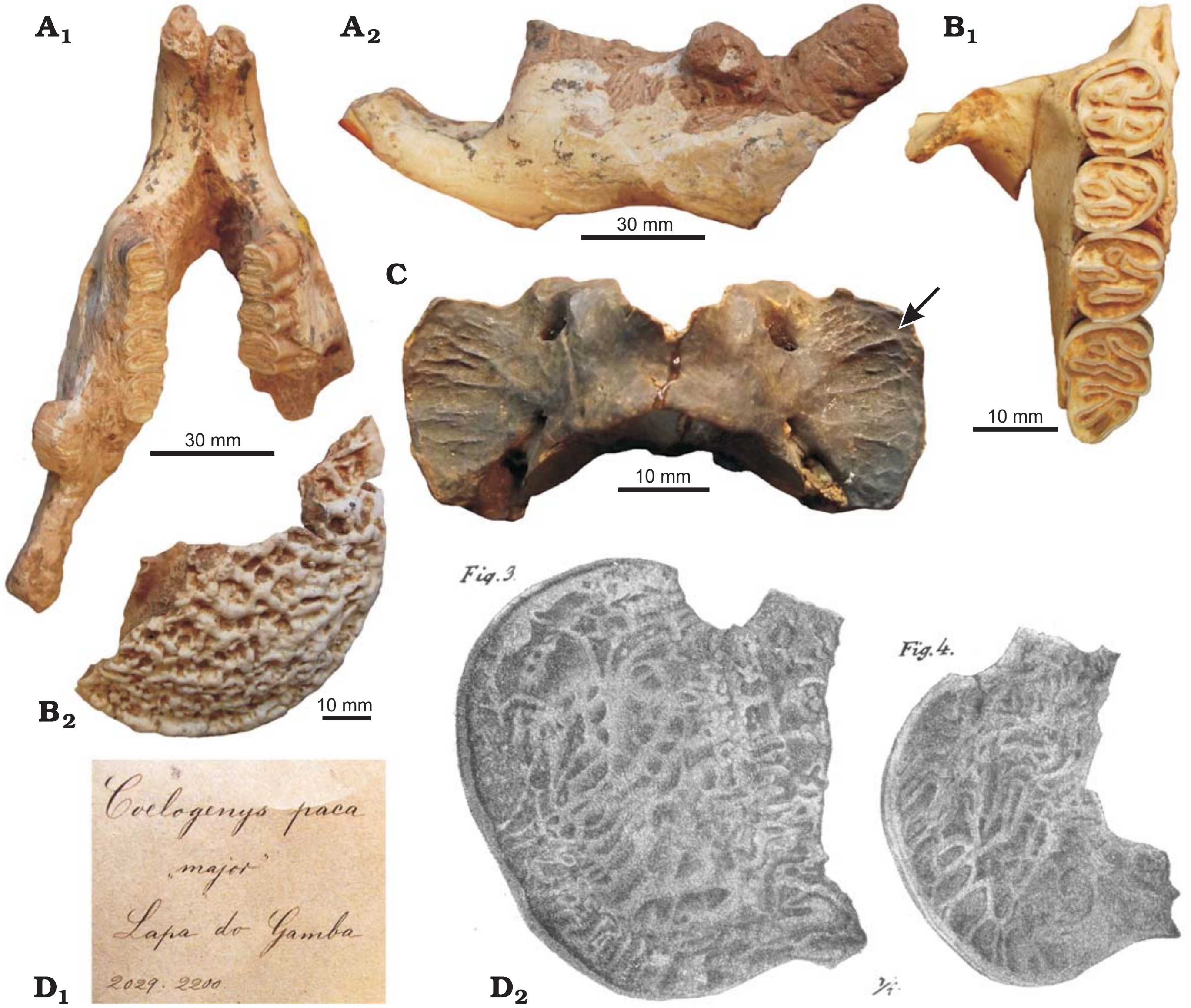

Fig. 2. Fossils from the Lagoa Santa, Minas Gerais, Brazil, attributed to extinct pacas (ages unknown). **A**, **B**. Specimens assigned to "*Cuniculus paca* forma *major*" Lund, 1839. **A**. ZMK 1/1845:2029, mandible in occlusal (A_1) and lateral (A_2) views. **B**. ZMK 1/1845:13450, maxilla with P4–M3 series in occlusal view (B_1); fragment of jugal in lateral view (B_2). **C**. Atlas (ZMK 1/1845:2989) assigned to "*Cuniculus paca* forma *laticeps*" by Winge (1887), which Lund (1837) described as *Cuniculus rugiceps*. Arrow is pointing to the rugosities on the dorsal surface. **D**. Syntypes of *Cuniculus rugiceps* from Lagoa Santa with the original label of Herluf Winge (D_1) and Lund's (1837) illustration (D_2) comparing the right jugal of *C. rugiceps* ("Fig. 3") with *C. paca* ("Fig. 4") (Lund 1837: pl. 3, 1840 [1841c]: pl. 20).

Hystricognathi Tullberg, 1899

Caviomorpha Wood and Patterson in Wood, 1955

Cuniculidae Miller and Gidley, 1918

Cuniculus Brisson, 1762

Type species: *Cuniculus paca* (Linnaeus, 1766); for type locality see Patton (2015); Recent of South America.

Cuniculus rugiceps (Lund, 1837)

1837 *Coelogenys rugiceps* Lund, 1837; Lund 1837: 332.
1839 *Coelogenys major* Lund, 1839; Lund 1839b: 228.
1839 *Coelogenys major* Lund, 1839; Lund 1839a: 42.
1841 *Coelogenys major* Lund, 1839; Lund 1841a: 102.
1887 *Cuniculus paca* forma *major* Winge, 1887; Winge 1887: 64–66.
1933 *Agouti major* (Lund, 1839); Rusconi 1933: 25.
1950 *Cuniculus paca major* (Winge, 1887); Paula Couto 1950: 64.
1986 *Coelogenys rugiceps* Lund, 1837; Mones 1986: 205.
1986 *Coelogenys major* Lund, 1839; Mones 1986: 205.
1999 *Agouti major* (Lund, 1839) Cartelle (1999): 32.
2015 *Cuniculus major* (Lund, 1839); Vasconcelos et al. 2015: 176.

