Cervidae and Tayassuidae of the Late Pleistocene from the Cuvieri Cave, Eastern Brazil

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ABSTRACT

The Pleistocene of the eastern Brazilian territory is characterized by a great diversity of extinct and living mammals. The Cuvieri Cave, part of the Lagoa Santa karst complex, presents an abundant amount of osteological material dated from the Pleistocene, resulting in an important record of changes in faunal composition and environmental settings. In this cave, Cervidae are represented by two extant species: *Mazama americana* and *Mazama* cf. *gouazoubira*, while the Tayassuidae family is the most abundant of Pleistocene macrovertebrates and is represented by two species. One of the species was identified as *Dicotyles tajacu*, showing anatomical features larger than recent specimens from the same region, but similar in size to Amazonian specimens. The most common observed species could not be identified and is much larger than the living *Tayassu pecari*, the largest Tayassuidae in the region and to the Pleistocene deposits of Cuvieri Cave. The Cervidae species are the same observed in the Holocene, but the differences of the Tayassuidae in relation to the living specimens suggest that paleoenvironmental changes occurred after the deposition.

1. Introduction

The Quaternary of South America was characterized by several species of large Nearctic mammals that migrated, after several phases of the Great American Biotic Interchange (GABI) initiated in the Pliocene (Woodburne, 2010). Among the various clades that migrated towards South are the Cervidae and the Tayassuidae.

The Family Cervidae constitutes a clade of taxonomic and environmental diversity, inhabiting almost all continents. Despite its relatively recent arrival and diversification in South America, with the first occurrences at the Pleistocene, several genera currently inhabit South America: *Hippocamelus*, *Blastocerus*, *Pudu*, *Odocoileus*, *Ozotoceros* and *Mazama* (Duarte, 1996; Duarte et al., 2008).

The Tayassuidae emerged in the Oligocene of Europe and Asia and were very common in the Neogene of North and South America, however, only three genera are observed in the present in South America: *Parachoerus*, *Dicotyles* and *Tayassu* (Dutra et al., 2017a; Gasparini et al., 2009, 2011, 2014; Acosta et al., 2020).

The Cuvieri Cave is part of the Lagoa Santa karst complex and the paleontological interest of this cave began in 1974 with the discovery of an articulated and almost complete specimen of ground sloth (Hubbe,

2008). However, only recently has been the subject of numerous paleoenvironmental, paleontological and sedimentological works (Mayer et al., 2016; Haddad-Martim et al., 2017; Chahud, 2020a, 2020b, 2021, 2022; Chahud et al., 2020; Chahud and Okumura, 2021a, 2021b).

Research with Cervidae and Tayassuidae from Cuvieri Cave has focused on taphonomy (Mayer et al., 2020), dating (Hubbe et al., 2011), taxonomy (Chahud and Okumura, 2023), and ontogeny (Chahud, 2020c) of the most recent specimens (from the Holocene or the Holocene-Pleistocene boundary). The osteological material from the Pleistocene deposits was reported by Mayer (2011), mostly describing taphonomic features, and little has been described in terms of the anatomy and taxonomic identification of these specimens.

The objective of this article is to present and described in details the osteological material of Tayassuidae and Cervidae of Pleistocene layers from Cuvieri Cave, and to contribute to the knowledge about the occurrence of these groups in Quaternary deposits in Brazil. We also make considerations and comments on the paleoenvironment and paleocology in which these two families lived in the Late Pleistocene of the Lagoa Santa region.

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2. Materials and methods

The Cuvieri Cave (UTM coordinates: 23 K 603756 E and 7846105 S) is located in the state of Minas Gerais (Hubbe, 2008; Hubbe et al., 2011), Brazil (Fig. 1). The present day open entrance measures approximately 1.5 m high by 1 m wide and ahead of it follows a horizontal, low and relatively short main conduit of about 15 m, presenting three unconnected abysses: *Locus* 1, 2, and 3, measuring approximately 16 m, 4 m, and 8 m, respectively (Hubbe et al., 2011, Fig. 1). The fossil specimens studied here come from Locus 3. The excavation of this site was carried in three distinct areas, *Locus* 3 A, 3 B and 3C, which were part of the evolution of the same sedimentary deposit.

The osteological material was collected between 2002 and 2009 and comes from different sedimentary facies of *Locus* 3, which, according to Hubbe (2008), Mayer (2011), Mayer et al. (2016) and Haddad-Martim et al. (2017), are dated from Pleistocene period.

The methodologies for taxonomic identification and establishment of ontogenetic stages used previously identified specimens from the "Renato Kipnis Reference Collection" and the "Awá-Guajá Ethnographic Collection", both housed at the Laboratory for Human Evolutionary Studies from the University of Sao Paulo (LEEH-IB-USP), the Laboratory of Systematic Paleontology of the Department of Sedimentary and Environmental Geology of the Institute of Geosciences of the University of São Paulo (IGc-USP), as well as, the Mastozoological Collection of the Museum of Zoology of the University of São Paulo. The works of Mayer and Wetzel (1987), Leeuwenberg and Resende (1994), Grubb and Groves (1996), Rossi (2000), Vogliotti (2003), Keuroghlian et al. (2004, 2009, 2012), Gasparini and Zurita (2005), Guérin and Faure (2009), Gasparini and Ferrero (2010), Gasparini et al. (2009, 2011, 2014), Desbiez et al. (2012), Duarte et al. (2012a, 2012b), Gasparini (2013), Missagia (2014), Oliveira et al. (2014), Dutra et al. (2017a, 2017b) Souza et al. (2017), González et al. (2018), Loponte et al. (2019) and Eltink et al. (2020) were also used for comparative analysis.

Data on specimens that could be measured are available in the supplementary material 1 dedicated to Cervidae and supplementary material 2 dedicated to Tayassuidae. For this study, we adapted the techniques for measurements suggested by Von den Driesch (1976) and Loponte et al. (2019).

For the taphonomical analysis, especially regarding the exposure to climatic weathering, the criteria presented by Behrensmeyer (1978) were used, who considered that bones with numerous cracks are indicative of exposure to sudden changes in humidity. In a cave environment like Cuvieri cave, the effects of exposure are very different from those observed in an open air surface and, therefore, the time associated to different levels of degradation (in an open air environment) could not be properly applied. Nevertheless, the information regarding the existence of periods of exposure associated to changes in humidity was considered to be important enough to be recorded, even if missing further details about the extension of time.

The specimens were numbered according to the field collection site, receiving the acronym CVL3-, for the material found in *Locus* 3 A, and CVL3B-, for specimens found in *Locus* 3 B. The numbers increase with the depth of the deposit, meaning that specimens with lower numbers were collected near the surface and specimens presenting higher numbers were excavated from the deeper parts.

All osteological material from Cuvieri Cave described in this article are housed at the Laboratory for Human Evolutionary Studies of the Institute of Biosciences of the University of São Paulo (LEEH-IB-USP).

3. Geological context

The Cuvieri Cave is a small cave located on the northeast side of a limestone massif, in the Lagoa Santa Karst. The cave was developed in lithotypes of the Sete Lagoas Formation, Bambuí Group (Neoproterozoic), part of the São Francisco Craton (Berbert-Born, 2000).

Due to the depositional characteristics of the cave, the accumulation of terrigenous sediment is poorly consolidated in each *loci*, which allowed the careful excavation of the sedimentary package. However, while *Locus* 2 presented a homogeneous sedimentary input composed by two sedimentary facies (Hubbe, 2008; Hubbe et al., 2011), *Locus* 3 was characterized by a greater variety of facies (Haddad-Martim et al., 2017).

Few were the ages obtained for *Locus* 3, but they indicate an older age in comparison to *Locus* 2. Two datings using the 14C-AMS technique were performed on osteological material near the surface, resulting in a date of 12,390 ± 50 BP (14,100–14,710 cal BP) for a Tapiridae and 12,510 ± 70 BP (14,230–15,040 cal BP) for a *Catonyx cuvieri* (Hubbe, 2008; Haddad-Martim et al., 2017). Three other datings were carried out, based on the analysis of material obtained in a stalagmite layer, using the U/Th technique, obtaining values between 27 and 31 thousand years (Hubbe, 2008), reinforcing that most of the deposition and osteological content of *Locus* 3 would be of Pleistocene age.

