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Quaternary ungulates of the Abismo Ponta de Flecha Cave, Ribeira of Iguape Valley, Southeast Brazil: Zooarchaeological and Paleoenvironmental aspects

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ABSTRACT

The Ribeira de Iguape Valley, located in the south of the state of São Paulo, presents a complex system of caves developed from Precambrian carbonate rocks. The presence of such karstic system favored the preservation of numerous fossilized remains of Quaternary mammals. The Abismo Ponta de Flecha Cave, located in the municipality of Iporanga, is a vertical cave divided into several lateral galleries with abundant vertebrate specimens. Among the most common are the ungulates, a clade of mammals characterized mainly by the presence of hooves, represented by the Holoarctic ungulates families Cervidae, Tayassuidae, Tapiridae, and the South American native ungulate Toxodontidae. The most common family in the deposit is Tayassuidae, with several individuals assigned to the species *Tayassu pecari*, *Dicotyles tajacu*, as well as an indeterminate large Tayassuidae. The Cervidae remains found in the cave have two species assigned to the genus *Mazama*; *M. americana* and *M. gouazoubira*. A specimen of the Tapiridae family, *Tapirus* sp., was also found. Only one species attributed to the extinct family Toxodontidae, *Toxodon platensis*, was recorded. Many specimens of Tayassuidae and Cervidae were subadults, and one individual of *Tayassu pecari* was very young. The origin of the specimens might be the result of the transport of individual bone parts, the death of accidently trapped animals as well as the disposal of such remains by human groups that inhabited the region in the past.

1. Introduction

The term Ungulate (*Ungulata* in Latin) is an informal denomination that groups placental mammals provided with a hoof. The origin of such group may have occurred during the Cretaceous, represented by a mandibular fragment of *Protougulatum* from Bug Creek Anthills, Montana (Sloan and Van Valen, 1965), but recent studies question this specimen as a true ungulate (Archibald et al., 2011). Ungulates are currently divided into the orders Perissodactyla, odd-toed ungulates, represented by Tapiridae (tapirs), Rhinocerotidae (rhinos), and Equidae (horses, zebras, and donkeys), and the Artiodactyla, even-toed ungulates, Tayassuidae (peccaries), Cervidae (deer), Suidae (pigs), Hippopotamidae (hippos), Camelidae (camels), Giraffidae (giraffes), Bovidae (cattle), Antilocapridae (antilocapra), Moschidae (musk deer), and Tragulidae (tragus). The Cetaceans (whales and dolphins) are also classified as even-toed ungulates based on evolutionary relationship, due to this clade is also called Cetartiodactyla (Cetaceae + Artiodactyla) (Spaulding et al., 2009).

The Ribeira de Iguape Valley has great potential for paleontological studies, given that it is a karstic region involving an extensive system of limestone caves. Many of these caves have revealed large numbers of fossils, but most of them have not been subject of such area of research. The first caves presenting Quaternary osteological material at the region were discovered still in the XIX century, revealing the presence of typical animals of the South American Pleistocene megafauna, such as extinct and actual terrestrial sloths and ungulates (Krone, 1898; Ameghino, 1907; Cardoso, 1914; Paula Couto, 1954, Paula Couto, 1973). Among the first works to describe remains of fossil ungulates in the Ribeira Valley region is that of Ameghino (1907) who reported the presence of Cervidae of the genus *Mazama* and Tayassuidae in the Monjolinho Cave.

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Paleontological research involving ungulates in the Ribeira Valley would happen only 70 years later with the work of Lino et al. (1979), who identified Cervidae, Tayassuidae and the extinct native ungulate *Toxodon platensis* in the Abismo do Fossil Cave. Later research in the region began to be common and several specimens of Cervidae, Tayassuidae, Equidae, Tapiridae, and *Toxodon* specimens were found in other caves (Paula Couto, 1979,1981; Sedor et al., 2004; Castro and Langer, 2011; Ghilardi et al., 2011).

The fossil materials from Abismo Ponta de Flecha Cave, a typical vertical cave of the region, had a preliminary taxonomic identification made by Barros-Barreto et al. (1982) and Chahud (2005), but the material was poorly described and only a few images were published. Besides the fossil and extant representatives of the Quaternary fauna found in the Abismo Ponta de Flecha Cave, bone cuts and archaeological artifacts were identified, which may suggest the contemporaneity of animals of the extinct fauna with human inhabitants. From these observations it was suggested that part of the bone concentration would originate from discards from ancient communities (Barros-Barreto et al., 1982).

Noting the lack of an accurate and detailed study of the ungulate fauna found in the Abismo Ponta de Flecha Cave the purpose of this contribution is to present comments on the taxonomy and origin of the bone material of Cervidae, Tayassuidae, Tapiridae, and Toxodontidae, adding information on the occurrence of these groups in South American Quaternary deposits.

2. Material and methods

The Abismo Ponta de Flecha Cave is located in Iporanga municipality, in the south of the state of São Paulo, southeastern Brazil (Fig. 1). The osteological material was collected between the years 1981 and 1982 and it consists of 1386 paleontological, and archaeological samples (Barros-Barreto et al., 1982).

The research in the Abismo Ponta de Flecha Cave consisted of the excavation of the sediments contained in its interior, its documentation, transport and preliminary treatment. The site was divided into 11 galleries, called “Jazidas”, which correspond to natural platforms. Numbers were giving to the materials in descending order, with the highest numbering in the deepest parts of the deposit. Each of the deposits was divided into concentrations and levels, with the purpose of systematizing and locating the material, or which traditional archaeological and paleontological techniques were used, adapted to the architecture of the cave (Barros-Barreto et al., 1982).

The specimens are deposited and cured at 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). The specimens received two valid numbering for the present study, the first being related to field collection with the acronym “PF-” and the second from the IGc-USP collection, “GP/2C-“”.

For taxonomic identification, specimens from the mastozoological and paleontological collections of the Museum of Zoology of the University of São Paulo, paleontological collection of the Cuvieri Cave, “Renato Kipnis” Reference Collection and the Guajá Collection, these three collections with known specimens of Cervidae, Tayassuidae and Tapiridae deposited at the Laboratory of Human Evolutionary Studies (LEEH).

The identification of specimens was made using the above-mentioned available specimens, as well as the works of Roth (1896), Duarte (1996), Vogliotti (2003), Gasparini and Zurita (2005), Mendonça (2007), Guérin and Faure (2009), Gasparini and Zurita (2005), Gasparini (2013), Gasparini et al. (2009, 2011, 2014), Desbiez et al. (2012), Duarte et al. (2012a, 2012b, 2012c, 2012d), Keuroghlian et al. (2012), Medici et al. (2012), Cozzuol et al. (2013), Cubas et al. (2014), Missagia (2014), Oliveira et al. (2014), Souza Junior et al. (2017), González et al. (2018), Loponte et al. (2019), Eltink et al. (2020) and Ferreira Figueiredo et al. (2022).