Material.—Cuvieri Cave: Fossil 1, right dentary, with the p4 erupting and m1–m3 series, without anterior region (CVL3 4052, CVL3 4080, CVL3 P7236); Fossil 2, right dentary with p4–m3 series, without angular process (CVL3 P11221, CVL3 P11178); Fossil 3, right dentary with p4–m3 series, without angular process (CVL3 P13149, CVL3 P13148); Fossil 4, right dentary, with the p4 erupting and m1–m3

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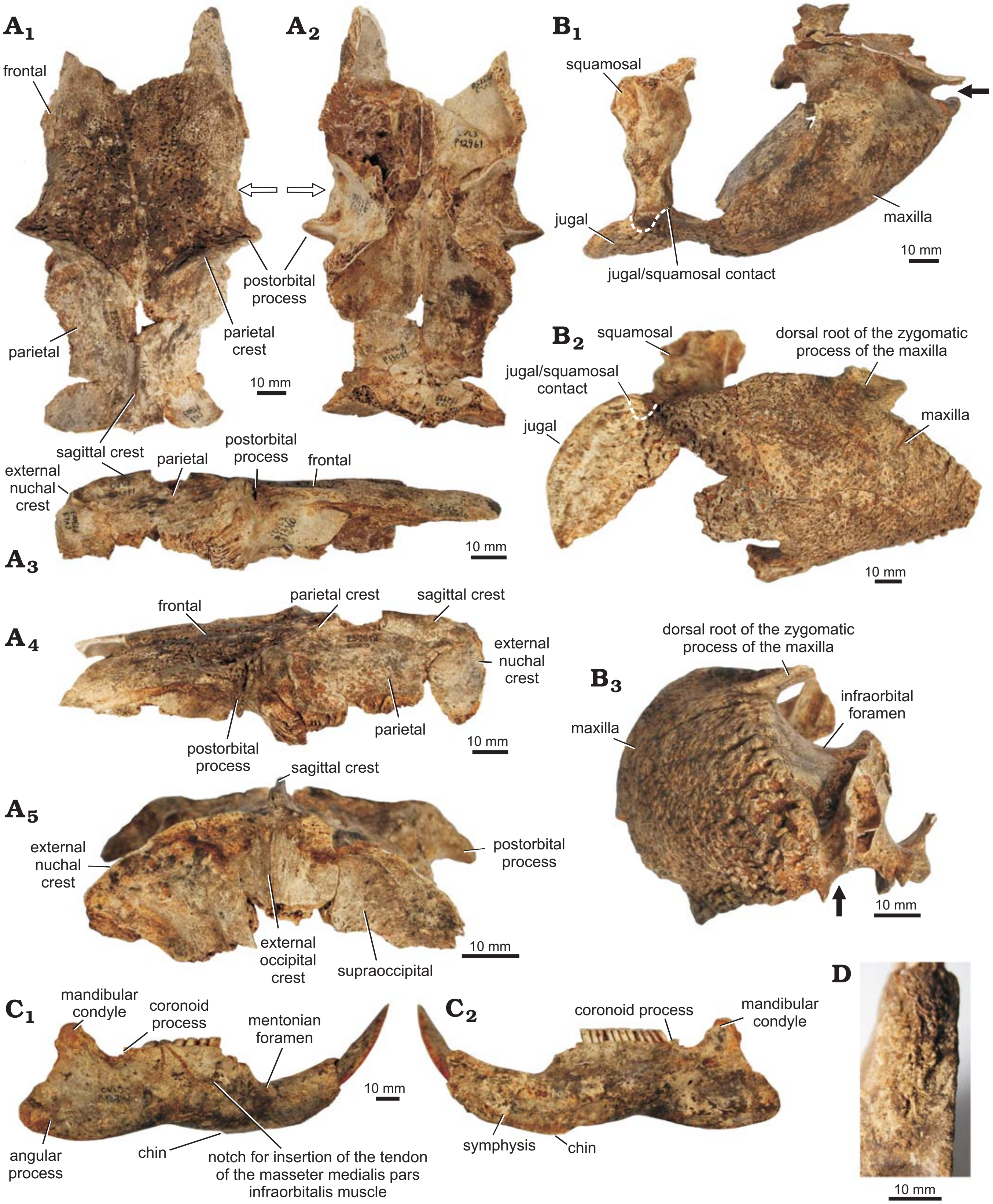

Fig. 3. Fossils of the extinct paca *Cuniculus rugiceps* (Lund, 1837) from Cuvieri Cave (minimum age of ~30 ky). **A**. Fossil 7 (CVL3 P13160), dorsal portion of the skull in dorsal (A_1), ventral (A_2), right lateral (A_3), left lateral (A_4), and posterior (A_5) views. **B**. Fossil 8 (CVL3 P13168), right zygomatic arch in dorsal (B_1), lateral (B_2), and anterior (B_3) views. **C**. Fossil 4 (CVL3 P13342), right dentary in lateral (C_1) and medial (C_2) views. **D**. Fossil 2 (CVL3 P11221), anteroventral face of the mentonian region of a right dentary showing rugosities. White arrows, discrete notch on the dorsal edges of the orbits; black arrows, large and deep notch on the bottom of the infraorbital foramen.

