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CINGULATA OF THE ABISMO PONTA DE FLECHA CAVE (PLEISTOCENE-HOLOCENE), RIBEIRA DE IGUAPE VALLEY, SOUTHEASTERN BRAZIL

ARTUR CHAHUD, PAULO RICARDO DE OLIVEIRA COSTA & MERCEDES OKUMURA

Laboratory for Human Evolutionary Studies, Department of Genetics and Evolutionary Biology, Institute of Biosciences, University of São Paulo, Rua do Matão 277, 05508-090, São Paulo, SP, Brazil. *arturchahud@yahoo.com* (Corresponding author), *paulo.rocta@gmail.com*, *okumuram@usp.br*

ABSTRACT – The Ribeira de Iguape Valley, located in southeastern Brazil, is an important karstic region, presenting a large number of caves containing fossil and subfossil vertebrate materials. The Abismo Ponta de Flecha Cave is a complex vertical cave divided into galleries where a large amount of osteological material was collected. The cave acted as a natural trap for several taxa and possibly as a disposal site for ancient human communities. Osteoderms and appendicular bones assigned to two genera of Cingulata were identified in the faunal assemblage. The most abundant bone material belongs to the family Chlamyphoridae, genus *Cabassous*, represented by the living species *C. tatouay* and by remains of a larger, but little-known species, cf. *C. antiquus*. The other identified genus belongs to the family Dasypodidae: *Dasypus* sp. Evidence of human activity was characterized in only one *C. tatouay* bone, while the other specimens were considered as being of natural origin.

Keywords: Quaternary, Chlamyphoridae, *Dasypus*, *Cabassous*, taxonomy.

RESUMO – O Vale do Ribeira de Iguape, localizado no sudeste do Brasil, é uma importante região cárstica, apresentando muitas cavernas contendo vertebrados fósseis e subfósseis. O Abismo Ponta de Flecha é uma caverna vertical complexa, dividida em galerias, onde foi observada uma grande quantidade de material osteológico. A caverna atuou como uma armadilha natural para vários táxons e possivelmente como um local de descarte para antigas comunidades humanas. Osteodermos e ossos apendiculares atribuídos a dois gêneros de Cingulata foram identificados na associação faunística. O material ósseo mais abundante pertence à família Chlamyphoridae, gênero *Cabassous*, representado pela espécie vivente *C. tatouay* e por restos de uma espécie maior, porém pouco conhecida, cf. *C. antiquus*. O outro gênero identificado pertence à família Dasypodidae, *Dasypus* sp. A evidência de atividade humana foi caracterizada em apenas um osso de *C. tatouay*, enquanto os demais espécimes foram considerados de origem natural.

Palavras-chave: Quaternário, Chlamyphoridae, *Dasypus*, *Cabassous*, taxonomia.

INTRODUCTION

The superorder Xenarthra represents a clade of mammals of South American origin consisting of two orders: Cingulata (armadillos, pampatheres and glyptodonts) and Pilosa (anteaters and sloths). Fossil remains are known from the Early Eocene (Fernicola *et al*., 2021), being restricted to the South American continent until the Neogene, when occurred the Great American Biotic Interchange (**GABI**) that allowed them to reach North America (Shapiro *et al*., 2015).

The order Cingulata is characterized by having an armor composed of dermal plates (osteoderms), being its living representatives colloquially known as armadillos. Currently, the order consists of twenty-two living species divided into two families: Dasypodidae, consisting of a single genus, *Dasypus* Linnaeus, 1758, and Chlamyphoridae, containing thirteen species grouped into eight genera; *Euphractus* Wagler, 1830, *Zaedyus* Ameghino, 1889, *Chaetophractus* Fitzinger, 1871, *Chlamyphorus* Harlan, 1825, *Calyptophractus* Fitzinger, 1871, *Priodontes* F. Cuvier, 1825, *Tolypeutes* Illiger, 1811 and *Cabassous* McMurtrie, 1831 (Delsuc *et al*., 2016; Feijó *et al*., 2018; Feijó & Anacleto, 2021).