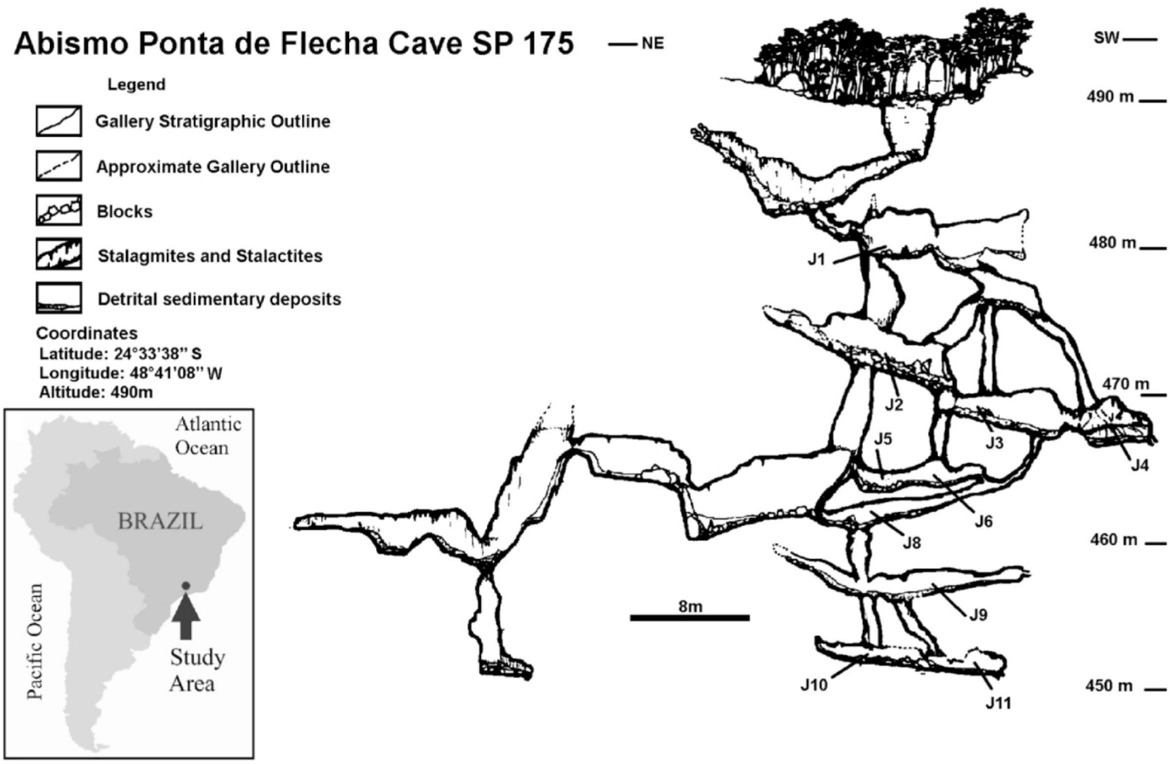

Fig. 1. Schematic profile of the Abismo Ponta de Flecha, SP 175. The location of the galleries (*Jazidas*, “J”) preserving osteological material (J1-J11) is indicated (Barros Barreto et al., 1982).

3. Geological context

The Abismo Ponta de Flecha Cave is a predominantly vertical cave located in an ancient polygonal depression with centripetal drainage (Karmann, 1994), formed in carbonate rocks from the Middle to Upper Proterozoic. The cave develops mainly along the N30-40 E and 70-80SE plane, coinciding with the main direction and valleys of the carbonate lens present in the Ribeira de Iguape Valley region (Barros-Barreto et al., 1982).

Sediment deposition occurs in a very irregular way both temporally and spatially, this characteristic is conditioned by its location, shape, entrance, by its internal morphology and by the nature of its sediment, which varies in all deposits (Barros-Barreto et al., 1982).

A dating using the AMS C14 technique was performed on specimens from Ribeira Valley, obtaining two ages for the same tooth of *Toxodon platensis*, PF-997/GP/2C-533 E, which showed evidence of human activity (Neves et al., 2007). The specimen had been previously dated from the Middle Holocene, a date of 6.700 ± 1300 BP was obtained from dentine and another of 5000 ± 1600 BP from dental enamel (ESR dating, Baffa et al., 2000), but two new C14 dates of bone collagen (11,380 ± 40 BP or 13,150–13,770 cal BP and 11,090 ± 40 BP or 12,900–13,180 cal BP) revealed that the specimen would have lived during the Pleistocene – Holocene boundary (Neves et al., 2007).

4. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Cervidae Goldfuss, 1820
Genus *Mazama Rafinesque*, 1817

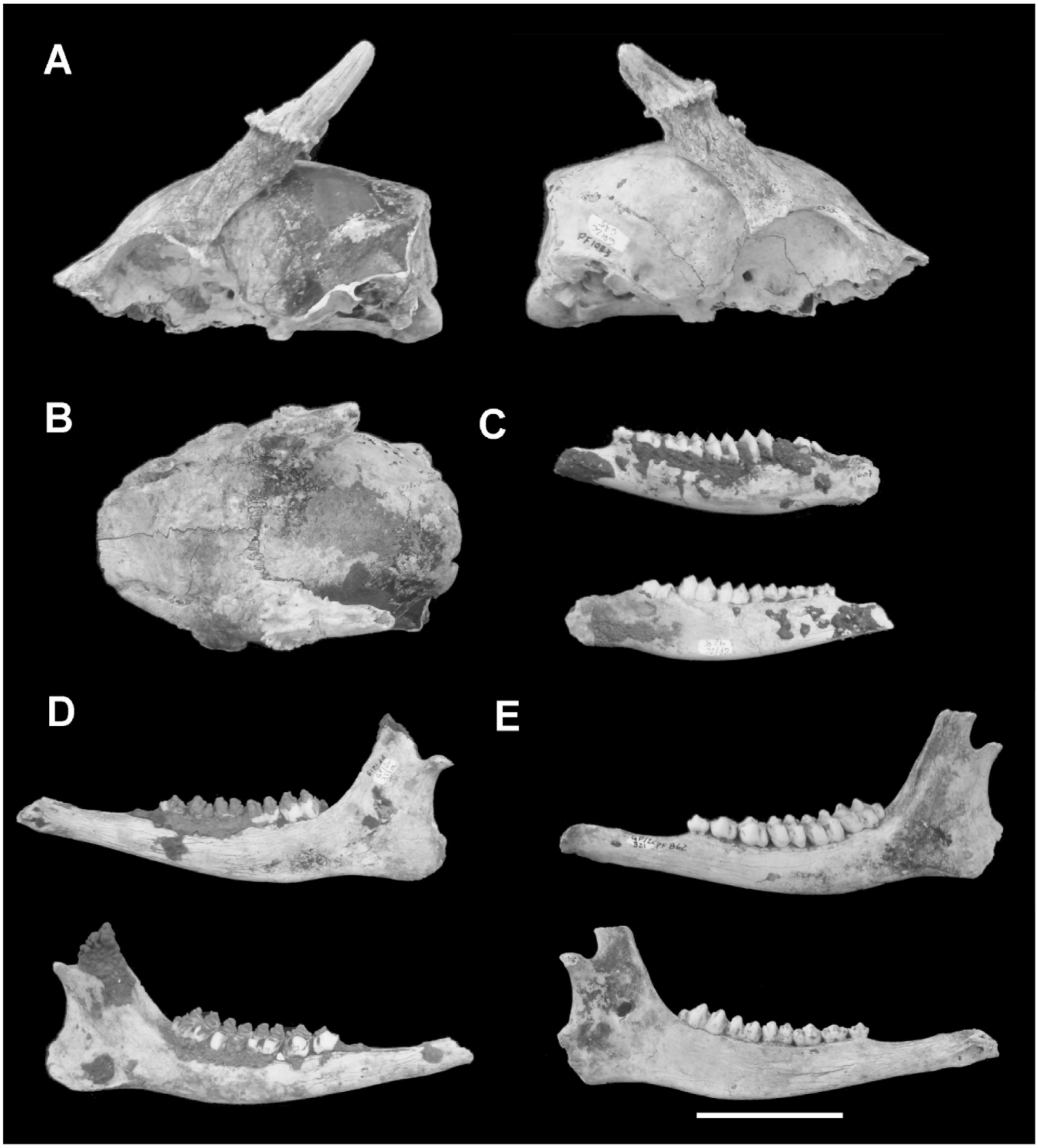

Fig. 2. Bone parts of *Mazama americana*. A-B) Skull of a young individual. (PF-1023/GP/2C-635) A) side views, B) superior view; C) subadult dentary (PF-607/GP/2C-428); D-E) right (PF-1213/GP/2C-313 A) and left (PF-862/GP/2C-321) dentaries of adults. Scale 50 mm.