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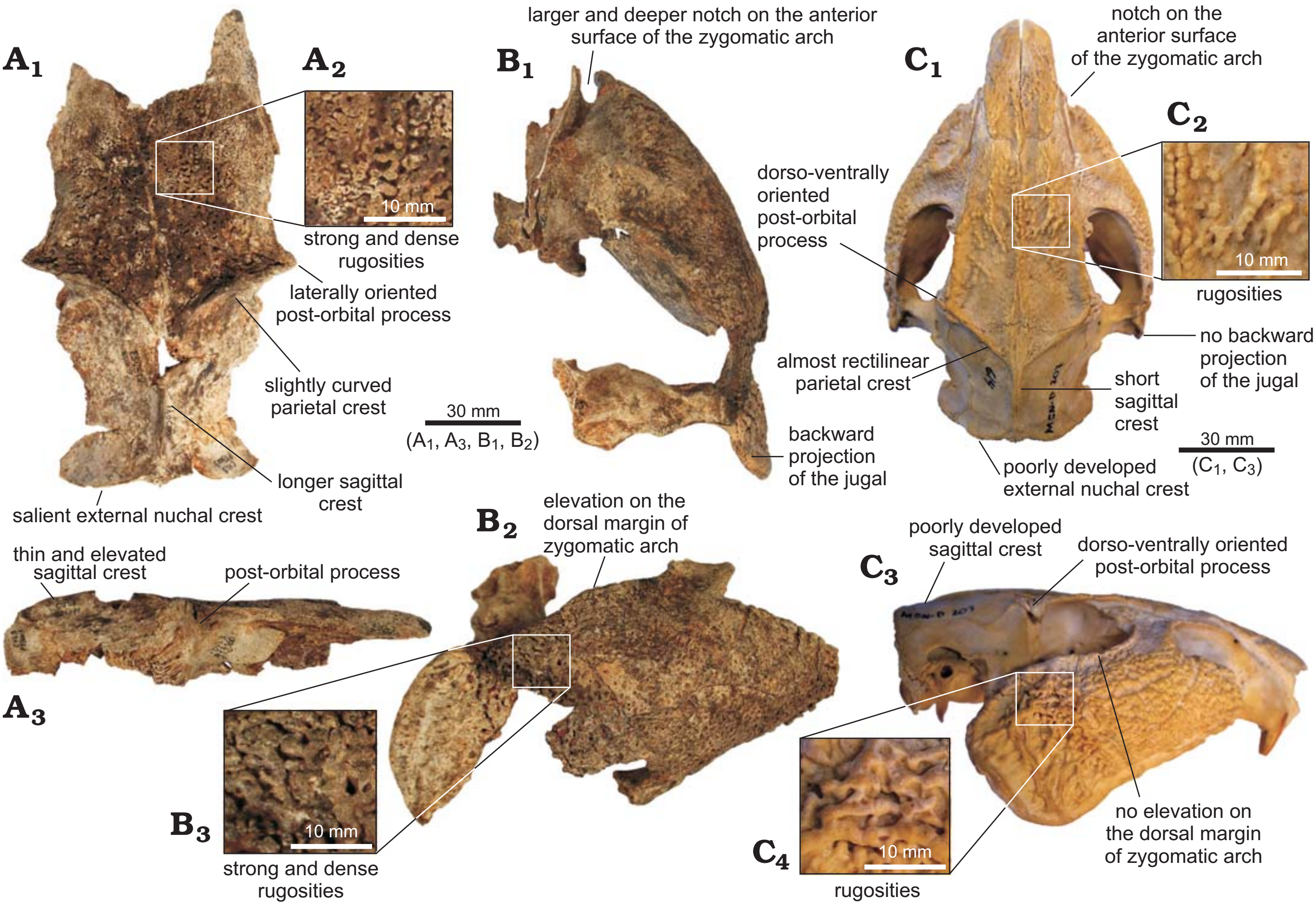

Fig. 4. Fossils of the extinct paca *Cuniculus rugiceps* (Lund, 1837) from Cuvieri Cave (minimum age of ~30 ky) (A, B) and modern specimen of *Cuniculus paca* Linnaeus, 1766 from Rio Grande do Sul (C). **A**. Fossil 7 (CVL3 P13160), cranial roof in dorsal (A_1) and lateral (A_3) views, detail (A_2). **B**. Fossil 8 (CVL3 P13168), right zygomatic arch in dorsal (B_1) and lateral (B_2) views, detail (B_3). **C**. MCN.D 207, skull in dorsal (C_1) and lateral (C_3) views, details (C_2, C_4).

series (CVL3 P13342); Fossil 5, left dentary, with p4–m3 series, lacking the posterior region (CVL3 P13145, CVL3 P12935, CVL3 P13007, CVL3 P13146, CVL3 P13147, CVL3 P13153, CVL3 P13157, CVL3 P13158); Fossil 6, left dentary with dp4–m3 series, lacking posterior region (CVL3 P13344); Fossil 7, dorsal portion of a skull (CVL3 P13160, CVL3 P13003, CVL3 P13041, CVL3 P13053, CVL3 P13158, CVL3 P12961, CVL3 P12998, CVL3 P13014); Fossil 8, almost complete right zygomatic arch (CVL3 P13168, CVL3 P12919, CVL3 P 12969, CVL3 P13110, CVL3 P13151, CVL3 P13152, CVL3 P13165, CVL3 P13169, CVL3 P13171). Toca de Cima dos Pilão: FUMDHAM 188-19521, possible right m2; FUMDHAM 188-19036, possible right m3.

Emended diagnosis.—*Cuniculus rugiceps* is distinguished from extant species in having: (i) a larger size; (ii) stronger and more densely distributed rugosities on the external skull surface; (iii) a more developed and laterally oriented post-orbital process; (iv) more developed and curved parietal crests; (v) a longer and elevated sagittal crest; (vi) a larger and deeper notch on the anterior surface of the groove on the bottom of the infraorbital foramen; (vii) the presence of a slight elevation on the dorsal margin of the zygomatic arch near to the central area of the orbit (not present in *C. paca*; apparently present but less developed in *C. taczanowskii*); (viii) a jugal more posteriorly elongated.

Description and comparison.—The morphology of the cranial portions and dentaries with lower cheek teeth is addressed here. The skull of *C. rugiceps* displays very strong and densely distributed rugosities on the dorsal area of the cranium and exterior face of the zygomatic arch, (Fossils 7 and 8; Figs. 3A1, B, and 4A1, B2). Although the presence of rugosities is a notable characteristic of Cuniculidae (Pocock 1922; Ellerman 1940; Moojen 1952; Hershkovitz 1955; Nelson and Schump 1978; Eisenberg and Redford 1999; Patton 2015), *C. rugiceps* shows extremely well-developed rugosities, far more pronounced than in the extant species. The variation in the rugosities within *C. paca* due to sexual dimorphism and/or ontogeny (Ellerman 1940; Mendes-Oliveira et al. 2012) suggests that variation in the rugosities of *C. rugiceps* may occur, and be due to the same reasons.

The post-orbital processes and parietal crests of *C. rugiceps* are more prominent than in *C. paca* (Fossil 7; Fig. 3A).

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The post-orbital process of *C. rugiceps* is laterally oriented, while in *C. paca* it is short and dorso-ventrally oriented. In this sense, the post-orbital process of *C. rugiceps* appears to be more similar to the extant *C. taczanowskii* (Ríos-Uzeda et al. 2004: fig. 2) and "*C. hernandezi*" (Castro et al. 2010: fig. 6). The parietal crests of *C. rugiceps* are slightly curved in comparison to *C. paca*, in which the parietal crest forms an almost rectilinear line (Figs. $3A_1$ and $4A_1$, C_1). The dorsal edges of the orbits show a discrete notch (Fossil 7; Fig. $3A_1$, A_2, white arrows; SOM 1: fig. 1). The sagittal crest of *C. rugiceps* is longer than in *C. paca*. This crest in *C. rugiceps* occupies a larger space on the dorsal posterior region of the skull than in the extant species (Figs. $3A_1$, A_3–A_5 and $4A_1$, A_2, C_1, C_2). In *C. rugiceps* this crest forms a thin and elevated lamina, while in *C. paca* this crest is poorly developed (Figs. 3A and $4A_2$, C_2).