4. Comments on the taphonomy

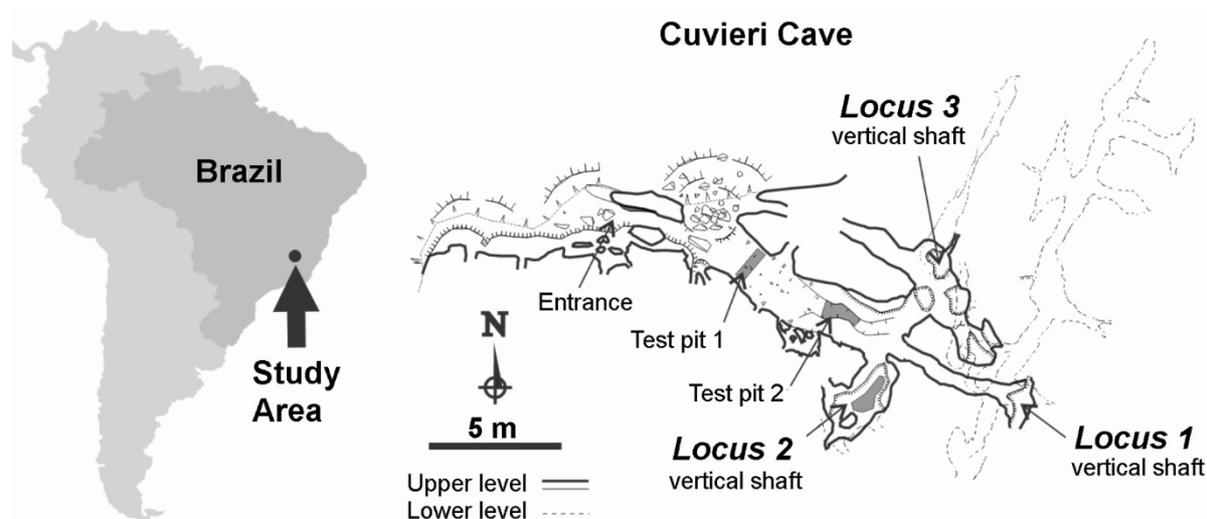The material found in Cuvieri Cave comprises teeth, cranial

Fig. 1. - Geographic location of the study area and of Cuvieri Cave showing the position of *Loci* 1, 2 and 3 (map courtesy of Alex Hubbe and Grupo Bambuí for Speleological Research).

fragments, mandibles, axial and appendicular bones of different sizes, some of them presenting articulation. According to Hubbe (2008), Mayer (2011) and Haddad-Martim et al. (2017), the presence of all the macrovertebrates can be explained as the result of accidental fall and subsequent entrapment of such individuals at *Locus* 3, given that there was no evidence of the transport by water. The lack of transport by water is supported by some specimens of Tayassuidae, which had some bones in a position showing anatomical articulation (Fig. 2).

Using the technique of the minimum number of individuals (MNI), a method that considers the size, ontogeny and laterality of each analyzed bone part (Badgley, 1986), nine Cervidae and 16 Tayassuidae were identified based on vertebrae, ribs, cranial bones and appendicular bones.

The dispersed materials that might belong to the same individual were interpreted as the result of either the activity of animals that fell into the cave and trampled on the bones of such animals or the feeding of scavengers (rodents or small carnivores) on the exposed carcasses (Mayer, 2011).

A few bones from *Locus* 3 presented cracks, indicating that some carcasses were exposed for some time before being buried. Some smaller bones such as astragali and phalanges presented a degree of roundness, but in general the material studied showed some abrasion.

Bones altered by biogenic activity are even rarer, and most cases were interpreted as being caused by rodents (Mayer, 2011) in long bones (Fig. 3).

The spatial distribution of the fossil material was described by Mayer (2011) and it indicated that the fossiliferous material attributed to Cervidae and Tayassuidae occurs in all layers of *Locus* 3, with no relevant concentrations.

5. Systematic Paleontology

Class Mammalia Linnaeus, 1758

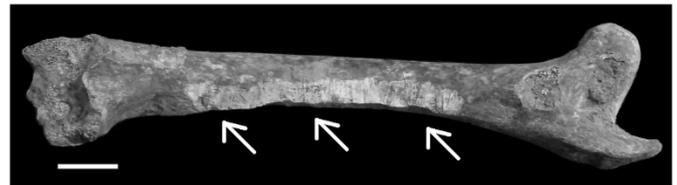**Fig. 2.** – Articulated appendicular limb of Tayassuidae (CVL3-2375 A). Scale 20 mm.

Fig. 3. – Femur of *Mazama americana* (CVL3B-1922) presenting tooth marks by rodents. Scale 20 mm.

Order Artiodactyla Owen, 1848
Family Cervidae Goldfuss, 1820
Genus *Mazama* Rafinesque, 1817

Material: The analyzed material consists of different osteological parts, including axial and appendicular bones, cranial and mandibular fragments attributed to nine individuals of at least two different species. The total number of bones of Cervidae was 470 specimens.

Only a few bones could be measured, preventing any statistical tests to be made. All measured specimens are presented with details in Supplemental Material 1.

Geographic distribution: The genus is very common in the Neotropics, extending from southern Mexico to northern central Argentina, and inhabiting diverse environments, including dense forests, high mountains, and savannas (Duarte et al., 2012a, 2012b, 2012c, 2012d).

Remarks: At least two species of *Mazama* (*M. americana* and *M. gouazoubira*) were identified based on the size of bones and dentaries (Fig. 4).

The two largest individuals have bones presenting length and width similar to specimens of *Mazama americana* (Guérin and Faure, 2009; Chahud and Okumura, 2023). However, no skull or mandibles were found and the classification is based only on the size and shape of appendicular bones, which are on average larger and more robust than any other species in the genus *Mazama*. The species *Mazama americana* is the largest species of the genus (Duarte et al., 2012a, 2012c) and such size difference can be observed in the analyzed osteological material (Fig. 4D, 4G and 4H).

Most of the osteological material presents equivalent proportions to adult individuals of *Mazama gouazoubira*, a small deer found in Quaternary deposits of Lagoa Santa (Chahud and Okumura, 2023) and in other Brazilian regions, such as Serra da Capivara in the State of Piauí (Guérin and Faure, 2009). The bone parts are medium-sized (Fig. 4A–C, 4E and 4I) for the specimens of *M. gouazoubira* (Souza et al., 2017).

Currently, in southern and southeastern Brazil, there are two other species of similar size and proportions to *Mazama gouazoubira, M. nana* and *M. bororo* (Duarte et al., 2012a, 2012c), however, they are restricted to small areas. The possibility that such species inhabited regions further north during the Pleistocene cannot be ruled out, and therefore it was chosen to classify the specimens from Cuvieri Cave as *Mazama* cf. *gouazoubira*. Such classification was made based only on the average size of the bones, slightly larger and thinner than the two abovementioned species, but such criteria was not enough to make the classification with accuracy.

Our suggestion that there were other species of *Mazama* in the deposits of the Cuvieri Cave is justified by the variation in size among some specimens, as evidenced in the femur CVL3-341-2838 (Fig. 4H), approximately 182 mm, representing a large *Mazama gouazoubira*.

Discussion: The oldest Pleistocene age dates for *Mazama* in the Lagoa Santa region are close to 15 ka BP (Auler et al., 2006) and both species already existed in the Early Holocene (Chahud and Okumura, 2023).