Cingulata remains are common in South American Quaternary deposits, with records in Brazil of the genera *Tolypeutes*, *Dasypus*, *Cabassous* and *Euphractus*, the last three being found in Holocene paleontological and archaeological sites (Paula-Couto, 1973, 1979; Chahud, 2005, 2021; Chahud *et al*., 2021). The genus *Tolypeutes* has its oldest record in the Late Pleistocene of Argentina (Paula-Couto, 1979), *Dasypus* is recorded in Pleistocene and Holocene deposits of Brazil and Argentina (Oliveira & Pereira, 2009), *Cabassous* occurs in the Quaternary of Southeast Brazil (Ameghino, 1907;

Chahud *et al*., 2021), and *Euphractus* was recorded in the Late Pleistocene/Holocene of Brazil (Chahud, 2021), plus occurrences in Argentina (Paula-Couto, 1979).

The region of the Ribeira de Iguape Valley, located in southeastern Brazil, is an important karstic region, with a large number of caves and potential for paleontological studies. The first remains of Cingulata from this important locality were reported by Ameghino (1907), who studied fossil and subfossil remains from the Gruta do Monjolinho, in the Municipality of Iporanga. Later, new materials were described and commented by Paula-Couto (1973), who conducted the first survey of Xenarthra occurrences in the State of São Paulo. However, among the living genera of Cingulata, only one humerus attributed to *Cabassous antiquus* Lund, 1840 identified by Ameghino (1907), in Ribeira de Iguape Valley, and bone parts of *Dasypus punctatus* Lund, 1840 (Castro *et al*., 2013), from the Municipality of Sorocaba, both described and commented by Paula-Couto (1973), were studied in the State of São Paulo; all other occurrences were limited to superficial descriptions and illustrations (Lino *et al*., 1979; Barros-Barreto *et al*., 1982).

Among the caves with a large volume of underexplored fossil material is the Abismo Ponta de Flecha Cave, a vertical cave (Figure 1) that served as a deposit for a large amount of osteological material of extinct and living animals, during the Holocene (Barros-Barreto *et al*., 1982; Chahud, 2001, 2005). The Cingulata were first observed and cited by Barros-Barreto *et al*. (1982) and Chahud (2001, 2005, 2012), but no specific study was performed. The present contribution aims to properly identify and comment on the Cingulata specimens found in this cave.

MATERIAL AND METHODS

The Abismo Ponta de Flecha Cave is located in the Municipality of Iporanga, in the south of the State of São Paulo, southeastern Brazil (Figure 1). The collected material consists of more than 1,300 samples of faunal and inorganic remains (Barros-Barreto *et al*., 1982). This study was part of a large speleological, archaeological, and paleontological study carried out by geologists and biologists in the Ribeira de Iguape Valley in the late 1970s and early 1980s.

The concentration of the Abismo Ponta de Flecha Cave is considered of mixed origin. Part of the material originating from anthropic activity and part from natural origin, such as natural traps (result of falling or entrapment of animals) and transport by physical and biological agents, such as hunting remains by predators and scavengers.

The specimens are deposited and curated 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). Initially, most of the material was organized and listed according to location and positioning in the internal galleries, called *Jazidas* (J), receiving the acronym PF-. Later all material received a new