In lateral view, we observed in *C. rugiceps* that there is an elevation on the dorsal margin of the zygomatic arch in nearly the central area of the orbit that is not present in *C. paca* and present but less developed in *C. taczanowskii* (Fig. $4B_2$, C_2; see also Ríos-Uzeda et al. 2004: fig. 3). In *C. rugiceps*, there is a large and deep notch on the anterior surface of the groove presumably for nerve and blood vessels (Patterson and Wood 1982) on the bottom of the infraorbital foramen (Figs. $3B_1$, B_3, black arrow and $4B_1$, C_1). In the posterior area of the zygomatic arch of *C. rugiceps*, the jugal forms a backward projection that exceeds the posterior limit of the zygomatic process of the squamosal, which is not observed in *C. paca* (Figs. $3B_1$, B_2 and 4B, C_1, C_2). In isolated jugal bones of *C. rugiceps* this projection could be perceptible relative to the position of the jugal/squamosal contact (Figs. 2, $3B_1$, B_2). The external nuchal crest of *C. rugiceps* is also more prominent than in *C. paca* (Fig. $3A_4$, A_5). In posterior view, the dorsal outline of the occipital region of *C. rugiceps* forms a more open angle than in *C. paca* (Fig. $3A_5$).

The dentary of *C. rugiceps* is similar to the extant pacas, except for its larger size (Fig. 3C; Table 1; SOM 2: table 1; size differentiation is also evident in our quantitative analysis, see next section). The coronoid process in *C. rugiceps* is located lateral to the m3 and is slightly lower than the condylar process (e.g., Fossil 3; not figured), a condition found also in *C. paca* and *C. taczanowskii* (Ellerman 1940; Ríos-Uzeda et al. 2004: fig. 3). The angular process of *C. rugiceps* is more developed than in *C. paca* (Fossil 4, Fig. 3C), such as described for *C. taczanowskii* (Ríos-Uzeda et al. 2004). However, it is important to note that this region has shown great variability in the analysed *C. paca* specimens. As in *C. paca*, *C. rugiceps* presents the notch for the insertion of the tendon of the masseter medialis pars infraorbitalis muscle located at the level of the m1 and the mentonian foramen placed on the posterior half of the dorsal area of the diastema (Fig. 3C). Some individuals of *C. rugiceps* show rugosities on the anteroventral face of the mentonian region (chin) (e.g., Fossil 2; Fig. 3D).

The lower cheek teeth of *C. rugiceps* are protohypsodont (sensu Mones 1968, 1982) and tetralophodont, showing a pattern with a main labial flexid (hypoflexid) not reaching the midline of the tooth, and possessing four lingual flexids that are longer, surpassing the midline, such as in the extant species (Fig. $5A_1$, B–F; Vucetich and Verzi 1994; Rusconi 1934). The mesial walls of the teeth are more rounded than the distal (Fig. $5A_1$, B–F). The last lophid of the m3 is more oblique than in the other teeth (Fig. $5A_1$, B–F).

The dp4 in *C. rugiceps* is pentalophodont and the p4 is tetralophodont, as in the extant species (Fossils 1–6; Fig. $5A_1$, B–F; Rusconi 1934; Ray 1964). The occlusal surface in *C. rugiceps* is quite variable during ontogeny, with the presence of isolated lophids in the early stages, and flexids becoming fossetids during ontogeny (Fig. $5A_1$, B–F; Rusconi 1933, 1934; Nelson and Schump 1978). The anteroflexid in

Table 1. Dentary measurements of the extant species of *Cuniculus* and the extinct *Cuniculus rugiceps* from Cuvieri Cave. Abbreviations: N, number of specimens analysed; Min/Max, minimum/maximum value measured; 1, maximum length; 2, tooth row length; 3, length between the distal margin of alveoli and base of incisive; 4, diastema length; 5, distance between mandibular condyle and ventral margin of angular process; 5a, vertical branch height (for details regarding the distances measured see SOM 1: fig. 1).

Taxon/measurements	1	2	3	4	5	5a
Cuniculus paca						
N	98	99	98	98	95	96
Mean (mm)	94.24	30.36	60.93	31.38	36.03	35.05
Min/Max (mm)	81.84/114.26	26.37/34.71	52.66/71.49	24.85/40.52	28.41/42.58	29.86/42.96
Standard deviation	5.92	1.77	3.51	3.35	2.47	2.73
Cuniculus taczanowskii						
N	10	10	10	10	10	10
Mean (mm)	91.86	30.24	58.11	28.53	33.76	34.47
Min/Max (mm)	86.04/99.19	26.35/32.71	51.97/61.2	25.75/31.81	31.88/35.91	32.67/36.61
Standard deviation	4.46	2.28	2.88	1.98	1.53	1.48
Cuniculus rugiceps						
N	2	3	4	3	3	2
Mean (mm)	129.37	38.41	81.12	44.09	48.81	45.99
Min/Max (mm)	118.39/140.34	38.26/38.53	78.58/83.06	42.4/45.3	44.47/51.06	42.94/49.04
Standard deviation	15.52	0.14	2.27	1.51	3.76	4.31