We emphasize that the species *Mazama americana* and *M. gouazoubira* are sympatric in several regions of South America and that the population ratio of each species varies according to the biome they inhabit (Duarte et al., 2012a, 2012c). At *Locus* 3, there are seven individuals identified as *M.* cf. *gouazoubira* and two as *M. americana*,
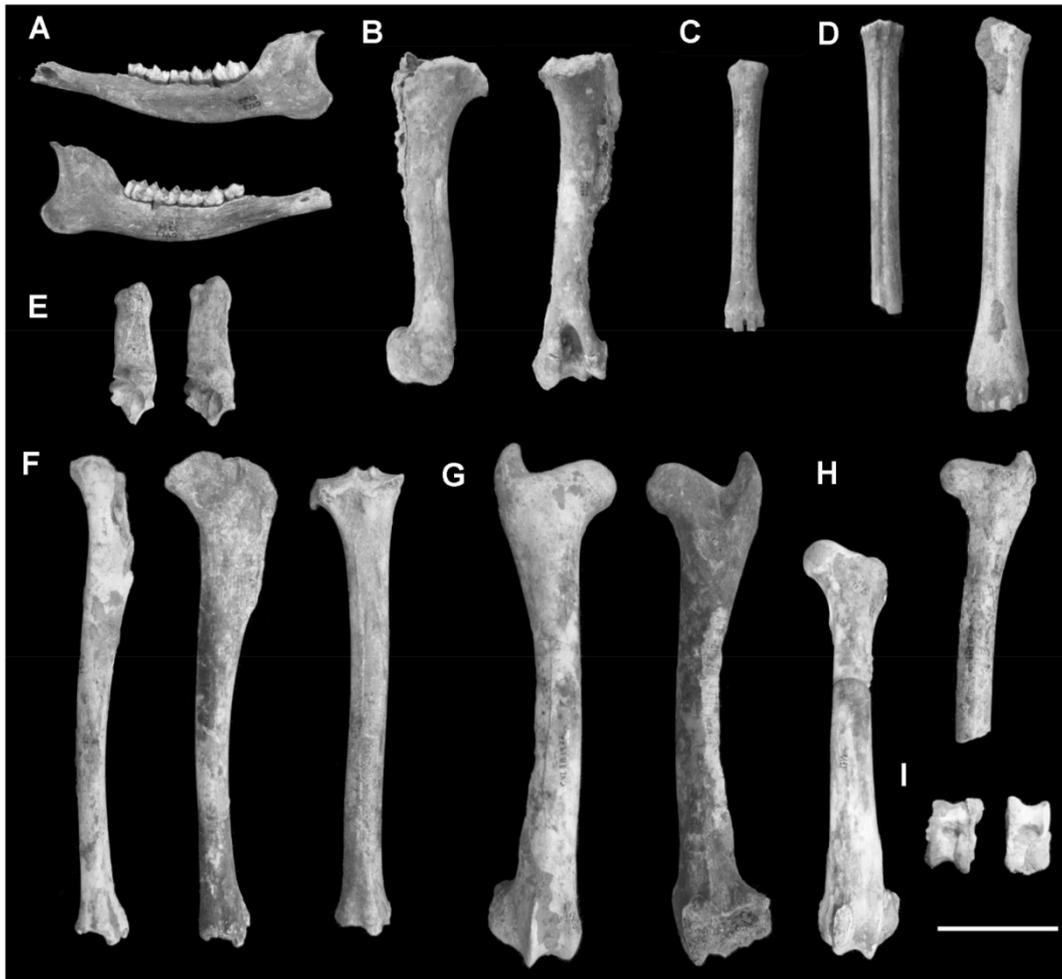
Fig. 4. – Osteological material attributed to specimens of the genus *Mazama*. A) right dentary of *Mazama* cf. *gouazoubira* (CVL3-3799-3722), internal (above) and external (below) views; B) right humerus of *M.* cf. *gouazoubira* (CVL3-2428); C) Left metacarpal of small *M.* cf. *gouazoubira* (CVL3-3795); D) Left metatarsal of *M.* cf. *gouazoubira* (minor) (CVL3-3691) and *M. americana* (major) (CVL3B-1287); E) Calcanes of *M.* cf. *gouazoubira* (CVL3B-158, CVL3-1972); F) Lateral views of the right tibiae of *M.* cf. *gouazoubira* (CVL3-1903, CVL3-3230) and dorsal view of the left tibia (CVL3-3743); G) right femur of *M. americana* (CVL3B-1922), two views, cranial and dorsal; H) Cranial views of two left femurs of *M.* cf. *gouazoubira* (CVL3-341-2838 and CVL3B-1744), I) Astragali of *M.* cf. *gouazoubira* (CVL3-1858, CVL3B-1757). Scale 20 mm.

however, given the small sample size, it is not possible to estimate the population ratio of these species in the Pleistocene. However, a greater difference between these two species was observed in the Holocene, when *M.* cf. *gouazoubira* seems to be much more abundant (Chahud and Okumura, 2023).

In the last 21 ka, the paleoenvironment of the Lagoa Santa region has changed from forest to savannah (Sobral-Souza and Lima-Ribeiro, 2017) and it would not be surprising that a greater amount of osteological material from Cuvieri Cave was attributed to *Mazama gouazoubira*, which is adapted to different environments and prefers ecotones between forest and savannahs. There is the possibility that these several environmental changes in the Quaternary limited the presence of *M. americana* in the Lagoa Santa region, during less favorable times. This species is much more sensitive to environmental changes than *M. gouazoubira*, which is much more resilient (Duarte et al., 2012a, 2012c) and, therefore, *M. americana* is not expected to be abundant in the Cuvieri Cave deposits.

Suborder Suiformes Jaeckel, 1911.
Family Tayassuidae Palmer, 1897

Material: The material consists of articulated and disarticulated osteological parts of at least 16 individuals. One individual was assigned to *Dicotyles* and 15 individuals were identified as indeterminate Tayassuidae. The total number of bones of Tayassuidae was 1379 specimens, but only four were attributed to *Dicotyles*.

Geographic distribution: Currently, the Tayassuidae occur from the southern United States, including Central America up to northern Argentina (Desbiez et al., 2012; Keuroghlian et al., 2012).

Remarks: The material found at *Locus* 3 can be attributed to two distinct species. The indeterminate Tayassuidae is largest and most abundant is distributed throughout the deposit while the other is represented by a smaller individual, identified as *Dicotyles tajacu*, found in intermediate portions of the deposit.

The name *Dicotyles tajacu* has always been a matter of discussion (Gasparini, 2013), but Acosta et al. (2020) considered the genus *Dicotyles* to be the only valid genus for the species. We agree with the authors regarding the classification and we will use it in the present study.

The anatomy of the specimens were compared with identified specimens of Tayassuidae from the Lagoa Santa region (Chahud and Okumura, 2023), from southern and southeastern Brazil (Chahud, 2005; Chahud et al., 2023), from the Amazon region (Ferreira Figueiredo et al., 2022), as well as with identified individuals from collections.

Dicotyles tajacu is represented by one fragmented dentary without teeth (Fig. 5A), two radioulnae of equal size and opposite laterality (Fig. 5B), and a fragment of the humerus (Fig. 5C). The specimen is larger than the extant *D. tajacu* found in the Lagoa Santa region and in previously described Holocene specimens (Chahud and Okumura,
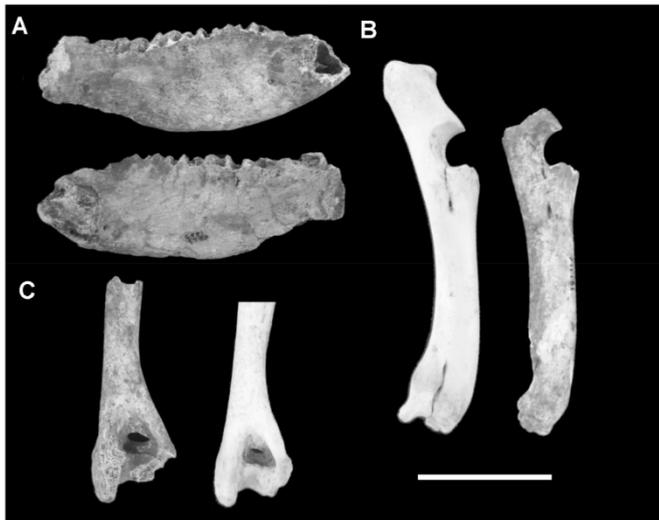
Fig. 5. - Remains of *Dicotyles* found in *Locus* 3 of Cuvieri Cave and in the eastern Amazon. A) Right dentary found in Cuvieri Cave (CVL3-1263), lateral, internal and external views, B) Right radioulna of a *Dicotyles tajacu* from eastern Amazon (left) (CS-13) and the specimen from Cuvieri Cave (CVL3-P11181) (right), C) right humerus of *Dicotyles tajacu* from eastern Amazon (O0/5N15/10/06) and the Cuvieri cave specimen (CVL3-P11115) (right). Scale 50 mm.

2023), however it is smaller than specimens of *Tayassu pecari*.