Fig. 3. Appendicular bones of Cervidae from the Abismo Ponta de Flecha Cave. A) Lateral view of the right humerus of *Mazama americana*, larger (PF-1185/GP/2C-310 and PF-598/GP/2C–370C), and lateral view of the right humerus of *M. gouazoubira*, smaller (PF-1279/GP/2C–311 B). B) Radius of *M. americana*, subadult (PF-860/GP/2C–369 B) and adult (PF-642/GP/2C-436 A). C) Dorsal and palmar views of left metacarpal of *M. americana* (PF-717/GP/2C-435 A). D) Front and back views of the right femur of *M americana* (PF-719-749/GP/2C-368 EC) and femur of *M. gouazoubira* (PF-1089/GP/2C–370 B). E) Posterior views of subadult (PF-605/GP/2C-370 E) and adult (PF-984/GP/2C-370 A) *M. americana* right tibiae. F) Dorsal views of left metatarsals of *Mazama americana* (PF-641/GP/2C-436c) and right *M. gouazoubira* (PF-1338/GP/2C–562 B) Scale 50 mm.

Figs. 2 and 3

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Material and number of individuals: The osteological material belongs to at least five individuals of two species of the genus *Mazama*, *Mazama gouazoubira* and *Mazama americana* (Figs. 2 and 3). Most of the material belonging to the species *M. americana*.

The material used for taxonomic identification included cranial bones, mandibles and large appendicular bones (femora, humeri, radii, ulnae, tibiae, metapodials), since these are easily recognizable and were in a better state of preservation. The main specimens analyzed included a *Mazama americana* skull (PF-1023/GP/2C-635), a subadult *M. americana* dentary (PF-607/GP/2C-428), two adult *M. americana* dentaries (PF-1213/GP/2C-313 A and PF-862/GP/2C-321), two *M. americana* humeri (PF-1185/GP/2C-310 and PF-598/GP/2C–370C), one *M. gouazoubira* humerus (PF-1279/GP/2C–311 B), two *M. americana* radii (PF-860/GP/2C–369 B and PF-642/GP/2C-436 A), one *M. americana* metacarpal (PF-717/GP/2C-435 A), one *M. americana* right femur (PF-719-749/GP/2C-368 EC), a femur of *M. gouazoubira* (PF-1089/GP2C–370 B), two tibiae of *M. americana* (PF-605/GP/2C-370 E and PF-984/GP/2C-370 A), a metatarsal of *M. americana* (PF-641/GP/2C-436c) and a metatarsal of *M. gouazoubira* (PF-1338/GP/2C–562 B).

Other bones, like calcanei, astragali, phalanges, vertebrae, and fragmented ribs that can be attributed to Cervidae but a more specific classification could not be done.

Geographic distribution and age: Cervidae endemic to the Neotropical Americas. The *Mazama* genus presents the oldest record at the beginning of the Pleistocene in El Salvador (Cisneros, 2005).

Remarks: The Cervidae material can be assigned to the genus *Mazama*, based on the proportion and morphology of the appendicular bones, the skull, jaw, teeth, and cranial fragments (Figs. 2 and 3) (Guérin and Faure, 2009; Chahud and Okumura, 2022). Altogether, the presence of two species could be recognized, with the larger specimens being attributed to *Mazama americana* Erxleben, 1777 (Chahud and Okumura, 2022) and a smaller one that can be attributed to *M. gouazoubira* Fischer, 1814 (Guérin and Faure, 2009; Chahud and Okumura, 2022). In addition to the identified species, the presence of other species is not ruled out, as at least two other species, *M. nana* and *M. bororo*, inhabited the region.

From the anatomy of the bones, it was possible to determine that the species with the greatest amount of osteological material identified is *Mazama americana* with 26 bones attributed to at least three individuals. The specimen with the greatest amount of bone parts belonged to a subadult individual (Fig. 3B and E) with deciduous dentition still present (Fig. 2C).

Two other identified specimens are represented by at least two individuals with proportions equivalent to adult specimens. One of the specimens had a dentary with a much worn dentition, indicating an older adult (Fig. 2D). The osteological material was found in several levels and galleries, suggesting that these bones were much remobilized and that the possibility of several individuals being present should not be ruled out.

The PF-1073/GP/2C-635 skull (Fig. 2A and B) did not preserve the maxilla and the frontal part and proportions are inferior to those of an adult *Mazama americana*, however the antlers are indistinguishable from that of a juvenile, which can be attributed to this species. The skull also differs from *Mazama gouazoubira, M. nana*, and *M. bororo*.

In the humerus PF-1279/GP/2C–311 B it is possible to see the difference between this specimen and the two larger ones of *Mazama americana* in the lateral view (Fig. 3A). This difference is compatible between what is known to the species *M. americana* Erxleben, 1777 and *M. gouazoubira* Fischer, 1814 (Guérin and Faure, 2009; Chahud and Okumura, 2022).

The PF-1089/GP/2C–370 B femur (Fig. 3E) presents a width and length of the distal part (approximately 34 mm) compatible with that of a large adult *Mazama gouazoubira* Fischer, 1814 (Loponte et al., 2019), therefore, we attributed this bone to this species.

The PF-641/GP/2C–436C metatarsal(Fig. 3F) is much more robust than that of *Mazama gouazoubira* of similar size, however it is shorter than that of *M. americana* and *M. bororo*, but both distal and proximal parts (22.4 mm and approximately 24 mm, respectively) are larger than that of an *M. bororo* (21.34 and 22.87, respectively) and can be attributed to a young or small *M. americana*.

The species *Mazama nana* and *M. bororo* are smaller and comparable in size to *M. gouazoubira* adults and could be related to part of the osteological material found, but no diagnostic features were observed that characterized either of these species.

Discussion: The Cervidae found in the Abismo Ponta de Flecha Cave are represented by two typical Holocene species from southeastern Brazil, *Mazama americana*, presenting greater size and robusticity and *Mazama gouazoubira*, and were found with specimens of various ages.

The species of the genus *Mazama* can present differences in habitat, size and weight, and *M. americana* is the largest of the genus. This species weighs an average of 30 kg (it can reach 65 kg), presenting an average of 70 cm in height and length that varies from 90 to 145 cm (Duarte et al., 2012a). It occurs in almost the entire Neotropical region, being present from southern Mexico to northern Argentina, and in all Brazilian biomes. This species lives both in forested areas and in savannas, as long as they are close to water bodies (Duarte et al., 2012a).