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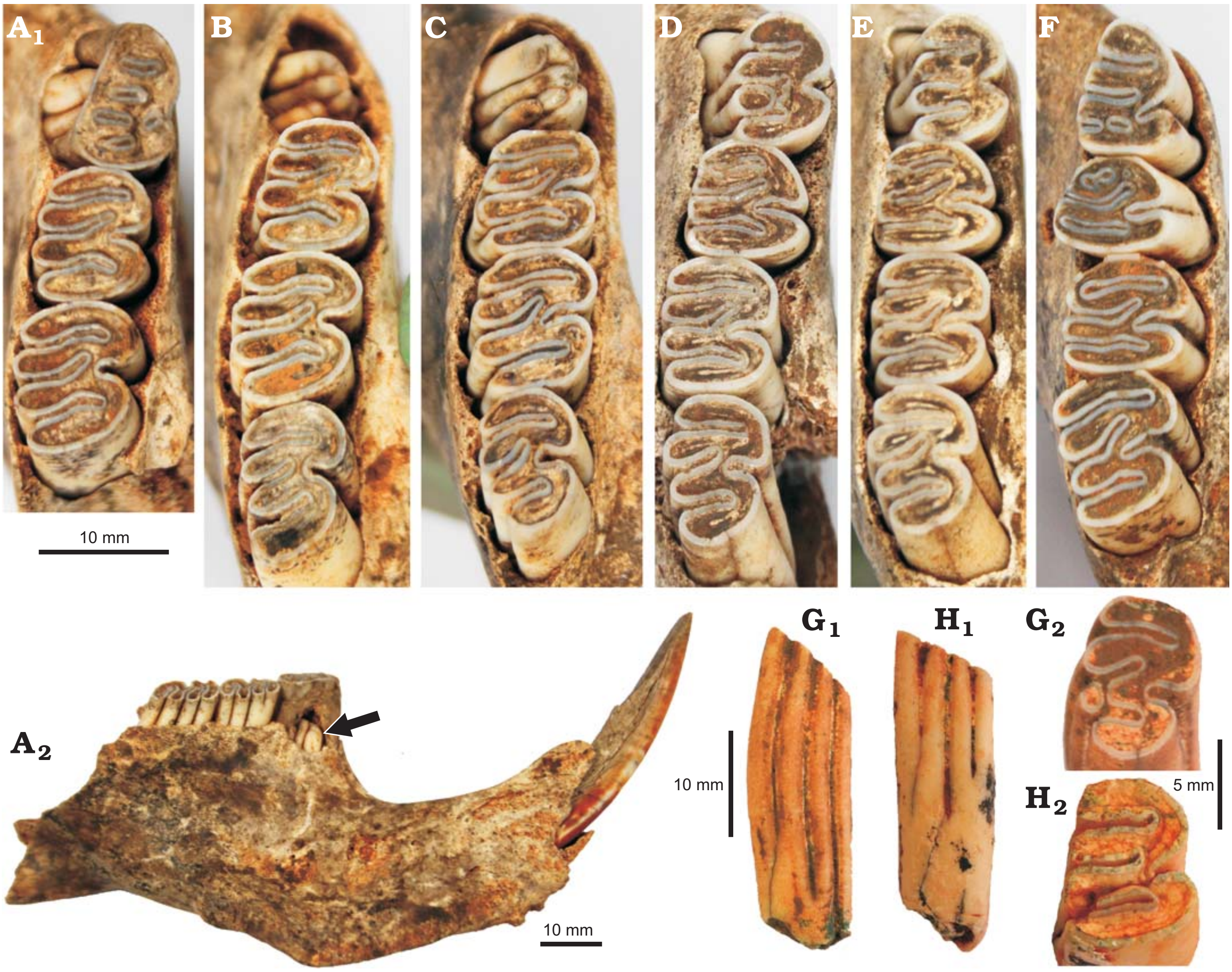

Fig. 5. Lower cheek teeth of the extinct paca *Cuniculus rugiceps* (Lund, 1837) from Cuvieri Cave (minimum age of ~30 ky). A_1, B–F, ontogenetic sequence of cheek teeth. **A**. Fossil 6 (CVL3 P13344) (image inverted). A_1, dp4–m2, the m3 is lacking due to fragmentation. A_2, dentary in medial view showing p4 replacing the dp4 (arrow). **B**. Fossil 4 (CVL3 P13342) (image inverted), showing dp4–m3. **C**. Fossil 1 (CVL3 4052), showing the p4 erupting and the m3 completely functional. **D**. Fossil 5 (CVL3 P13145), showing p4–m3. **E**. Fossil 3 (CVL3 P13149), showing p4–m3. **F**. Fossil 2 (CVL3 P11221), showing p4–m3. **G**, **H**. Isolated molars from Toca de Cima dos Pilão deposits; in occlusal (G_1, H_1) and lingual (G_2, H_2) views. **G**. FUMDHAM 188-19036, possible right m3. **H**. FUMDHAM 188-19521, possible right m2.

C. rugiceps is the first to close, followed by the second and third flexids (Fig. 5A_1, B–F). With wear, the cheek teeth of *C. rugiceps* reduce in mesio-distal length (Fig. 5A_1, B–F). The *C. rugiceps* hemimandibles from Cuvieri Cave show the replacement of the premolar (Fig. 5A_2, arrow), allowing us to reconstruct the sequence of dental eruption, which is the same of the extant species: dp4–m1–m2–m3–p4 (Fig. 5A_1, B–F).

As noted by Rusconi (1933), there is no evident difference between the cheek teeth morphology of *C. rugiceps* and *C. paca*, but the molars of *C. rugiceps* (= *Agouti major*; Rusconi 1933: 25) present a larger size than *C. paca*, as can be seen in the material from Cuvieri Cave and Toca de Cima do Pilão.

Stratigraphic and geographic range.—Tentatively Quaternary (see below section Chronology) of tropical Brazil (from approximately 10 to 20 south latitude; see below section Biogeographic remarks).

Discussion

Quantitative analysis.—To quantitatively characterize the extinct and extant species we performed a principal component analysis comparing dentaries from extinct *Cuniculus rugiceps* and "*Cuniculus laticeps*", and extant *Cuniculus paca* and *Cuniculus taczanowskii*. Our analysis shows that the averaged measurements of *C. rugiceps* (Lund, 1837) dentaries are clearly larger than the other species, thus supporting our interpretation that *C. rugiceps* is a valid species. On the other hand, the two "*C. laticeps*" (= *C. paca lati-*

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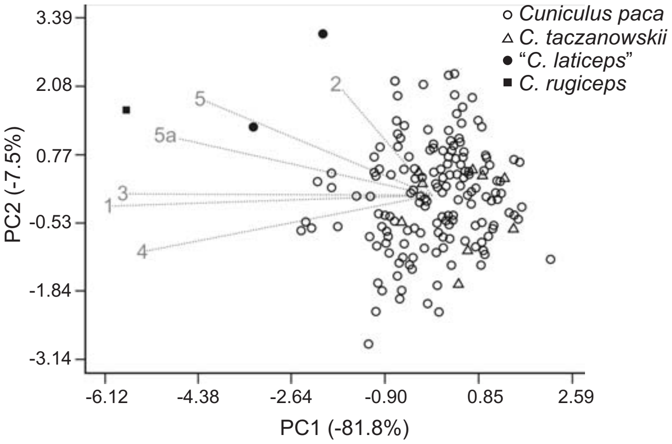

Fig. 6. Principal component analysis performed using the pooled-within species covariance matrix based on six dentary linear distances. Gray-dotted lines and associated numbers show the variables that have high correlations (r > 0.5) with each of the PCs. The gray numbers represent the measurements described in SOM 1.

ceps) dentaries match in size with the larger *C. paca* or are slightly larger than the extant species. Based on the limited number of dentaries of "*C. laticeps*" it is hard to sustain any conspicuous difference between this taxonomic unit and extant species regarding the second axis of major variation. One of the "*C. laticeps*" specimens is outside the distribution of the extant species, so there might be a tendency towards shape differences beyond size (Fig. 6). As mentioned earlier, further studies are required to characterize the size of "*C. laticeps*".