This specimen is similar in terms of external morphology, size, and robusticity to *D. tajacu* from the eastern part of the Amazon region (Table 1 and Fig. 5B and C). Some specimens of *Dicotyles tajacu* found in the eastern part of the Amazon region have a slightly larger size than those from other localities (Table 1), however, they are smaller than specimens of *Tayassu pecari* (Fig. 6A and B). This difference was observed by Roosmalen et al. (2007) who suggested the creation of a new species, *Pecari maximus*, but Gongorra et al. (2011) observed that there was not enough genetic differentiation to support this new species and commented that variations in size and proportion can be observed within the species *Dicotyles tajacu* and that would represent regional differences.

The similarity between the abovementioned specimen from Cuvieri Cave and the specimens from *Dicotyles tajacu* from the Amazon region (Table 1 and suplementary file 2), supports the classification of such specimen as *D. tajacu*. However, this individual is larger than specimens from Quaternary deposits of Lagoa Santa (Chahud and Okumura, 2023) and in southeastern regions of Brazil, such as the Abismo Ponta de Flecha Cave, located at the Ribeira de Iguape River Valley (Chahud, 2005; Chahud et al., 2023).

The most abundant species of Tayassuidae found at *Locus* 3, and in the deposits of Cuvieri Cave, are large than any current member of the family in the region and cannot be associated with any living species. In all, 15 individuals were identified, and three were subadults that had not yet reached their maximum size.

The identification of subadult specimens was based on the presence of unfused epiphyses as well as the overall robustness, as the bones were similar in length to that of adult specimens of *Tayassu pecari*.

Fig. 6. - Humeri and radioulnae of Quaternary Tayassuidae. A) Lateral view of the humeri and B) lateral view of the radioulnae. From left to right; Tayassuidae Indeterminate from *Locus* 3 of the Cuvieri Cave, Quaternary *Tayassu pecari* from Abismo Ponta de Flecha Cave, southeastern Brazil, *Dicotyles tajacu* from eastern Amazonia, *D. tajacu* of the Middle Holocene from *Locus* 2 of the Cuvieri Cave, living *D. tajacu* from region of Lagoa Santa. Scale 50 mm. Registration numbers: A) right humeri: CVL3B-1306, PF-417/GP2C–43 S O0/5N15/10/06, CVL2-6709, MR-3-3; B) right radioulnae: CVL3-2314, PF -408/GP2C43P, CS-13, CVL2-6710, MR-3-7.

The postcranial elements were compared with living species (Figs. 6 and 7), the difference being in the much larger size. This difference was observed in all postcranial bones, including humeri, radioulnae (Fig. 6A-B), femora and tibiae (Fig. 7A-B), as well as in small appendicular bones such as calcanei, astragali and patellae (Fig. 7C–E).

All the dentaries and maxillas of the specimens (Fig. 8A) are incomplete or fragmented. They are slightly larger than those of *Tayassu pecari*, but present dentition compatible with this species. The comparison was made using a known specimen of *Tayassu pecari* of the Quaternary (Fig. 8B) and there was a small difference in the length of the dental sequence, which is greater in specimens from *Locus* 3 of Cuvieri Cave. Comparing to specimens of *Dicotyles tajacu*, all teeth are much larger and more robust.

These specimens were also compared with the specimen of *Tayassu*

Table 1
Comparative mean measures of radioulnae of *Dicotyles tajacu*. Measurements in mm. Abbreviations: BP - Breadth of the proximal, DP - Depth of the proximal, BD - Breadth of the distal, DD - Depth of the distal. * Measurements of a single individual.

	CVL3-P11181	*Dicotyles tajacu* Amazon (n = 3)	*Dicotyles tajacu* Lagoa Santa (n = 4)	*Dicotyles tajacu* Ribeira de Iguape River Valley (n = 1)
BP (radius)	19.8	19.8	18.2	18.3
DP (radius)	12.1	12.4	11.8	11.8
BD	21.6	20.6*	18.7	19.0
DD (radius)	15.2	15.1*	14.8	14.6

Fig. 7. - Bones of Tayassuidae A) Femora, B) Tibiae, C) Calcanei, D) Astragali, E) Patellas. From left to right; Tayassuidae Indeterminate from *Locus* 3 of Cuvieri Cave, *Tayassu pecari* from the Quaternary of the Abismo Ponta de Flecha Cave, southeastern Brazil, current *D. tajacu* from the Lagoa Santa region. Scale 50 mm. Registration number: A) Left femora: CVL3-2176, PF-410/GP2C-43 T, MR-3-13; B) Left tibiae: CVL3B-1927, PF-409/GP2C-43 R, MR-3-11; C) Left calcanei: CVL3B 1536, PF-390/GP2C-43 E, MR-3-17; D) Right Astragali: CVL3B-1318 b, PF-365/GP2C-43 E, MR-3-18; E) Right patellas: CVL3B–P3742, PF-402/GP2C–43I, MR-3-14.

pecari from the Pleistocene-Holocene boundary of Cuvieri Cave, found at *Locus* 2 (Chahud and Okumura, 2023). The *Locus* 2 specimen was smaller than the specimens studied here and of identical proportions to those observed in current *T. pecari*. Therefore, it was possible to infer that no specimens of this large Tayassuidae were found in the Holocene deposits of Cuvieri Cave and that the indeterminate variation is restricted to Pleistocene deposits.

Data on measurements of the indeterminate specimens of Tayassuidae are available in the supplementary material 2.

Discussion: The observation of proportionally larger appendicular bones is observed in the genus *Parachoerus* (Mayer and Wetzel, 1987), currently observed in Paraguay, and in the extinct *Brasiliochoerus* (Paula Couto, 1979, 1981; Cartelle, 1994, 1999; Missagia et al., 2016). As previously mentioned, the dentition, mandible and maxilla are slightly larger than those observed in *Tayassu pecari* and no complete skulls were found, only a fragmented occipital region that is also similar to that observed in specimens of *T. pecari*.

During the Pleistocene in Lagoa Santa, there were at least three species of Tayassuidae: two recent, *Tayassu pecari* and *Dicotyles tajacu*, and the extinct species, *Brasiliochoerus stenocephalus* (Dutra et al., 2017a, 2017b; Acosta et al., 2020; Copetti et al., 2021). The species *Brasiliochoerus stenocephalus* is the largest of the three Tayassuidae species and was reported between the Middle Pleistocene and the Early Holocene in Argentina, Uruguay, Brazil, and Bolivia (Avilla et al., 2013; Dutra et al., 2017a, 2017b; Copetti et al., 2021) and living species, *Tayassu pecari* and *Dicotyles tajacu* have the oldest record in the Middle Pleistocene of Argentina, Brazil, Uruguay, and Venezuela (Gasparini, 2013; Gasparini et al., 2014; Dutra et al., 2017a, 2017b).

The main difference between the genera *Brasiliochoerus* and *Tayassu* lies in the external morphology of the skull and, given that there were no
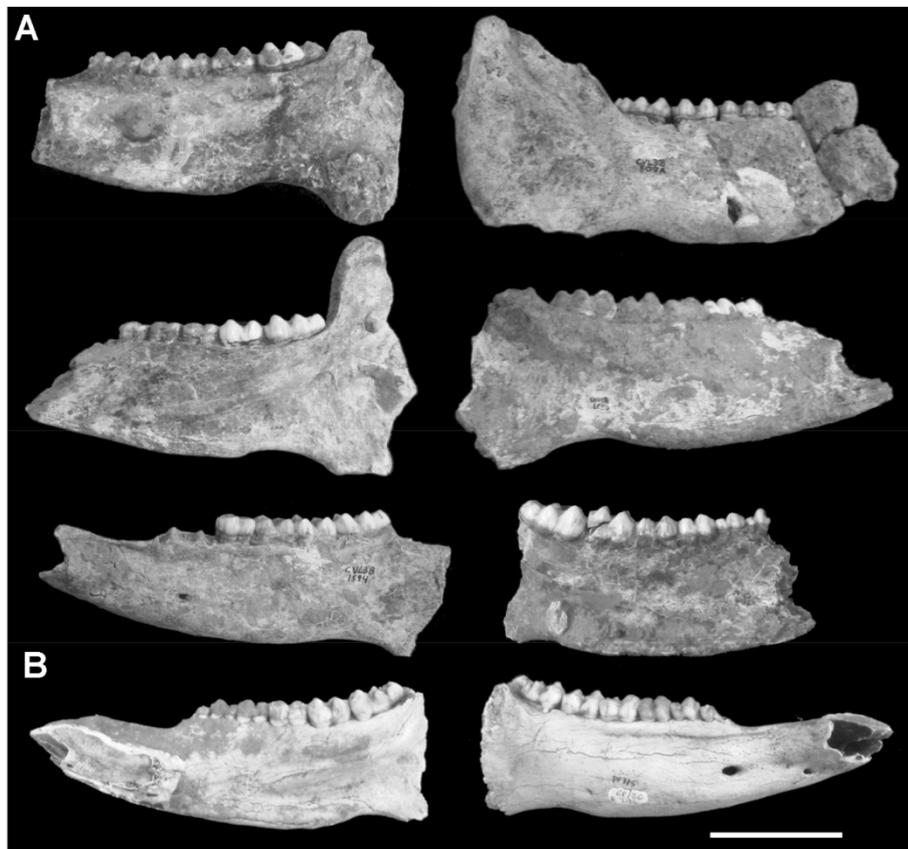
Fig. 8. - Dentaries of Tayassuidae. A) indeterminate Tayassuidae dentary from the Pleistocene of *Locus* 3. B) *Tayassu pecari* dentary of the Quaternary from Abismo Ponta de Flecha Cave. Scale 50 mm. Number of records: A) Side views; Right teeth; CVL3-2515 A, CVL3B-507 A, CVL3-2445, Left Tooth; CVL3B-2650, CVL3B-1594, CVL3-2055, B) Lingual and labial views; PF-335/GP2C-335 A.