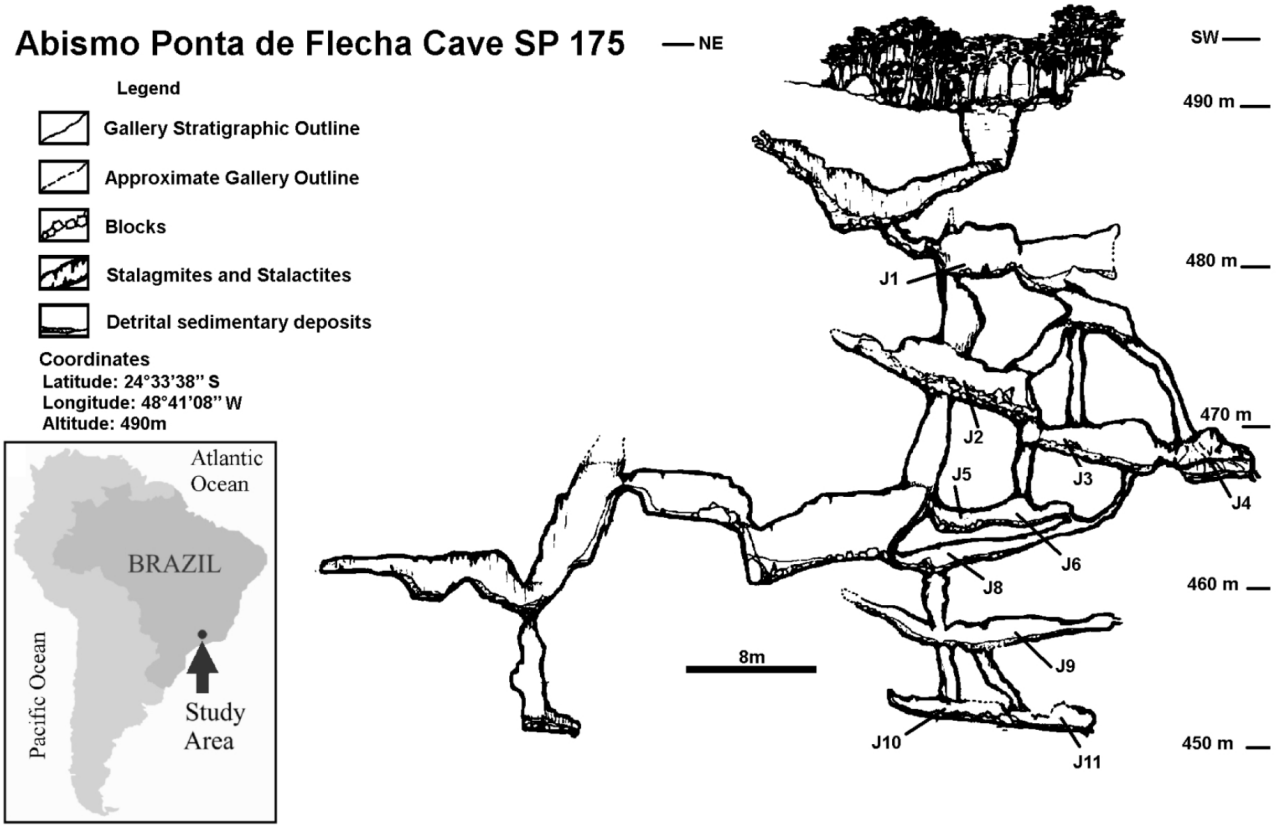

Figure 1. Schematic profile of the Abismo Ponta de Flecha, SP 175. The location of the galleries (*Jazidas*, "**J-**") preserving osteological material (**J1–J11**) is indicated. The material studied here comes from J10 and J11. Adapted from Barros-Barreto *et al*. (1982).

classification, **GP/2C**. Observing the two existing numbers, all material studied will present both records.

The osteological material referring to the Cingulata of the Abismo Ponta de Flecha Cave consists of eight appendicular bones (femora, humeri and ulnae), and 112 disarticulated osteoderms, totaling 120 identifiable bone parts. These specimens come mainly from J10 and J11, and only two osteoderms were found in J5, indicating that most of the material is concentrated in the deepest parts of the Abismo Ponta de Flecha (Figure 1)

The study of material preservation followed the taphonomic techniques proposed by Voorhies (1969), Behrensmeyer (1978, 1991), and Lyman (1994). For the analysis of the marks, a digital microscope DinoLite 2.0 was used, and for the morphological identification of the marks the works of Binford (1981) and Lyman (1994) were consulted.

For the taxonomic identification of the material, comparisons were made with known specimens from scientific collections, such as the "Renato Kipnis Collection" and "Guajá Collection", both curated at the Laboratory of Human Evolutionary Studies of the Institute of Biosciences of USP (IB-USP) and Mastozoological Collection from the Museum of Zoology USP, as well as with the descriptions and figures from the works of Ameghino (1907), Paula-Couto (1979), Wetzel (1980), McBee & Baker (1982), Ciancio *et al*. (2012), Hayssen (2014a, b), Delsuc *et al*. (2016), Feijó & Cordeiro-Estrela (2016), Feijó *et al*. (2018), Feijó & Anacleto (2021) and Chahud (2021, 2022).