To quantitatively compare teeth from Cuvieri Cave and Toca de Cima do Pilão we measured their mesio-distal length and linguo-labial width. The comparison shows similar values for teeth from both localities (SOM 2: table 2). Based on the similar values (associated with the compatible morphology; see description and comparison), we assigned the material excavated at Toca de Cima dos Pilão to the extinct species *C. rugiceps.*

To provide a metric reference for further analysis and future attempts to recognize *C. rugiceps* we measured six distances on the skull. The measurements of the skull remains from Cuvieri Cave are characterized preliminarily by two widths on the frontal bone and four linear distances between structures on the zygomatic arch (SOM 2: table 3).

Biogeographic remarks.—The current distribution of *Cuniculus* encompasses the tropical and subtropical portions of South America and part of Central America. *Cuniculus paca* has the broader range, covering an area from Mexico to southern Brazil and northeast Uruguay (Pérez 1992; Queirolo et al. 2008 and references therein; Fig. 7). *Cuniculus taczanowskii* is restricted to the Andean region, covering Peru, Ecuador, Colombia, Bolivia, and northwest Venezuela (Ríos-Uzeda et al. 2004; Tirira et al. 2008; Fig. 7). "*Cuniculus hernandezi*" is to date restricted to its type localities in Colombia (Castro et al. 2010; Fig. 7). Fossils of extant *Cuniculus* were found only in presumed Quaternary deposits (Auler et al. 2006), and, as far as we know, are only of *C. paca*. All *C. paca* fossils were reported within the tropical region of Brazil, including the states of Minas Gerais (Lund 1837, 1839a; Souza-Cunha and Guimarães 1986; Hubbe et al. 2011); Bahia (Lessa et al. 2008); Mato Grosso do Sul (Salles et al. 2006); Goiás (Salles et al. 1999); São Paulo (Chahud 2005); Paraná (Kerber et al. 2013; see SOM 1: fig. 2); Acre (no published data, see SOM 1: fig. 2) and Pará (Toledo et al. 1999; Fig. 7). Guérin et al. (1996) cited the presence of *Agouti paca* (= *Cuniculus paca*) in Serra da Capivara, state of Piauí, northeastern Brazil, but did not refer to any material. However, at least some of these reports could be referable to *C. rugiceps*, and a detailed revision is needed. For example, according to Lessa et al. (2008), material of *Cuniculus* collected in Bahia has larger dimensions than the Recent exemplars of *C. paca*.

To date, reports of extinct cuniculids, which according to our interpretation belong solely to *C. rugiceps* (Lund, 1837), were restricted to the Lagoa Santa caves (including Cuvieri Cave) (Lund 1837, 1839; Winge 1887; Rusconi 1933; Vasconcellos et al. 2015; this work). Our morphological and quantitative analyses suggest the at least two specimens from Toca de Cima dos Pilão cave belong to *C. rugiceps* (Fig. 5G_1–H_2; SOM 2: table 2). Thus, the newly diagnosed *C. rugiceps* remains from Serra da Capivara represent the

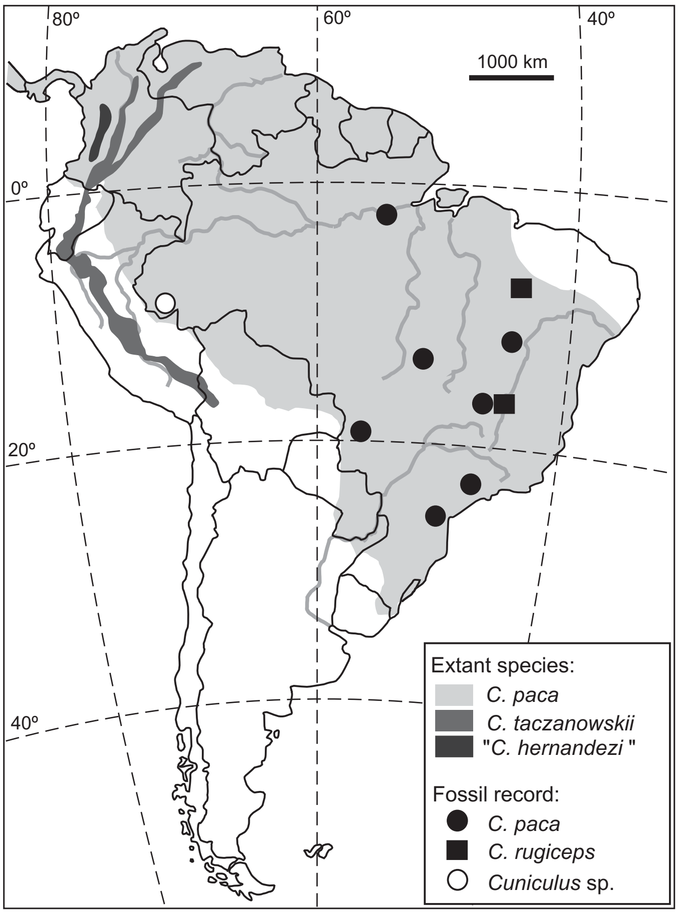

Fig. 7. Distribution of the extinct *Cuniculus rugiceps* and extant species of *Cuniculus* and its fossil record. References in the text.

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northernmost limit of *C. rugiceps*' range, expanding the geographic distribution of this taxon almost 1500 km away from Lagoa Santa. The record from Toca de Cima dos Pilão cave also contributes to knowledge of the ancient fauna from the Serra da Capivara region, since this rodent was not recognized in the sample analysed in a recent review of the late Quaternary caviomorph fauna (Kerber et al. 2016). The available records of *C. rugiceps* are restricted to the tropical region of Brazil.