The adult individuals of *Mazama gouazoubira* weight approximately 18 kg (rarely more than 20 kg), presenting an average height of 50 cm and length between 80 and 105 cm. The small deer *Mazama gouazoubira* is the most abundant species in South America, found in almost all Brazilian biomes. The species is present in various types of habitats from dense forests to open savannah areas associated with small forest patches, indicating easy adaptation to different environments. It prefers transitional areas between the forest and the grasslands (Vogliotti, 2003; Duarte et al., 2012c).

Despite the mentioned species being the most common in the Ribeira Valley region, two other species have already been recorded and, despite not having been recognized in the material described here, their presence in the deposits cannot be completely ruled out. The *Mazama bororo* species has an average weight of 25 kg and a height of about 50 cm, it is an endemic species from the states of São Paulo and Paraná and is restricted to the ombrophilous forest. The species *Mazama nana* is the smallest existing species of the genus *Mazama*, weighing 15 kg and 45 cm in height (Duarte, 1996; Duarte et al., 2012b, 2012d) and apparently can be found in more varied environments than *M. bororo* and *M. americana*, but little is known about its species, including its original geographic distribution (Duarte and Reis, 2012).

The specimens of *Mazama americana* observed in the Ribeira Valley are slightly smaller than the largest one recorded in the Holocene of the Lagoa Santa region, identified by Chahud and Okumura (2022). This difference may be related to the regional variation that exists in the species (Varela et al., 2010 and Cifuentes-Rincón et al., 2020).

Suborder Suiformes Jaeckel, 1911.
Infraorder Suoidea Gray, 1821
Family Tayassuidae Palmer, 1897
Genus *Tayassu* Fischer von Waldheim, 1814.
Tayassu pecari (Link, 1795).
Figs. 4 and 5.

Material and number of individuals: The *Tayassu pecari* are represented by six individuals, one of which is very young, presenting bones scattered through several galleries of the Abismo Ponta de Flecha Cave. One of the specimens was found articulated (Barros-Barreto et al., 1982) presenting most of the bones well preserved (PF-310 – PF-424/GP/2C-43).

Complete or fragmented mandibles (PF-728-878-727/GP-2C-301ABC, PF-17/GP/2C-637, PF-1367/GP/2C–612 B, PF-164-173/GP/2C-631), frontal part of skull (PF-3/GP/2C-610), left dentary (PF-880/GP/2C-301D), dentary (PF-1366/GP/2C-612 A), right dentary from a very young individual (PF-657/GP/2C-438 A), three humeri (PF-718/GP/2C–369C, PF-858/GP/2C–436 B and PF-1/GP/2C-569 A), one tibia (PF-859/GP/2C–429C), two radioulnae (PF-720/GP/2C-429D and PF-5/GP/2C–569C) and an articulated humerus and radioulna (PF-7/GP2C–569 B–623C). Other bones like calcanei, astragali, phalanges, vertebrae, and fragmented ribs that can be attributed to Tayassuidae were observed but could not have specific classification.

Geographic distribution: The species is found in the tropical regions of Central and South America. The range extends from the Yucatán Peninsula to state of Rio Grande do Sul in Brazil and northeastern of Argentina (Keuroghlian et al., 2012).

Remarks: The specimens attributed to *Tayassu pecari* are the most abundant among the macrovertebrates found in the Abismo Ponta de Flecha Cave and presented the greatest age range between the observed specimens. The identification is based on the cranial material, teeth, mandibles (Figs. 4A and 5and supplementary material) and on the length and width of the bones, as they are similar in size to those found in current specimens attributed to this species.

Four specimens are adults of similar size, with little variation, and at least two specimens had not yet reached adulthood, one very young with deciduous dentition (Fig. 4G) and a subadult with a size close to that of an adult, but with the epiphyses unfused (Fig. 5A, C, 5E).

At least four specimens had several bone parts preserved, such as mandibles, maxillary and associated appendicular bones, indicating that most of these specimens probably fell and died as a result of these accidental falls.

The most remarkable specimen was found in J6, an individual with more than 110 bones (PF-310-424/GP/2C-43) found articulated and with most of the osteological material preserved (supplementary material). The presence of this specimen in this cave position is mysterious, as it was the only macrovertebrate found at that level (only an isolated *Toxodon* tooth, shells, and few microvertebrate bones were found in J6) and access to that part of the cave is difficult. Probably in an attempt to find a way out, the individual was trapped in J6 and perished there.

Another outstanding specimen was found in J1, near the cave entrance and with a great part of the bones presenting carbonate incrustations (Fig. 4A, B, 5B, 5F, 5G). Together with another specimen found in J11, they are among the largest specimens of *Tayassu pecari* of the Abismo Ponta de Flecha cave.

The specimen found in J1 presents an almost complete mandible (Fig. 4A and B) where it was observed a tooth agenesis with the absence of the right p1, which apparently never developed. Absence of premolars have already been observed in mammals and usually on both sides of the mandible, but the reason in Tayassuidae is unknown and may be related to the tooth developmental pattern of the specimen.

Initially, we assumed that the very young specimen (Fig. 4G)preserved only the right dentary, but it is possible that some small, very fragmented, indeterminate appendicular bones may belong to this individual. The presence of very young specimens is very rare in Brazilian deposits and so far have only been recorded in Cervidae (Chahud, 2020) and Tapiridae (Chahud and Okumura, 2021), this being specimen probably the youngest Tayassuidae specimen found in a Quaternary deposit in the Americas.

Genus *Dicotyles* Cuvier, 1816
Dicotyles tajacu (Linnaeus, 1758).
Figs. 5 and 6B-6D.

Material and number of individuals: The species is represented by at least two individuals. The bone material corresponds to a complete skull, cranial fragments, mandibles, maxilla and several axial and appendicular bone parts.

Among the specimens are two right dentaries (PF-861/GP/2C–436C, PF-726/GP/2C-322), left dentary (PF-636/GP/2C430B), fragment of dentary (PF-881/GP/2C-471) and skull (PF-1071/GP/2C-636 A). The appendicular bones analyzed included fragments of a femur (PF-731/GP/2C346A), a tibia (PF-724/GP/2C282C), a humerus (PF-716/GP/2C–346 B) and a radioulna (PF-723/GP2C–435 B).

Geographic distribution: Currently occur from the south of the United States, passing through Central America to the north of Argentina, not inhabiting high altitude regions, including the Andes (Desbiez et al., 2012).

Zoological nomenclature: Problems involving the classification of this species have always been a reason for discussion, but Acosta et al. (2020) considered the genus *Dicotyles* to be the only valid genus for the species. We agree with the classification of Acosta et al. (2020) and will use it in the present study, however we emphasize that the genus *Pecari* has been the most used in recent years and, until the present work, was still recognized by the International Commission on Zoological Nomenclature (ICZN).