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889
Order CINGULATA Illiger, 1811
Family CHLAMYPHORIDAE Bonaparte, 1850

Cabassous McMurtrie, 1831
(Figures 2A–E, 3, 4A)

Material. Osteological materials include a left ulna (PF-1124/GP2C-551g) and a right humerus (PF-638/GP2C-551c) attributed to *Cabassous tatouay* Desmarest, 1804 and two left femora (PF-963/GP2C-551a and PF-755/GP2C-551e), and a right femur (PF-654/GP2C-552) assigned to cf. *Cabassous antiquus* Lund, 1840. The osteoderms can be attributed to the family Chlamyphoridae, being composed of 104 specimens (PF-1300/GP2C-102, PF-1313/GP2C-104, PF-1216/GP2C-83, PF-776/GP2C-256, PF-706/GP2C-226, PF-537/GP2C-211, PF-1133/GP2C-219, PF-1330/GP2C-98, PF-1078/GP2C-255, PF-1180/GP2C-96, PF-914/GP2C-212, PF-301/GP2C-11, PF-1253/GP2C-85, PF-1111/GP2C-326N).

Remarks. The four long bones found have an external morphology indistinguishable from *Cabassous* and can be safely assigned to this genus. However, differences were observed in the length, ontogenetic stages, and preservation of each bone part, suggesting at least two different species for the remains found in the Abismo Ponta de Flecha Cave.

The right humerus (PF-638/GP2C-551c) presents broken extremities and part of the deltopectoral tuberosity (Figure 2A). From the size of its deltoid tuberosity, it was possible to infer that the specimen would have proportions compatible with that of a *Cabassous tatouay*, the largest living *Cabassous* (Wetzel, 1980; Hayssen, 2014a). Due to the conditions of the specimen, it is not possible to suggest a more detailed age class, although it shows similar proportions to an adult individual. It is important to note that the specimen presents several cut marks.

The left ulna PF-1124/GP2C-551g belonged to a subadult individual, due to the (missing) unfused epiphyses, however the length of the preserved part is like that of an adult *Cabassous tatouay* and the assignation to this species is possible. We emphasize that the ulna of the genus *Cabassous* differs from other genera of the family Chlamyphoridae in the proportions and positions of the olecranon and sigmoid fossa, even in early ontogenetic stages.

The three femora can be attributed to adult specimens and, despite their very different preservation (PF-755/GP2C-551e, PF-654/GP2C-552 and PF-963/GP2C-551a), all present the same proportions and probably represent the same species. The assignation to *Cabassous* is based on the curvature of the diaphysis and the more robust distal part, compatible with the observed morphology of this genus. On the other hand, the assignation of these three femora to some species of *Cabassous* is not certain, as it is possible to observe these characteristics in *Cabassous unicinctus* Linnaeus, 1758, *Cabassous squamicaudis* Lund, 1845 and *Cabassous tatouay* Desmarest, 1804 (Hayssen, 2014a, b; Feijó & Anacleto, 2021). However, the specimens studied here are much larger than adult specimens of *C. tatouay*, considered the largest species of the genus, and have similar proportions to the femora of *Euphractus*, the second largest extant Cingulata that occurs in the area (Chahud, 2021, 2022).

Cabassous bones larger than those of living species were observed in Ribeira de Iguape Valley by Ameghino (1907), who adopted Lund's classification, *Cabassous antiquus*. In a review of the genus *Cabassous*, Wetzel (1980) commented that *C. antiquus* differed from recent species only by its larger size and no other distinguishing feature has been found. The specimen described by Ameghino (1907) was compared with *C. unicinctus*, however Ameghino (1907) considered this the largest species of the region. It is important to emphasize that *C. unicinctus* is not found in the Ribeira de Iguape Valley (Wetzel, 1980; Anacleto *et al*., 2014; Hayssen, 2014b; Feijó & Anacleto, 2021; Rocha *et al*., 2022) and that the region is inhabited by the species *C. tatouay* (Gonzalez & Abba, 2014). However, Paula-Couto (1975) comments on the existence of *C. unicinctus* in Iporanga. Still, the author did not differentiate this species from *C. tatouay*, considering *C. unicinctus* as the only extant species of the genus *Cabassous* in the area (Paula-Couto, 1973, 1975, 1979).