preserved skulls from Cuvieri, it was not feasible to assign a genus for these specimens. The presence of regional variations in size in Tayassuidae was suggested by Gongorra et al. (2011), therefore, there is a possibility of these specimens representing large individuals of the genus *Tayassu*. The dentaries were not complete and had many breaks (Fig. 8) and, in several specimens, the dentition was broken or worn.

The genera *Brasiliochoerus* and *Tayassu* were considered as contemporaneous, as according to Dutra et al. (2017a) Pleistocene deposits with both species were reported. The *Tayassu pecari* is very well adapted to tropical and subtropical forests, but can also be found in arid regions, as long as they are close to water sources (Keuroghlian et al., 2012). However, regardless of their preference for forests, their presence cannot be considered a precise environmental indicator, due to the species being found in different environments. The *Brasiliochoerus stenocephalus* species would have inhabited dry or semi-arid environments such as the current *Parachoerus* (Gasparini et al., 2009).

6. Paleoenvironmental considerations

The assemblage described in *Locus* 3 of Cuvieri Cave was considered of Pleistocene age by Hubbe (2008), Mayer (2011), Mayer et al. (2016) based on the dates ranging from 31 ka BP and 12 ka BP (Hubbe, 2008). During this period, the paleoenvironment in Lagoa Santa changed from a humid and dense forest to dry savanna, at least more than once (Ledru, 1993; Ledru et al., 1996; Araujo et al., 2005; Barros et al., 2011; Sobral-Souza et al., 2015; Sobral-Souza and Lima-Ribeiro, 2017).

Our taphonomic observations support the previous hypothesis that the macrovertebrates were the result of individuals falling on *Locus* 3 and that there was little dispersion of the bone parts, with articulated specimens being observed. However it is important to emphasize the occurrence of few specimens presenting abrasion and breaks and given that they were in a cave environment, it is possible that the remobilization of individuals has occurred.

The study of the spatial distribution of osteological material carried out by Mayer (2011) for Cervidae and Tayassuidae in the *Locus* 3 deposit suggests that the two families were contemporary, as their remains were found at the same levels. There are also remains of typical animals of the extant fauna, including microvertebrates (reptiles, birds, amphibians, armadillos, and small rodents), a specimen of *Panthera onca* (Chahud and Okumura, 2021b), Tapiridae (Chahud et al., 2022), rabbits (Chahud et al., 2020; Chahud and Okumura, 2022) as well as large rodents (Chahud, 2020a), *Dasyprocta* and *Cuniculus paca*. Moreover, extinct Pleistocene biota such as the ground sloths (Hubbe, 2008) *Catonyx cuvieri* and *Valgipes bucklandii*, and *Cuniculus rugiceps* were also observed (Mayer et al., 2016)..

Most of the remains of *Cuniculus rugiceps* occur in the deeper levels of *Locus* 3 (Mayer, 2011) and, therefore, it is suggestive that *C. rugiceps* must be one of the oldest specimens found in Cuvieri Cave. Mayer (2011) suggested that the paleoecology of *C. rugiceps* would be similar to that of current *C. paca*, although *C. rugiceps* was supposed to be more sensitive to environmental changes. The current *Cuniculus paca* is a typical forest animal that lives near water courses and, considering that *C. rugiceps* had the same ecology, it is possible that in the period in which it lived, the region of Lagoa Santa could have been similar to that of the Atlantic Forest, which would have expanded during the Pleistocene and may even have had contact with the Amazon (Sobral-Souza et al., 2015; Sobral-Souza and Lima-Ribeiro, 2017).

The region where the Cuvieri Cave is located underwent several environmental changes during the Pleistocene. According to Ledru et al. (1996), during the period between 40 ka BP and 27 ka BP, the paleoenvironment of the state of Minas Gerais was composed of lowland forests, however Silva et al. (2004) extends this period to 21 ka AP. The presence of a wetter period and conditions similar to those of present-day Amazon may be reinforced by the presence of a specimen of *Dicotyles tajacu* indistinguishable of specimens from eastern Amazonia. This variety of *D. tajacu* are slightly larger than the collared peccaries

from Lagoa Santa do Holocene and are currently restricted to the Amazon region. The possibility that a large *D. tajacu* similar to the Amazonian ones inhabited Lagoa Santa may be indicative of a possible connection between the Atlantic Forest and Amazonian biomes, as Sobral-Souza et al. (2015) and Sobral-Souza and Lima-Ribeiro (2017) suggest that it occurred around 21 ka years.

According to Ab'Saber (1977), it was during the Pleistocene that a diagonal of dry vegetation was formed in South America, which would have separated the Amazon and the Atlantic Forest (Sobral-Souza and Lima-Ribeiro, 2017). According to Ledru (1993), this drier period may have occurred between 17 ka - 13 ka, when there was a significant drop in the amount of tree pollen in Minas Gerais state. A drier period could favor the presence of large animals, including the genus *Brasiliochoerus*. Such idea supports the hypothesis that the large indeterminate Tayassuidae specimens could belong to this genus. The hypothesis that *Brasiliochoerus* would be typical of drier climates, as proposed by Kerber and Oliveira (2008), Gasparini et al. (2009, 2010), Avilla et al. (2013) and Dutra et al. (2017a), would indicate that they would not have lived with specimens from more humid forests, such as the Amazonian variation of *Dicotyles tajacu*, and that the occurrence of both at the same levels would be the result of taphonomic processes.

The Pleistocene-Holocene boundary in the Lagoa Santa region was apparently marked by a wet period that would have started in the early Holocene (11,700–8200 BP) followed by a dry period that would have started in 8000 BP (Araujo et al., 2005). In this period, the Tayassuidae observed in the Pleistocene from Cuvieri Cave are no longer present and they were replaced by the living species observed in the region, *Dicotyles tajacu* of savanna and *Tayassu pecari*. However, the Cervidae diversity remained the same (Chahud et al., 2021; Chahud and Okumura, 2023), presenting few (if any) changes until the present.

The 14C-AMS dates obtained for the *Tapirus* of 12,390 ± 50 BP and 12,510 ± 70 BP for *Catonyx cuvieri* (Hubbe, 2008), suggest that this species would have inhabited the Lagoa Santa region at the end of the driest period and beginning of the wettest (Ledru, 1993). However, it is important to remark that these specimens were found in the more superior parts of the stratigraphy (Hubbe, 2008) and they could be the most recent animals of *Locus* 3.

7. Conclusions

The material found in *Locus* 3 of Cuvieri Cave comprises nine specimens of Cervidae with at least two species, *Mazama americana* and *Mazama* cf. *gouazoubira*, and 16 specimens of Tayassuidae, one individual of *Dicotyles tajacu* of similar size of those found in eastern Amazonia, and 15 individuals of a large indeterminate Tayassuidae.