Remarks: The specimens recovered from Abismo Ponta de Flecha

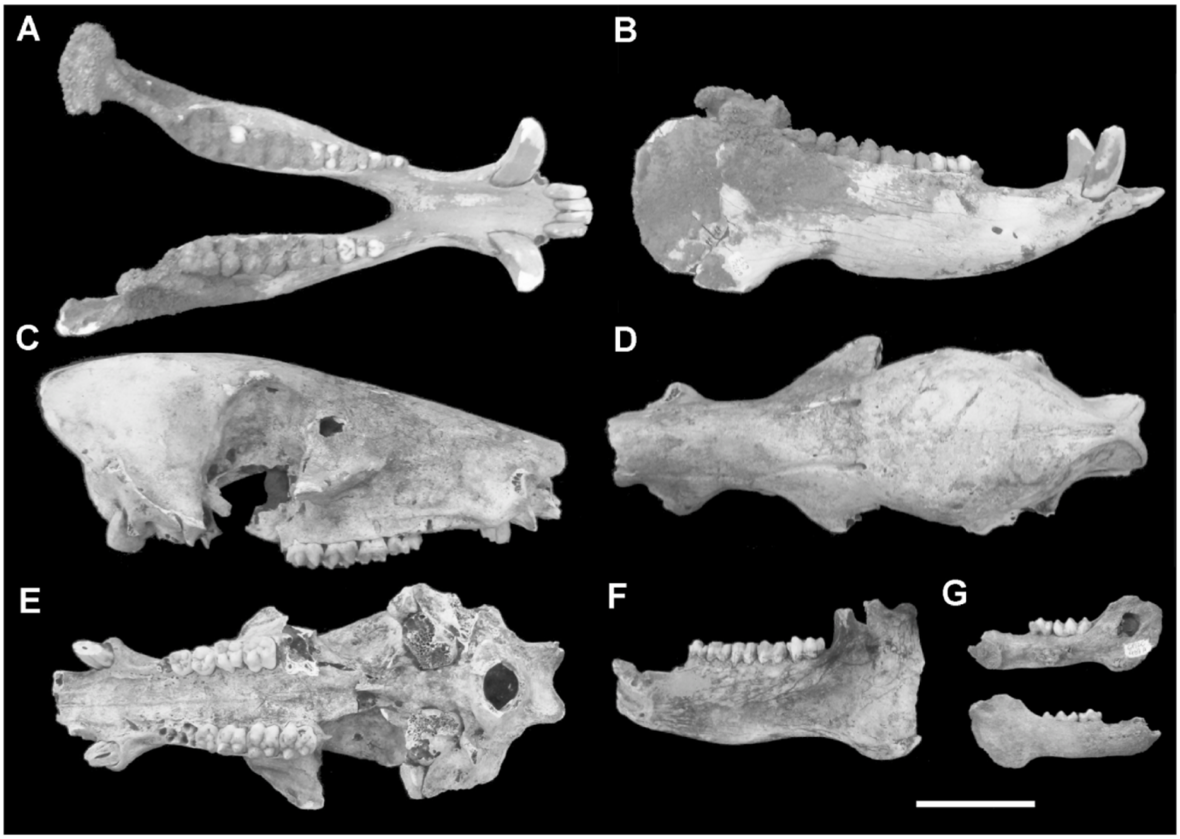

Fig. 4. Mandibles and skull of Tayassuidae. A-B) Occlusal and lateral views of the mandible of *Tayassu pecari* (PF-17/GP/2C-637). C-E) Skull of *Dicotyles tajacu* (PF-1071/GP/2C-636 A). F) Internal lateral view of the left dentary of *Dicotyles tajacu* (PF-636/GP/2C–430 B). G) Lateral view of the right dentary of a very young *Tayassu pecari* (PF-657/GP/2C-438 A). Scale: 50 mm.

Cave can be properly assigned to the species *Dicotyles tajacu*. The length and width of the postcranial bones are indistinguishable from those of current specimens found in the southeastern region of Brazil and also from subfossil specimens from the Holocene of Lagoa Santa, Minas Gerais state (Chahud and Okumura, 2022), a Brazilian region that recorded the species' presence between 5000 and 6000 years BP and also in the Pleistocene-Holocene boundary.

Although the specimens here described are similar in size to the current ones in the region, we emphasize that the species presents a great regional morphological variation, although no important differences are observed in genetic studies (Gongorra et al., 2011).

The PF-726/GP/2C-322 dentary (Fig. 4F) has numerous surface cracks indicating exposure to environmental changes in temperature and humidity, as observed in specimens studied by Behrensmeyer (1978), suggesting that such bone part may have been transported disarticulated to the Abismo Ponta de Flecha Cave. The same was observed in an isolated radioulna (Fig. 5D). The PF-1071/GP/2C-636 skull (Fig. 4C–E) has few exposure cracks, however, a large amount of sediment found in the endocranium suggests that the specimen was buried quickly after death.

All bones here described belong to adult individuals and some of them present marks, mainly from physical transport, suggesting an intense remobilization of materials. In addition, it was noted in a few specimens that some marks can be interpreted as the result of predation.

Tayassuidae indeterminate.

Material and number of individuals: The specimens are represented by two individuals, represented by two radioulnae (PF-1152/GP/2C-347 A and PF-1280/GP/2C-311 A), a femur (PF-1359/GP/2C-623 A), and fractured bones.

Remarks: Represented by some fragmented appendicular bones and two right radioulnae of two adult individuals (Fig. 6), the specimens represent a large and unknown species of Tayassuidae.

The specimen is larger than *Tayassu pecari*, the largest living species of Tayassuidae in Brazil, and comparisons with bones of this species