Taphonomic contextualization

Bone accumulation and main modifications.—Based on the analysis of the bone assembly found in Locus 2, Hubbe et al. (2011) argued that the main process of bone accumulation inside Cuvieri Cave was most likely pitfall entrapment. Our findings for *Cuniculus rugiceps* (Lund, 1837) agree with this interpretation. First, we found some *C. rugiceps* articulated skeleton segments during excavations. In Locus 3A, cranial fragments are associated with a dentary, long bones and vertebrae, while in Locus 3B there was a clustered set of a sacrum, lumbar vertebrae and a femur (Fig. 8A, B). Second, most of the *C. rugiceps* remains were excavated from the subdivision A of Locus 3 (92% of the total amount of specimens, ~323 bones/m^3; Fig. 8) and the remaining specimens (8%, ~42 bones/m^3) came from the southern region of Locus 3B, with very few fossils in the northern region. This data reinforces the interpretation of pitfall entrapment because *C. rugiceps* fossils occur more densely in the area located immediately below the vertical shaft entrance in direct communication with the main passage (~8 m above; Figs. 1, 8A: black arrow). One possible explanation, although not the only one, is that this area is the most likely one where a carcass would be deposited if an animal fell and died after falling into Locus 3. One possibility that we can rule out is bone transport leading to specimen concentration in Locus 3A, because the deposit stratigraphy and sediment characteristics do not indicate the occurrence of water flows capable of transporting bones.

The integrity of the fossils was similar for the three fragmentation categories. Almost complete, incomplete and fragments represented 228 (31%), 282 (38%), and 230 (31%) specimens, respectively. The majority of the fragmentation and movement of the remains is probably due to falling and trampling by other individual *C. rugiceps* and/or other taxa represented in the deposit (Hubbe 2008; Mayer 2011). The falling of detached limestone blocks, which were recorded embedded in sedimentary facies during excavation, possibly acted as another relevant factor (Fig. 8A).

Only rodent gnawing marks were detected on *C. rugiceps* remains (Fig. 8C). These marks were detected on less than 1% of the remains and probably occurred relatively soon after death inside Locus 3, as indicated by observations of modern local fauna that reveals fresh bones are recurrently gnawed by small rodents (Lund 1836: 243–244).

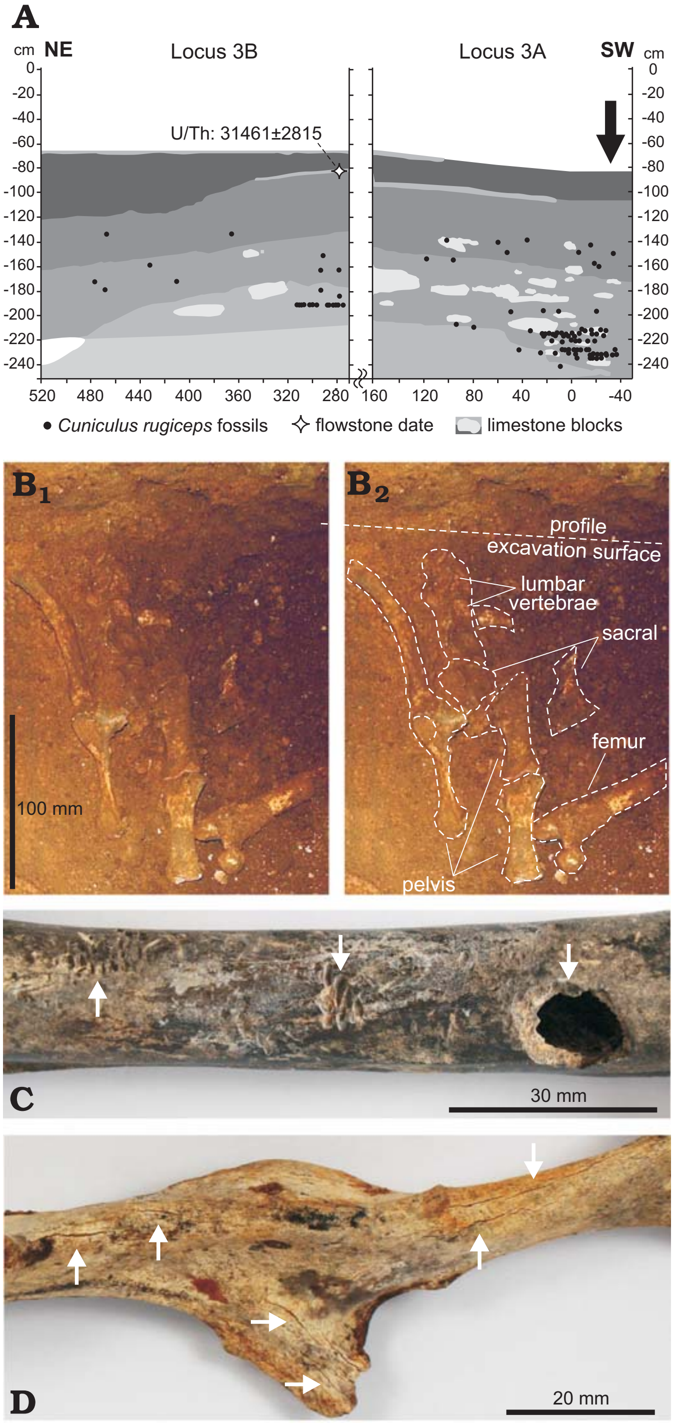

Fig. 8. Taphonomic aspects of the extinct paca *Cuniculus rugiceps* (Lund, 1837) from Cuvieri Cave (minimum age of ~30 ky), Lagoa Santa. **A**. Stratigraphic distribution of plotted specimens (specimens recovered by sieving are not represented) relative to the flowstone dated. Clusters of dots in the lower layers of Locus 3A and 3B represent bones preserved in anatomical association. Black arrow indicates the position of the 8 m deep pitfall. **B**. Excavation record of specimens in anatomical association (B$_1$) with schematic indication of bone elements (B$_2$). **C**. Left femur in posterior view (CVL3P13911), showing bone modifications caused by rodent gnawing (arrows; see the remarkable circular opening of diaphysis). **D**. Right innominate in medial view (CVL3B2165a), showing initial cracking caused by weathering (arrows).

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The low percentage of remains gnawed indicates that the processes of bone accumulation by predators and scavengers (i.e., rodents) did not play a major role in the deposition of *C. rugiceps* skeletons in Locus 3.