The Cervidae of the genus *Mazama* are very common in the Neotropics and their presence in the Pleistocene had already been recognized in region, but there was never a concern in the differentiation of species living in Lagoa Santa. The largest Cervidae can be attributed to the species *Mazama americana* based on the size and shape of osteological material when compared to identified specimens (Chahud and Okumura, 2023). The other individuals have similar size to *Mazama gouazoubira*, a species observed in the present, however due to the existence of other *Mazama* species and the absence of a well-preserved skull does not reliably identify the species and, therefore, we chose to classify it as *Mazama* cf. *gouazoubira*.

The *Dicotyles tajacu* is similar to eastern Amazon specimens and larger than Holocene specimens from Lagoa Santa. The specimen may represent one of the last specimens of this lineage of *Dicotyles tajacu* that inhabited the Lagoa Santa region, being replaced by modern forms in the Late Pleistocene and Early Holocene (Chahud and Okumura, 2023).

The indeterminate Tayassuidae bone parts (dentaries, teeth, appendicular and axial bones) present a much greater size than the current *Tayassu pecari*, suggesting either the presence of a regional variation of *T. pecari* or that may these individuals represent the extinct Tayassuidae of the region, *Brasiliochoerus stenocephalus*. Unfortunately, given the

absence of a skull and a well-preserved dentition, it was not possible to further classify these specimens.

Bones proportionally larger than those of the genus *Tayassu* are characteristic of *Brasiliochoerus* or of the current *Parachoerus*, considered a Tayassuidae of dry and arid environments (Mayer and Wetzel, 1987; Gasparini et al., 2009, 2010; Avilla et al., 2013; Dutra et al., 2017b). The possibility of the indeterminate Tayassuidae from Cuvieri Cave belonging to any of these genera would be indicative of a drier period during the Pleistocene of Lagoa Santa.

CRediT authorship contribution statement

Artur Chahud: Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gisele Ferreira Figueiredo:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Mercedes Okumura:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2023.104195.

References

Ab'Saber, A.N., 1977. Os domínios morfoclimáticos na América do Sul: primeira aproximação. Geomorfologia, São Paulo, Brazil. Universidade de São Paulo, Instituto de Geografia 52, 1–21.

Acosta, L.E., Garbino, G.S.T., Gasparini, G.M., Dutra, R.P., 2020. Unraveling the nomenclatural puzzle of the collared and white-lipped peccaries (Mammalia, Cetartiodactyla, Tayassuidae). Zootaxa 4851 (1), 60–80. https://doi.org/10.11646/zootaxa.4851.1.2.

Araujo, A.G.M., Neves, W.A., Pilo, L., Atui, J.P., 2005. Holocene dryness and human occupation in Brazil during the "Archaic Gap. Quat. Res. 64, 298–307. https://doi.org/10.1016/j.yqres.2005.08.002.

Auler, A.S., Piló, L.B., Smart, P.L., Wang, X., Hoffmann, D., Richards, D.A., Edwards, R.L., Neves, W.A., Cheng, H., 2006. U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves. Palaeogeogr. Palaeoclimatol. Palaeoecol. 240, 508–522. https://doi.org/10.1016/j.palaeo.2006.03.002.

Avilla, L.S., Müller, L., Gasparini, G.M., Soibelzon, L., Absolon, B., Pêgo, F.B., Silva, R.C., Kinoshita, A., Figueiredo, A.M.G., Baffa, O., 2013. The northernmost record of *Catagonus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Cetartiodactyla) and its palaeoenvironmental and palaeobiogeographical significance. J. S. Am. Earth Sci. 42, 39–46. https://doi.org/10.1016/j.jsames.2012.10.001.

Badgley, C., 1986. Counting individuals in mammalian fossil assemblages from fluvial environments. Palaios 12 (3), 328–338. https://doi.org/10.2307/3514695.

Barros, L., Lavarini, C., Lima, L., Júnior, A., 2011. Synthesis of the late-quaternary palaeobioclimatic scenarios in Minas Gerais state/southeastern Brazil. Sociedade e Natureza 23, 371–386. https://doi.org/10.1590/S1982-45132011000300001.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4 (2), 150–162. https://doi.org/10.1017/S0094837300005820.

Berbert-Born, M., 2000. Carste de Lagoa Santa. In: Schobbenhaus, C., Campos, D.A., Queiroz, E.T., Winge, M., Berbert-Born, M. (Eds.), Sítios Geológicos e Paleontológicos do Brasil, vol. 16.

Cartelle, C., 1994. Tempo Passado. Mamíferos Do Pleistoceno Em Minas Gerais. Editora Palco: Acesita, Belo Horizonte, p. 132p.

Cartelle, C., 1999. Pleistocene mammals of the cerrado and caatinga of Brazil. In: Eisenberg, J.F., Redford, K.H. (Eds.), Mammals of the Neotropicals: the Central Neotropicals, vol. 3. University of Chicago Press, Chicago, pp. 27–46.

Chahud, A., 2005. Paleomastozoologia do Abismo Ponta da Flecha, Iporanga, SP. In: Congresso Latino-americano de Paleontologia de Vertebrados, Resumos. UFRJ, Rio de Janeiro, pp. 76–78.

Chahud, A., 2020a. Dasyproctidae e Cuniculidae (Cavioidea, Rodentia) do Pleistoceno da Gruta Cuvieri, Estado de Minas Gerais, Brasil. Bioterra 20 (1), 29–37.

Chahud, A., 2020b. Occurrence of the sabretooth cat *smilodon* (felidae, machairodontinae) in the cuvieri cave, eastern Brazil. Palaeontol. Electron. 23 (2), a24. https://doi.org/10.26879/1056.

Chahud, A., 2020c. Um exemplar muito jovem de *Mazama* sp. encontrado na Gruta Cuvieri, Região de Lagoa Santa, Estado de Minas Gerais, Brasil. Rev. Bras. Zoociencias 21 (1), 1–10. https://doi.org/10.34019/2596-3325.2020.v21.29276.

Chahud, A., 2021. Ocorrência de *Euphractus sexcinctus* Linnaeus, 1758 na Gruta Cuvieri, região de Lagoa Santa, MG, Brasil. Acta Biológica Catarinense 8 (3), 72–82. https://doi.org/10.21726/abc.v8i3.1528.

Chahud, A., 2022. *Cuniculus paca* Linnaeus, 1766 (Cuniculidae, Rodentia) no Holoceno da Gruta Cuvieri, Brasil. Revista de Biologia Neotropical/Journal of Neotropical Biology 19 (1), 1–8. https://doi.org/10.5216/rbn.v19i1.69286.

Chahud, A., Figueiredo, G.F., Mingatos, G.S., Okumura, M., 2021. Taxonomic analysis of the Quaternary archaeofauna found at the Lapa do Santo site, Lagoa Santa region, Brazil. J. Quat. Sci. 36, 1268–1278. https://doi.org/10.1002/jqs.3372.

Chahud, A., Costa, P.R.O., Figueiredo, G.F., Okumura, M., 2023. Quaternary ungulates of the Abismo Ponta de Flecha cave, Ribeira of Iguape valley, southeast Brazil: zooarchaeological and paleoenvironmental aspects. J. S. Am. Earth Sci. 121, 104107 https://doi.org/10.1016/j.jsames.2022.104107.

Chahud, A., Figueiredo, G.F., Okumura, M., 2022. Tapiridae (perissodactyla) in the late Pleistocene of the cuvieri cave, eastern Brazil. Hist. Biol. https://doi.org/10.1080/08912963.2022.2140422.

Chahud, A., Mingatos, G.S., Okumura, M., 2020. Leporidae Fischer, 1817 (Mammalia: Lagomorpha) de um depósito Quaternário do Brasil: comentários taxonômicos e tafonômicos. Boletim do Museu Paraense Emílio Goeldi. Cienc. Nat. 15 (3), 795–806. https://doi.org/10.46357/bcnaturais.v15i3.299.

Chahud, A., Okumura, M., 2021a. The presence of *Panthera onca* Linnaeus 1758 (felidae) in the Pleistocene of the region of Lagoa Santa, state of Minas Gerais, Brazil. Hist. Biol. 33 (10), 2496–2503. https://doi.org/10.1080/08912963.2020.1808975.

Chahud, A., Okumura, M., 2021b. The youngest Tapir of a quaternary deposit of the Americas. Hist. Biol. 33 (10), 2400–2405. https://doi.org/10.1080/08912963.2020.1798420.