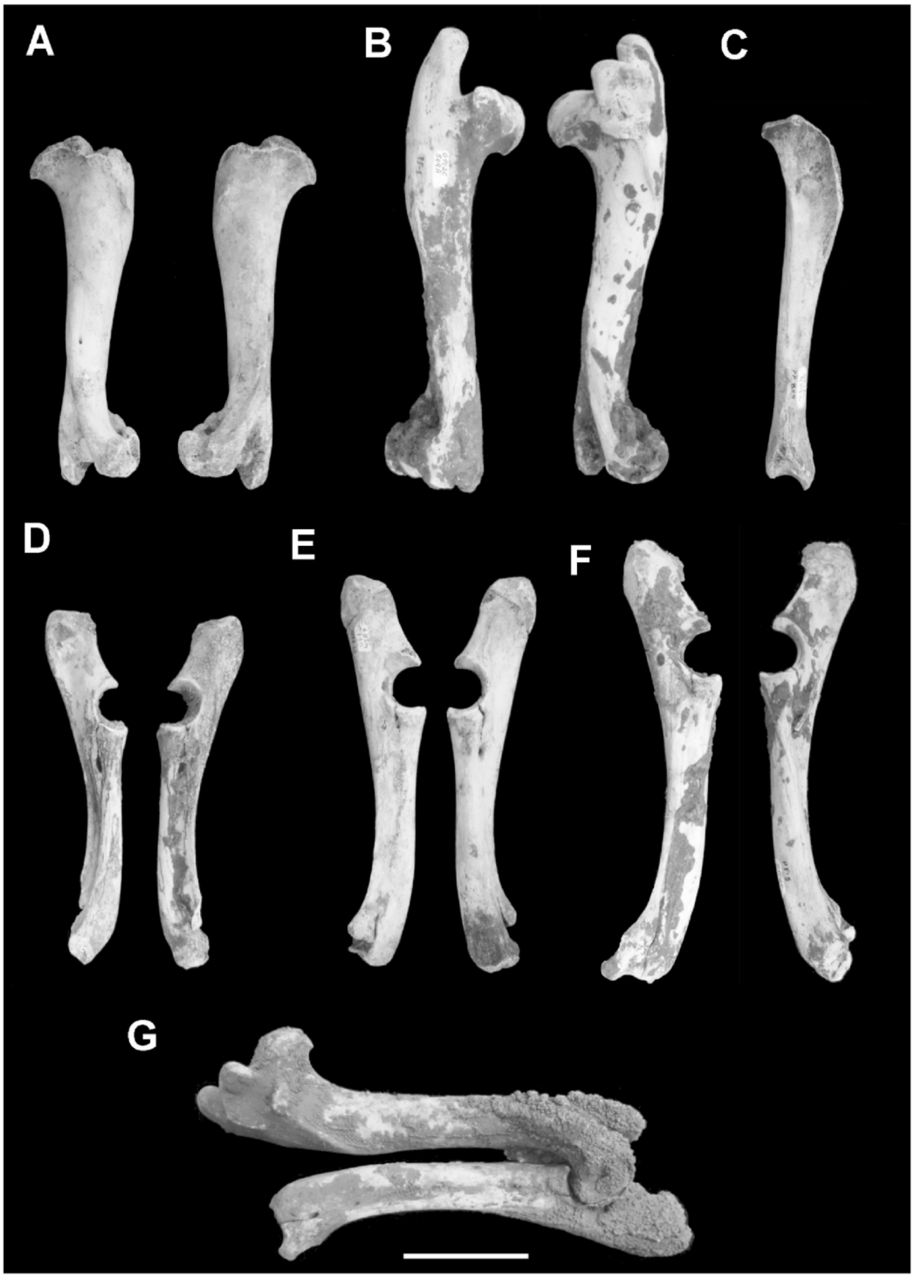

Fig. 5. Appendicular bones of Tayassuidae. A) Lateral views of the right (PF-718/GP/2C–369C) and left (PF-858/GP/2C–436 B) humeri of a subadult Tayassu pecari. B) Lateral views of the humerus (PF-1/GP/2C-569 A) of an adult *T. pecari*. C) Lateral view of the tibia (PF-859/GP/2C–429C) of subadult *T. pecari*. D) Lateral views of the left radioulna (PF-723/GP/2C–435 B) of Dicotyles tajacu. E) Lateral views of the left radioulna (PF-720/GP/2C-429D) of subadult *T. pecari*. F) Lateral views of the left radioulna (PF-5/GP/2C–569C) of adult *T. pecari*. G) Articulated humerus and radioulna (PF-7/GP/2C–569 B–623C) of *T. pecari*. Scale 50 mm.

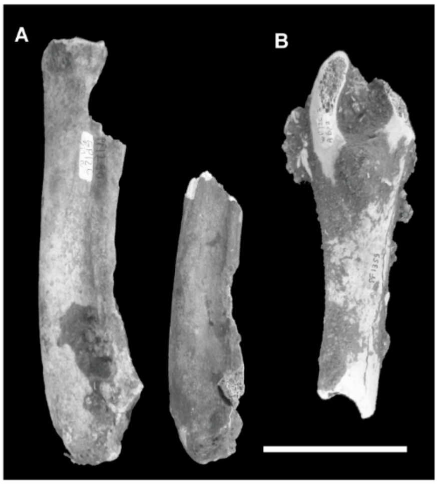

Fig. 6. Bone parts of indeterminate Tayassuidae. A) Lateral views of the left radioulnae (PF-1280/GP/2C-311 A and PF-1152/GP/2C-347 A). B) Fragmented left femur (PF-1359/GP/2C-623 A). Scale 50 mm.

show that this specimen is much larger.

Discussion of Tayassuidae: The specimens attributed to the living species, *Tayassu pecari* and *Dicotyles tajacu*, represent individuals of different ontogenetic stages. Both species are currently common in the region of Ribeira de Iguape Valley as well as in the Brazilian territory in general.

The *Dicotyles tajacu* are the smallest living tayassuids measuring approximately 90 cm and weighing from 15 to 28 kg. They live in a wide diversity of habitats, from dry and humid tropical forests, to desert regions. Its temperature tolerance is also great, supporting a variation from 0 °C to over 45 °C (Keuroghlian et al., 2004, 2012; Cubas et al., 2014).

The *Tayassu pecari* are larger than *Dicotyles tajacu*, measuring an average of 110 cm in length and an average weight between 30 and 50 kg. They live in a wide variety of habitats, being found from forests to savannah regions, always close to water courses and making use of a large area for foraging (Cubas et al., 2014).

The presence of individuals with indistinguishable characteristics from the current ones suggests that the specimens from the Abismo Ponta de Flecha Cave must not have lived in environments different from the current ones, or that they could be recent.

The few bones attributed to an undetermined Tayassuidae could be a representative of an extinct species. A Late Pleistocene species identified as *Brasiliochoerus stenocephalus* (or *Catagonus stenocephalus*) would have been larger than the living Tayassuidae (Cartelle et al., 1999), but variation in the size of species of this family can be observed in living species (Gongorra et al., 2011) and therefore, the possibility that these specimens belong to current large-sized species cannot be ruled out. However, this much larger dimension, not observed in current specimens from the region, may represent that the specimens are not recent or that they have lived in a different environment allowing for larger individuals.

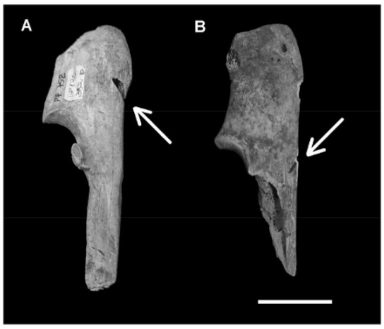

Fig. 7. Ulnae of Cervidae with cut marks. A) PF-752/GP/2C-473 and B) PF-1059/GP/2C–469 B. Arrow indicates the cut mark. Scale 50 mm.

5. Evidence of human activity in cervidae and tayassuidae

Human activities in animal bones found at the Abismo Ponta de Flecha cave were previously described by Barros-Barreto et al. (1982). The Cervidae specimens analyzed by Barros-Barreto et al. (1982) are illustrated in Fig. 3A, D, and 3F (the latter is a *Mazama americana*), and a detailed analysis revealed that no marks could be safely be attributed to human activity. The Tayassuidae specimen is represented by a small distal fragment of humerus that, due to abrasion and rounding, was not possible to find cut marks.

The only materials in which cuts could be identified were in two cervid ulnae, PF-752/GP/2C-473 and PF-1059/GP/2C–469 B (Fig. 7). In both bones, cut marks are located in the proximal epiphysis and diaphysis. In the epiphysis of PF-752/GP/2C-473, the incision is deep, starting from the external side of the bone, while in the ulna PF-1059/GP/2C–469 B there is a group of parallel, elongated and V-shaped section marks in the central part of the epiphysis. In the diaphysis of PF-752/GP/2C-473, it is possible to observe impact marks that are elongated and parallel and superimposed on each other, suggesting repetitive movements. In the diaphysis of PF-1059/GP/2C–469 B, there is a single incision that is elongated, transversally oriented, has a V-shaped section, and presents flaking at the edge of the incision. In both bones we suggest that the purpose of the cuts was a possible attempt to extract meat from the bones, in ulna PF-752/GP/2C-473 by a dynamic percussion process and in ulna PF-1059/GP/2C–469 B by a slicing process (Lyman, 1994).