Bone modifications associated with weathering were identified on 15% of *C. rugiceps* specimens, which represent modifications compatible only with stage 1 weathering (Behrensmeyer 1978; Fig. 8D). Despite the low intensity of these weathering marks, it indicates that at least part of the bones remained on the surface for some time before burial. Moreover, since caves are underground environments, the weathering probably occurred at a slower rate than would occur on surface (as was the experiment conducted by Behrensmeyer 1978), and potentially even bones that do not present weathering modifications could have been exposed on the surface of Locus 3 for a relatively long time. This suggests that the falling and entrapment of other animals and the falling of limestone blocks allied with rodent scavenging probably played the major roles in modifying the deposits. Currently, a broader taphonomic study based on all taxa recovered from Locus 3 is underway and will add new information to this issue.

Quantification of fossils.—The NISP calculated for *C. rugiceps* is 740 and several skull and postcranial elements are represented. The left calcaneus is the most abundant element in the sample and served as the basis to calculate the MNI, resulting in at least seven individuals. There is some discussion about the adequacy of these indexes in relation to different bone accumulation processes (Badgley 1986; Castro and Langer 2011). The NISP method is appropriate to count individuals from assemblages whose remains suffered wide-ranging transportation and are deposited as scattered pieces, displaying a low probability of association. In contrast, the MNI method assumes a high probability of association and is suitable to infer the number of individuals contained in assemblages formed in natural traps (Badgley 1986). As such, we argue that MNI is a better estimate for the number of *C. rugiceps* individuals in Locus 3, since falling and entrapment is the most likely cause of the bone accumulation.

Some evidence suggests that the seven individuals of *C. rugiceps* did not fall into Locus 3 in a single event. First, the specimens exposed during excavations were vertically distributed in at least two distinct sedimentary facies encompassing ~1.10 m of the ~1.80 m total excavated depth in Locus 3 (Fig. 8A). Despite some burial perturbations of a lesser range being identified through the mechanical refitting of medium-sized mammal bones, the breadth of the movements are mainly near the horizontal plane or subparallel to inferred facies boundaries (Mayer 2011), reinforcing trampling as an important taphonomic process. Since there was no mixing of the sedimentary facies, the idea of independent entrapment of the individuals appears plausible. Second, considering the behavioural aspects of *C. paca*, the solitary habits of this cursorial rodent support the idea of individual independent entrapment in Locus 3. Moreover, the presence of *C. paca* inside caves is commonly recorded (Lund 1838, 1841b; Nowak 1999; Zeppelini Filho et al. 2003) and this behaviour could be shared by the extinct *C. rugiceps*, which would facilitate eventual falling of individuals over relatively long periods of time.

Chronology.—The chronological information available so far for *C. rugiceps* is insufficient to allow any solid interpretation about the temporal distribution of the species. The flowstone formed above the deposits containing the fossils of *C. rugiceps* from Cuvieri Cave (Fig. 8A) suggests a Late Pleistocene minimum age of ~30 ky for our findings. However, since bone remains from Lagoa Santa caves range from older than 300 ky to as young as the present, more dating will be required to allow a better understanding of the chronological distribution of *C. rugiceps* in the fossil record (Auler et al. 2006; Hubbe et al. 2011).

Conclusions

We propose that the only valid name for the extinct Cuniculidae is *Cuniculus rugiceps.* The new fossil remains of *C. rugiceps* presented by us from Cuvieri Cave, Minas Gerais state, Brazil suggest that at least seven individuals of *C. rugiceps* accumulated asynchronously by pitfall entrapment inside Locus 3, and were buried after some undetermined time of exposure on the surface. The stratigraphically controlled excavations and dating of the Cuvieri Cave deposits allowed the establishment of a Late Pleistocene minimum age (~30 ky) for these specimens. Furthermore, remains of *C. rugiceps* from Toca de Cima dos Pilão cave, Piauí state allowed us to tentatively assign a tropical geographic distribution for this species.

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Appendix 1

Comparative fossil specimens from Lagoa Santa.

The material reported herein was compared with extant specimens from several institutions (see SOM). Besides these specimens, our sample was compared with the ontogenetic series of *Cuniculus paca*: MCN-M(D) 076 (adult); MCN-M 1051; MCN-M 3001 (senile); MCN-M 1052 (adult female); MCN-M(D) 096 (newborn/juvenile); MCN-M(D) 088 (adult).

"*Cuniculus paca* forma *laticeps*": ZMK 1/1845:3832 (Lapa da Cerca Grande), palatal portions; ZMK 1/1845:13441 (Lapa da Cerca Grande), left zygomatic arch; ZMK 1/1845:1340 (Lapa da Cerca Grande), two dorsal portions of the skull (young specimens); ZMK 1/1845: 13426 (Lapa da Cerca Grande), portion of a skull; ZMK 1/1845: 13428 (Lapa da Cerca Grande), four dentaries of adult specimens and four young specimens; ZMK 1/1845:2989 (Lapa da Cerca Grande), eleven atlas; ZMK 1/1845:13439 (Lapa da Cerca Grande), fragmented skull; ZMK 1/1845:3823 (Lapa da Cerca Grande), right dentary; ZMK 1/1845:3820 (Lapa da Cerca Grande), right dentary lacking the m3 and right dentary; ZMK 1/1845:3818 (Lapa da Cerca Grande), right dentary associated with three left dentaries and two right dentaries; ZMK, unnumbered specimen (Lapa da Cerca Grande), fragmented skull.

"*Cuniculus paca* forma *major*": ZMK 1/1845: 2029 (Lapa do Gambá), mandible with left p4–m3 series and right p4–m2; ZMK 1/1845: 2200 (Lapa do Gambá), jugal portion; ZMK, unnumbered specimen (Lapa da Escrivânia nº 11), left dentary; ZMK 1/1845:13450 (Lapa do Periperi), cranial fragments including portions of the zygomatic arch and maxilla, besides other fragments. One of them is a right maxilla with P4–M3 series; ZMK 1/1845: 1154 (Lapa do Bahu), fragment of left dentary with p4–m1; ZMK 1/1845: 1065 (Lagoa Santa), right dentary and cheek teeth (m3 in eruption); ZMK 1/1845: 2065 (Lagoa Santa), fragment of dentary with p4–m3; ZMK 1/1845:2639 (Lagoa Santa), fragment of right dentary; ZMK 1/1845: 11064 (Lapa da Escrivânia nº 5), fragment of right dentary associated with postcranial remains, and a fragment of dentary.

"*Cuniculus paca* forma *typica*": ZMK, unnumbered specimen (Lapa do Bahu), cranial portion.

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