Chahud, A., Okumura, M., 2022. Reavaliação dos materiais de Leporidae (Mammalia; Lagomorpha) do Quaternário da Gruta Cuvieri, Minas Gerais, Brasil. Acta Biol. Parana. 51 (1), 1–8. https://doi.org/10.5380/abp.v51i1.86907.

Chahud, A., Okumura, M., 2023. Cervidae and Tayassuidae from the Holocene deposits of the cuvieri cave, state of Minas Gerais, eastern Brazil; taxonomic and paleoenvironmental considerations. Hist. Biol. 35 (1), 74–83. https://doi.org/10.1080/08912963.2021.2022134.

Copetti, P.L., Gasparini, G.M., Pereira, J.C., Fontoura, E., Lopes, R.P., Kerber, L., 2021. A skull of the extinct tayassuid *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880) (Mammalia, Cetartiodactyla) from the Late Pleistocene of southern Brazil: morphology and taxonomy. Hist. Biol. 33 (9), 1898–1910. https://doi.org/10.1080/08912963.2020.1751837.

Desbiez, A.L.J., Keuroghlian, A., Beisiegel, B.M., Medici, E.P., Gatti, A., Pontes, A.R.M., Campos, C.B., Tófoli, C.F., Moraes Junior, E.A., Azevedo, F.C., Pinho, G.M., Cordeiro, J.L.P., Santos Júnior, T.S., Morais, A.A., Mangini, P.R., Flesher, K., Rodrigues, L.F., Almeida, L.B., 2012. Avaliação do risco de extinção do cateto *Pecari tajacu* Linnaeus, 1758, no Brasil. Biodiversidade Brasileira 1, 74–83.

Duarte, J.M.B., 1996. Guia de identificação de cervídeos brasileiros. Jaboticabal, FUNEP 14.

Duarte, J.M.B., González, S., Maldonado, J.E., 2008. The surprising evolutionary history of South American deer. Mol. Phylogenet. Evol. 49, 17–22. https://doi.org/10.1016/j.ympev.2008.07.009.

Duarte, J.M.B., Vogliotti, A., Zanetti, E.S., Oliveira, M.L., Tiepolo, L.M., Rodrigues, L.F., Almeida, L.B., 2012a. Avaliação do risco de extinção do veado-mateiro *Mazama americana* Erxleben, 1777, no Brasil. Biodiversidade Brasileira 1, 33–41.

Duarte, J.M.B., Vogliotti, A., Zanetti, E.S., Oliveira, M.L., Tiepolo, L.M., Rodrigues, L.F., Almeida, L.B., 2012b. Avaliação do risco de extinção do veado-mateiro-pequeno *Mazama bororo* Duarte, 1996, no Brasil. Biodiversidade Brasileira 1, 42–49.

Duarte, J.M.B., Vogliotti, A., Zanetti, E.S., Oliveira, M.L., Tiepolo, L.M., Rodrigues, L.F., Almeida, L.B., 2012c. Avaliação do risco de extinção do veado-catingueiro *Mazama gouazoubira* g. Fischer von Waldheim, 1814, no Brasil. Biodiversidade Brasileira 1, 50–58.

Duarte, J.M.B., Vogliotti, A., Zanetti, E.S., Oliveira, M.L., Tiepolo, L.M., Rodrigues, L.F., Almeida, L.B., 2012d. Avaliação do risco de extinção do veado-cambuta *Mazama nana* Hensel, 1872, no Brasil. Biodiversidade Brasileira 1, 59–67.

Dutra, R.P., de Melo Casali, D., Missagia, R.V., Gasparini, G.M., Perini, F.A., Cozzuol, M. A., 2017a. Phylogenetic systematics of peccaries (Tayassuidae: Artiodactyla) and a classification of South American tayassuids. J. Mamm. Evol. 24 (3), 345–358. https://doi.org/10.1007/s10914-016-9347-8.

Dutra, R.P., Missagia, R.V., Perini, F.A., Cozzuol, M.A., Gasparini, G.M., Guedes, P.G., Salles, L.D.O., 2017b. Fossil peccaries of Late Pleistocene/Holocene (Cetartiodactyla,

Tayassuidae) from underwater caves of Serra da Bodoquena (Mato Grosso do Sul State, Brazil). Hist. Biol. 29 (1), 85–92. https://doi.org/10.1080/08912963.2015.1125898.

Eltink, E., Castro, M., Montefeltro, F.C., Dantas, M.A.T., Scherer, C.S., de Oliveira, P.V., Langer, M.C., 2020. Mammalian fossils from Gruta do Ioiô cave and past of the Chapada Diamantina, northeastern Brazil, using taphonomy, radiocarbon dating and paleoecology. J. S. Am. Earth Sci. 98, 102379 https://doi.org/10.1016/j.jsames.2019.102379.

Ferreira Figueiredo, G., Chahud, A., Okumura, M., 2022. Taxonomia e Tafonomia dos remanescentes ósseos de ungulados da coleção Awá-Guajá do estado do Maranhão, Brasil. Revista Etnobiología 20 (2), 84–99.

Gasparini, G.M., 2013. Records and stratigraphic ranges of South American Tayassuidae (Mammalia, Artiodactyla). J. Mamm. Evol. 20 (1), 57–68. https://doi.org/10.1007/s10914-011-9172-z.

Gasparini, G.M., Ferrero, B., 2010. The Tayassuidae (Mammalia, Artiodactyla) from the quaternary of Entre rios province. A palaeofaunal review in Argentina. Neues Jahrbuch Geol. Palaontol. Abhand. 256, 151–160. https://doi.org/10.1127/0077-7749/2010/0040.

Gasparini, G.M., Ferrero, B., Vezzosi, R., Brunetto, E., 2011. El registro de *Tayassu pecari* (Link, 1795) (Artiodactyla, Tayassuidae) en El Pleistoceno Tardío de la provincia de Santa Fe, Argentina. Aspectos biogeográficos y de distribución de una especie em retracción. Rev. Mex. Ciencias Geol. 28 (2), 203–211.

Gasparini, G.M., Kerber, L., Oliveira, E., 2009. *Catagonus stenocephalus* (Lund in reinhardt, 1880) (Mammalia, Tayassuidae) in the Touro passo formation (late Pleistocene), rio grande do sul, Brazil. Taxonomic and palaeoenvironmental comments. Neues Jahrbuch Geol. Palaontol. Abhand. 254 (3), 261–273. https://doi.org/10.1127/0077-7749/2009/0016.

Gasparini, G.M., Rodriguez, S.G., Soibelzon, L.H., Beilinson, E., Soibelzon, E., Missagia, R.V., 2014. *Tayassu pecari* (Link, 1795) (Mammalia, Cetartiodactyla): comments on its South American fossil record, taxonomy and paleobiogeography. Hist. Biol. 26 (6), 785–800. https://doi.org/10.1080/08912963.2013.858247.

Gasparini, G.M., Soibelzon, E., Zurita, A.E., Miño-Boilini, A.R., 2010. A review of the quaternary Tayassuidae (Mammalia, Artiodactyla) from the Tarija valley, Bolivia. Alcheringa 34 (1), 7–20. https://doi.org/10.1080/03115510903277717.

Gasparini, G.M., Zurita, A.E., 2005. Primero registro fósil de *Tayassu pecari* (Link) (Mammalia, Artiodactyla) en la Argentina. Ameghiniana 42, 473–480.

Gongorra, J., Biondo, C., Cooper, J.D., Taber, A., Keuroghlian, A., Altrichter, M., Do Nascimento, F.F., Chong, A.Y., Miyaki, C.Y., Bodmer, R., Mayor, P., González, S., 2011. Revisiting the species status of *Pecari maximus* van Roosmalen et al., 2007 (Mammalia) from the Brazilian Amazon. Bonn zoological Bulletin 60 (1), 95–101.

González, S., Mantellatto, A.M.B., Duarte, J.M.B., 2018. Craniometrical differentiation of gray brocket deer species from Brazil. Rev. Mus. Argent. Ciencias Nat. Nueva Ser. 20, 179–193. https://doi.org/10.22179/REVMACN.20.561.

Grubb, P., Groves, C.P., 1996. Los Dicotylidae del Neotrópico (*Tayassu* and *Catagonus*). Taxonomía y Descripción. In: Plan de acción y evaluación de la condición actual de los pecaríes (Olivier WLR. NYZS-the Wildlife Conservation Society and UICN-SUR, pp. 1–5.