It is important to note that specimens presenting numerous cut marks according to Barros-Barreto et al. (1982), as well as the arrowhead that gave the cave its name were not analyzed in this article.

Order Perissodactyla Owen, 1848
Family Tapiridae Burnett, 1830
Genus *Tapirus* Brisson, 1762
Tapirus sp.
Fig. 8

Material and number of individuals: The material attributed to the genus consists of a fragment of the tibia (PF-1137GP/2C-524) that belonged to an adult individual.

Geographic distribution: Currently, the genus *Tapirus* is typical of tropical regions in the Americas and had its original geographical distribution from the southern United States (Florida and California) to northern Argentina and Uruguay and may have reached the south of the Rio da Plata at the beginning of the Pleistocene (Hulbert Jr., 2010;

Table 1
Comparison of the specimen PF-1137GP/2C-524 from the Abismo Ponta de Flecha Cave with recent specimens of Tapirus terrestris (16 specimens of HOLANDA, 2011 and two specimens from the CRK reference collection). Measurements are in millimeters.

	Abismo Ponta de Flecha Cave PF-1137GP/2C-524	Range of recent *Tapirus terrestris* (N = 18)
Mediolateral diameter of the body	29.2	23.2–28.7
Mediolateral diameter of distal portion	53.1	44.9–53.0
Craniocaudal diameter of distal portion;	40.2	35.8–45.0
Mediolateral diameter of distal articular surface	46.5	34.3–46.8

Fig. 8. Tapiridae specimen PF-1137/GP/2C-524 (dark color) compared to a current specimen (white color). Scale 50 mm. Dorsal view and cranial view.

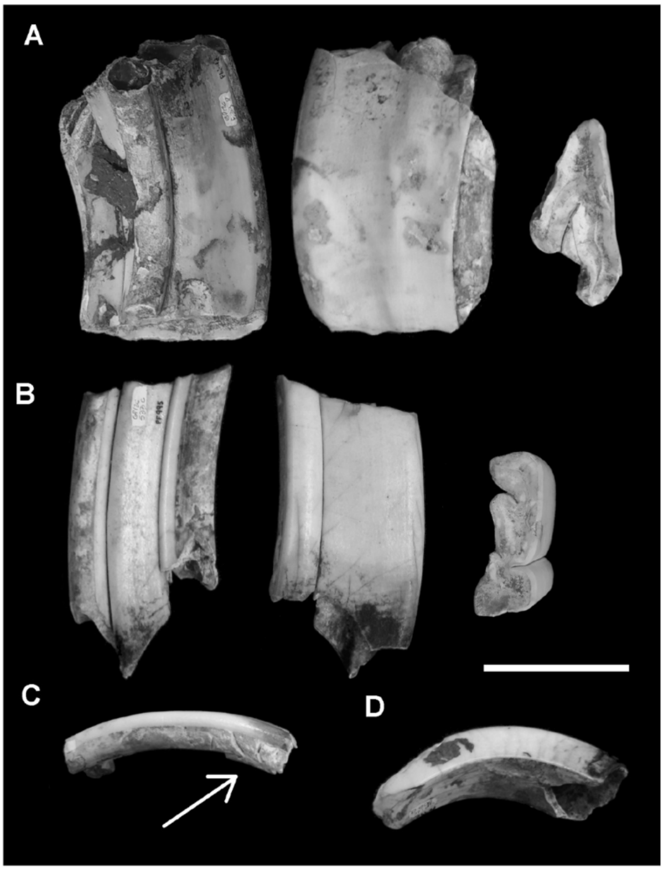

Fig. 9. Teeth of *Toxodon platensis*. A) Upper molar in lingual, labial and occlusal views (PF-993/GP/2C–533 F). B) Lower molar in lingual, labial and occlusal views (PF-995/GP/2C–533C). C) Lower premolar in lateral view (PF-997/GP/2C-533 E). D) Upper incisor in lateral view (PF-940/GP/2C-306 A). Arrow indicates the cut marks at the base of the tooth. Scale 50 mm.

Holanda and Ferrero, 2013).

Remarks: The specimen is represented by the central-distal part of the right tibia of an adult animal. The measurements of the specimen are among the largest ones (Table 1) when compared to the range of variation estimated by recent specimens (Holanda, 2011 and the CRK Reference Collection). However, other than the large size, this specimen is indistinguishable from the living specimens (Fig. 8) (see Fig. 9).

The specimen is similar to Pleistocene Tapiridae, which presented limbs larger than extant specimens (Holanda, 2011). However, the values obtained for the fossil specimen are close to the ones observed in the living species and the lack of diagnostic characteristics (found only in the skull) make it impossible to make any further comparisons of this specimen with any fossil or current species.

Tapirids, unlike other perissodactyls, are associated with forest environments, yet they can be found in various types of biomes, including savannahs near water courses (Cubas et al., 2014).

Order Notoungulata Roth, 1903
Family Toxodontidae Owen, 1845
Genus *Toxodon* Owen, 1837
Toxodon platensis Owen, 1837
Fig. 9

Material and number of individuals: The species is represented by one individual. The material attributed consists of eleven teeth (GP/2C-533 A, PF-856/GP/2C–533 B, PF-995/GP/2C–533C, PF-430/GP/2C-533D, PF-997/GP/2C-533 E, PF-993/GP/2C–533 F, PF-1123/GP/2C-107, PF-1368/GP/2C-312, PF-1214/GP/2C-316, PF-940/GP/2C-306 A and PF-994/GP/2C–306 B).

Geographic distribution: The genus *Toxodon* is endemic to South America and its fossils are found only in Plio-Pleistocene deposits in Brazil, Peru, Uruguay, Argentina, Bolivia and Venezuela. At the end of the Pleistocene they reached Central America, being found in Honduras, El Salvador and Nicaragua (Mendonça, 2007).

Recognized species: There are currently five species assigned to the genus *Toxodon*; *Toxodon chapalmalensis* Ameghino, 1907, occurring only in the Pliocene, *T. ensenadensis* Ameghino, 1907, *T. gracilis* Guérin and Faure, 2009, *T. burmeisteri* Gasparini, 2010 and *T. platensis* Oliveira et al., 2014, the last one is the only one to occur in Brazil.

Remarks: The described material is composed of teeth and it is undoubtedly identified as *Toxodon platensis* based on the comparison with the anatomical descriptions by Miño Boilini et al. (2006) (Table 2). Some teeth, such as PF-856/GP/2C–533 B, PF-997/GP/2C-533 E, and PF-1214/GP/2C-316, had part of the occlusal surface fragmented or covered with concretion, making it difficult to accurately obtain some

Table 2
Toxodon platensis teeth measurement data and comparison with reference values. Measurements are in millimeters. TD: transverse diameter; APD: antero-posterior diameter. Question marks signal estimated measures. The measurement range was based on the works by Roth (1896), Fariña et al. (1998) and Miño Boilini et al. (2006).

Upper Dentition					
Identification	Tooth type	Measure TD	Range	Measure APD	Range
PF-940/GP/2C-306 A	I1	27.50	–	–	–
PF-993/GP/2C–533 F	M1	30.23	28–30	63.4	40–65
PF-856/GP/2C–533 B	M2	29.44?	29–45	64.68	51–72
GP/2C-533 A	M2	29	29–45	65.39	51–72
Lower Dentition					
Identification	Tooth type	Measure TD	Range	Measure APD	Range
PF-1123/GP/2C-107	i1	21.90	21–22	–	–
PF-994/GP/2C–306 B	i2	22.2	22	–	–
PF-1368/GP/2C-312	pm3	13.30	12–14	26.30	20–26
PF-997/GP/2C-533 E	pm3	14.26	12–14	25.17?	20–26
PF-1214/GP/2C-316	pm4	18.40?	17–18	32.79?	22–32
PF-995/GP/2C–533C	m2	14.32	14–20	47.54	34–50
PF-430/GP/2C-533D	m2	14.47	14–20	45.55	34–50

measurements.

In general, the materials found at Abismo Ponta de Flecha Cave are within the expected range for adult individuals of *T. platensis*, compared to reference values found in the literature such as Roth (1896), Fariña et al. (1998) and Miño Boilini et al. (2006), and can be safely associated with this species.

Small variations in tooth size, as seen in Table 2, are common in this species as has been pointed out by several authors, including Mendonça (2007), Dantas (2012) and Silva (2019), and that may be related to regional morphological variation.

Some of the teeth had fragmented parts, indicating that these materials were heavily remobilized. All teeth that were found in J11 present important calcite deposits on the surface. A premolar found in J10 (PF-997/GP/2C-533 E) presents several marks on the posterior portion of the root (Fig. 9C). The marks are curved and elongated, with a V-shaped section. Although they have characteristics of marks produced by human action, the curved direction of this incision differs from several marks found in the literature (Binford, 1981; Lyman, 1994; Domínguez-Rodrigo et al., 2009; Chichkoyan et al., 2017), moreover, anthropic incisions are not common to be identified in teeth. Therefore, it is not possible to safely suggest that the presence of *Toxodon* osteological materials in the deposits the Abismo Ponta de Flecha Cave are related to humans or not.

Based on Carbon isotopic analyses and on the comparative anatomy of the skeleton, it is proposed that *Toxodon platensis* were terrestrial animals, found both in more open environments and in forest edges, making the best habitats for toxodontids the mixed regions presenting the Atlantic Forest and a dry forest (Mendonça, 2012; Dantas et al., 2017; Silva, 2019).

6. Paleoenvironmental discussion

The dating obtained for the specimen of *Toxodon platensis* from the Abismo Ponta de Flecha Cave (Neves et al., 2007) is indicative that its entrance was unobstructed at least since the late Pleistocene.

Taphonomic studies have considered that there has been remobilization of many specimens since the Pleistocene, but such transportation was different among the deposits, ranging from an articulated specimen of *Tayassu pecari* (supplementary material) to others partially destroyed in other deposits of the cave.

In addition to ungulates, the Abismo Ponta de Flecha Cave yielded several species of microvertebrates, including frogs, snakes, lizards, birds, marsupials, rodents, and bats (Barros-Barreto et al., 1982; Chahud, 2003, 2005, 2012, 2021, 2022b; Camolez and Zaher, 2010). These microvertebrates are still present in the region, suggesting that the environment in which they lived should have been similar to the current one, but the material showed bone selection (most of them consisted of appendicular bones) and fragmentation (Chahud, 2003, 2012) suggesting that it has been reworked. It is important to emphasize that smaller and fragile bone parts are easily lost in high energy environments (Voorhies, 1969; Behrensmeyer, 1991) and that, probably, most specimens are recent.

On the other hand, the macrovertebrates of the current fauna present a different state of preservation and some specimens still have fragile bone elements still preserved. However, extinct species, such as the Toxodontidae and the typical animals of the Pleistocene megafauna, are represented only by teeth or have few preserved bone parts, most of them being worn or fragmented (Chahud, 2005, 2021, 2022a). Such pattern suggests that many current ungulates belong to recent individuals or who have been deposited in more protected locations.

The ungulates of extant species found in the Abismo Ponta de Flecha Cave are still common in the dense forest of the Ribeira de Iguape Valley and have representatives since the Pleistocene period in southeastern Brazil (Auler et al., 2006). The dense forest in the region of the Ribeira de Iguape Valley suffered very few climatic changes through the Holocene and it would have been present in the last 14,000 years BP. Before that, the region where the Abismo Ponta de Flecha Cave is located would have a drier climate (Saia, 2006).

Current interpretations for the Pleistocene paleoenvironment of megafauna species suggest the existence of savanna and open grassland habitats. However, the AMS C14 dates obtained for the *Toxodon* from the Abismo Ponta de Flecha Cave, for another specimen of *Toxodon* from the Abismo do Fossil Cave, and for the sloth *Catonyx cuvieri* from the Abismo Iguatemi Cave (all caves in the Ribeira de Iguape Valley) are younger than 14,000 years BP (Hubbe et al., 2013), when the forest would already be established in the region (Saia, 2006).

As previously mentioned, *Toxodon* could have inhabited transitional regions between forest and dry ecotones (MacFadden, 2005; Dantas et al., 2017). The possibility of such species having inhabited regions close to forests could justify its presence around 13,000 years, when the establishment of a forest (Saia, 2006) could have resulted in transitional environments including forest and open fields. Unfortunately, it was not possible to date other megafauna specimens, but it is likely that they are older than 14,000 years, given that dates made on other specimens from other locations showed older ages (Hubbe et al., 2013).

7. Conclusions

The material found at Abismo Ponta de Flecha Cave is represented by four families of ungulates: Cervidae, Tayassuidae, Tapiridae, and Toxodontidae, the latter being the only taxon currently extinct.

The family Cervidae consists of at least two species assigned to the genus *Mazama*, with the larger specimens being attributed to *Mazama americana* and a smaller one that can be tentatively attributed to *M. gouazoubira*.

The Tayassuidae is the most abundant family with at least ten individuals and are represented by three species. Most of the material can be attributed to *Tayassu pecari*, with six specimens, but it was also possible to identify materials that were identified as *Dicotyles tajacu* and an undetermined large species.

The Tapiridae family is represented by a tibia fragment from an indeterminate adult animal. Due to the absence of diagnostic features, it was not possible to associate the specimen with any fossil or extant species, but it was possible to observe that it is a large animal compared to current Tapiridae individuals.

The Abismo Ponta de Flecha Cave also presented the only family of an South American native ungulate from the Pleistocene - Holocene boundary, the Toxodontidae. All the material is composed of teeth and can be safely associated with the species *Toxodon platensis*, representing a single adult specimen.

The extant species of ungulates found in the Abismo Ponta de Flecha Cave are common in the local forest, which might have been present in the region for the last 14,000 years (Saia, 2006). The specimen of *Toxodon platensis* may have inhabited the region at times when there was an ecotone between biomes that occurred in the Late Pleistocene and Early Holocene.

The presence of human communities around Abismo Ponta de Flecha Cave is notable by the identification of bone elements with cut marks, but their presence was not the main factor for the origin of this deposit because of the low representativeness of materials with cut marks in the whole assembly, being more likely that these materials have ended up inside the cave accidently.

CRediT authorship contribution statement

Artur Chahud: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Paulo Ricardo de Oliveira Costa:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gisele Ferreira Figueiredo:** Writing – review & editing, Writing – original draft, Methodology,

Investigation, Formal analysis, Data curation, Conceptualization. **Mercedes Okumura:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, 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

A figure of a complete specimen has been added

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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.2022.104107.

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