Guérin, C., Faure, M., 2009. Les Cervidae (Mammalia, Artiodactyla) du Pléistocène supérieur-Holocène ancien de la région du Parc National Serra da Capivara (Piauí, Brésil). Geobios 42 (2), 169–195. https://doi.org/10.1016/j.geobios.2008.06.004.

Haddad-Martim, P.M., Hubbe, A., Giannini, P.C.F., Auler, A.S., Piló, L.B., Hubbe, M., Mayer, E., Wang, X., Cheng, H., Edward, E.L., Neves, W.A., 2017. Quaternary depositional facies in cave entrances and their relation to landscape evolution: the example of Cuvieri Cave, eastern Brazil. Catena 157, 372–387. https://doi.org/10.1016/j.catena.2017.05.029.

Hubbe, A., 2008. Contextualização taxonômica, tafonômica e morfométrica dos remanescentes ósseos da megamastofauna da gruta Cuvieri (MG) um sitio paleontológico do pleistoceno tardio. In: Master Dissertation. Instituto de Biociências da USP. São Paulo.

Hubbe, A., Haddad-Martim, P.M., Hubbe, M., Mayer, E.L., Strauss, A., Auler, A.S., Pilo, L.B., Neves, W.A., 2011. Identification and importance of critical depositional gaps in pitfall cave environments: the fossiliferous deposit of Cuvieri Cave, eastern Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 312, 66–78. https://doi.org/10.1016/j.palaeo.2011.09.010.

Kerber, L., Oliveira, E.V., 2008. Fósseis de vertebrados da Formação Touro Passo (Pleistoceno Superior), Rio Grande do Sul, Brasil: atualização dos dados e novas contribuições. Gaea-Journal of Geoscience 4 (2), 49–64. https://doi.org/10.4013/gaea.20082.02.

Keuroghlian, A., Desbiez, A.L.J., Beisiegel, B.M., Medici, E.P., Gatti, A., Pontes, A.R.M., Campos, C.B., Tófoli, C.F., Moraes Junior, E.A., Azevedo, F.C., Pinho, G.M., Cordeiro, J.L.P., Santos Júnior, T.S., Morais, A.A., Mangini, P.R., Flesher, K., Rodrigues, L.F., Almeida, L.B., 2012. Avaliação do risco de extinção do queixada *Tayassu pecari* Link, 1795, no Brasil. Biodiversidade Brasileira 1, 84–102.

Keuroghlian, A., Eaton, D.P., Desbiez, A.L.J., 2009. The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian Pantanal. Int. J. Biodivers. Conserv. 1 (4), 87–97.

Keuroghlian, A., Eaton, D.P., Longland, W.S., 2004. Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biol. Conserv. 120, 411–425. https://doi.org/10.1016/j.biocon.2004.03.016.

Ledru, M.P., 1993. Late Quaternary environmental and climatic changes in central Brazil. Quat. Res. 39, 90–98. https://doi.org/10.1006/qres.1993.1011.

Ledru, M.P., Soares Braga, P.I., Soubie'S, F., Fournier, M., Martin, L., Suguio, K., Turcq, B., 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 123, 239–257. https://doi.org/10.1016/0031-0182(96)00105-8.

Leeuwenberg, F., Resende, S.L., 1994. Ecologia de cervídeos na Reserva Ecológica do IBGE/DF: manejo e densidade de populações. Cad. Geociencias 11, 89–95.

Loponte, D., Corriale, M.J., Mucciolo, L., Acosta, A., 2019. Sex and age-biased exploitation and metric characterization of medium-sized deer in the lower Paraná wetland, South America. Int. J. Osteoarchaeol. 29, 889–907. https://doi.org/10.1002/oa.2767.

Mayer, E.L., 2011. Processos de formação de um depósito fossilífero, um abismo na Gruta Cuvieri (MG): Taxonomia, Tafonomia e distribuição espacial. Master Dissertation. Instituto de Biociências, Universidade de São Paulo.

Mayer, E.L., Hubbe, A., Botha-Brink, J., Ribeiro, A.M., Haddad-Martim, P.M., Neves, W., 2020. Diagenetic changes on bone histology of Quaternary mammals from a tropical cave deposit in southeastern Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 537, 109372 https://doi.org/10.1016/j.palaeo.2019.109372.

Mayer, E.L., Hubbe, A., Kerber, L., Haddad-Martim, P., Neves, W., 2016. Taxonomic, biogeographic, and taphonomic reassessment of a large extinct species of paca from the Pleistocene of Brazil. Acta Palaeontol. Pol. 61 (4), 743–758. https://doi.org/10.4202/app.00236.2015.

Mayer, J.J., Wetzel, R.M., 1987. Tayassu pecari. Mamm. Species 293, 1–7. https://doi.org/10.2307/3503865.

Missagia, R.V., 2014. Taiassuídeos (Mammalia: Artiodactyla) do Quaternário da Região Intertropical Brasileira: morfometria cranial e implicações taxonômicas. In: Master Dissertation. Federal University of Minas Gerais (UFMG).

Missagia, R.V., Parisi-Dutra, R., Cozzuol, M.A., 2016. Morphometry of *Catagonus stenocephalus* (Lund in reinhardt 1880) (Artiodactyla: Tayassuidae) and taxonomical considerations about *catagonus* ameghino 1904. Lundiana. International Journal of Biodiversity 12 (1), 39–44.

Oliveira, P.V., Ribeiro, A.M., Viana, M.S.S., Holanda, E.C., 2014. Tayassuidae, Cervidae e Tapiridae da gruta do urso fóssil, Holoceno, parque nacional de Ubajara, Ceará, Brasil. Rev. Bras. Palaeontol. 17 (3), 417–434. https://doi.org/10.4072/rbp.2014.3.11.

Paula Couto, C., 1979. Tratado de Paleomastozoologia. Academia Brasileira de Ciências, Rio de Janeiro.

Paula Couto, C., 1981. On an extinct peccary from the Pleistocene of Minas Gerais. Iheringia Ser. Geol. 6, 75–78.

Roosmalen, M.G.M., Frenz, L., Van Hooft, P., De Iongh, H.H., Leirs, H., 2007. A new species of living peccary (Mammalia: Tayassuidae) from the Brazilian Amazon. Bonn. Zool. Beitrage 55, 105–112.

Rossi, R.V., 2000. Taxonomia de Mazama Rafinesque, 1817 do Brasil (Artiodactyla, Cervidae). In: Master Dissertation. Instituto de Biociências, Universidade de São Paulo.

Silva, A.C., Vidal-Torrado, P., Martinez Cortizas, A., Garcia Rodeja, E., 2004. Solos do topo da Serra São José (Minas Gerais) e suas relações com o paleoclima no sudeste do Brasil. Revista Brasileira de Ciências do Solo 28, 455–466. https://doi.org/10.1590/S0100-06832004000300007.

Sobral-Souza, T., Lima-Ribeiro, M.S., 2017. De volta ao passado: revisitando a história biogeográfica das florestas neotropicais úmidas. Oecologia Australis 21 (2), 93–107. https://doi.org/10.4257/oeco.2017.2102.01.

Sobral-Souza, T., Lima-Ribeiro, M.S., Solferini, V.N., 2015. Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. Evol. Ecol. 29 (5), 643–655. https://doi.org/10.1007/s10682-015-9780-9.

Souza, P., Ribeiro, M.G.F., Dutra, L.J., Mattos, K.D., Carvalho, N.D.C.D., Abidu-Figueiredo, M., Santos, A.L.Q., 2017. Osteología del miembro torácico de la corzuela parda *Mazama gouazoubira* (G. Fischer, 1814) (Cetartiodactyla: Cervidae). Int. J. Morphol. 35 (3), 1000–1009. https://doi.org/10.4067/S0717-95022017000300031.

Vogliotti, A., 2003. História natural de *Mazama bororo* (Artiodáctyla: Cervidae) através da etnozoología, monitoramento fotográfico e rádio-telemetria. Master Dissertation. Universidade de São Paulo, Piracicaba, Brazil.

Von den Driesch, A., 1976. A guide to the measurement of animal bones from archaeological sites: as developed by the Institut für Palaeoanatomie, vol. 1. Domestikationsforschung und Geschichte der Tiermedizin of the University of Munich, Peabody Museum Press, p. 136.

Woodburne, M.O., 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. J. Mamm. Evol. 17 (4), 245–264. https://doi.org/10.1007/s10914-010-9144-8.