The specimens studied here were compared with a recent adult *Cabassous tatouay*, and they show a much larger size, as described by Ameghino (1907) and confirmed by Wetzel (1980). The humerus of *C. antiquus* described by Ameghino

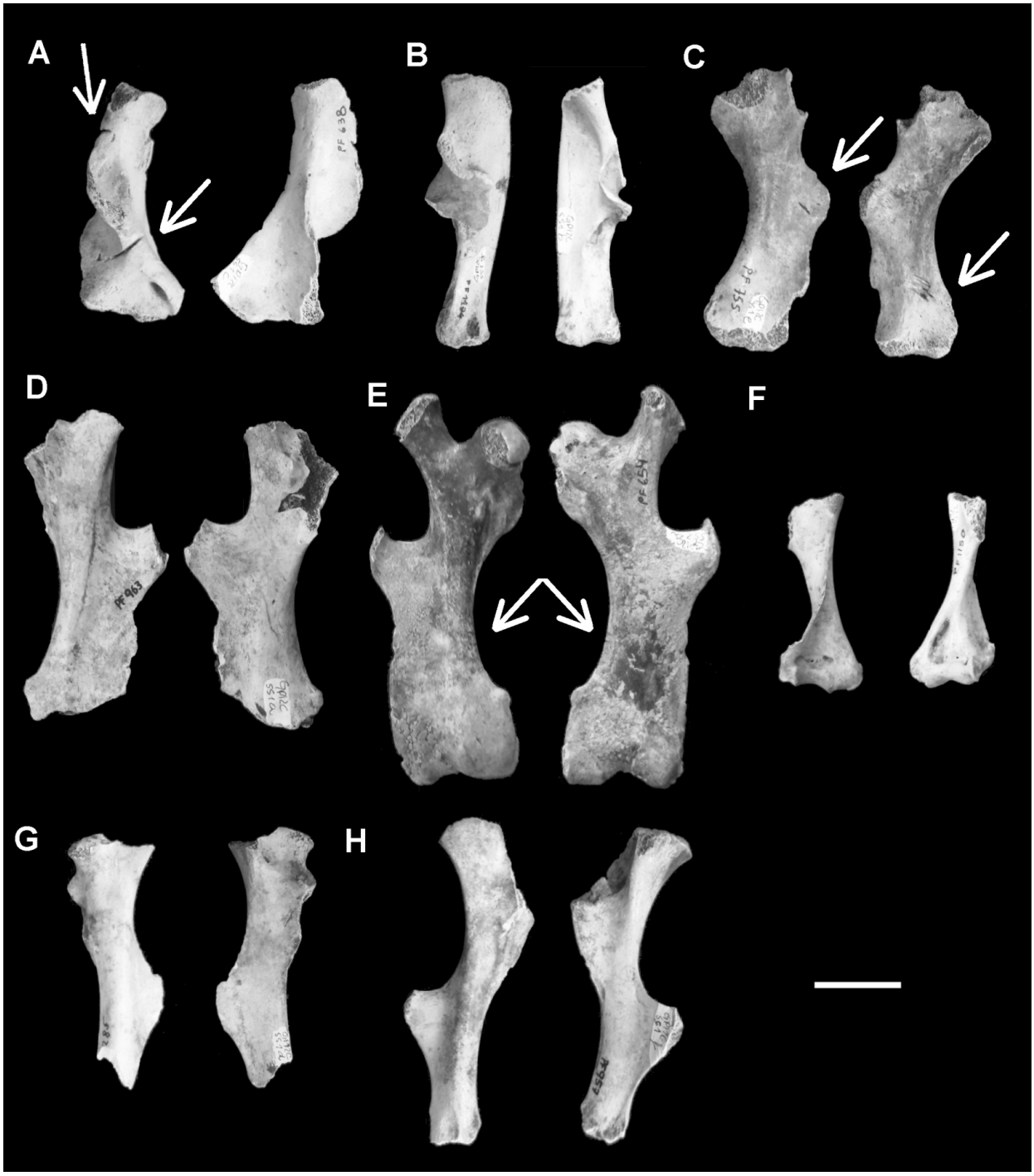

Figure 2. Cingulata found in the Abismo Ponta de Flecha Cave. **A**, Right humerus (PF-638/GP2C-551c); **B**, Left ulna (PF1124/GP2C-551g); **C**, Left femur (PF-755/GP2C-551e) from *Cabassous tatouay*; **D**, Left femur (PF-963/GP2C-551a); **E**, Right femur (PF-654/GP2C-552) from *Cabassou antiquus*; **F**, Left humerus (PF-1150/GP2C-551h); **G**, Left femur (PF-1285/GP2C-551d); **H**, Right femur (PF-957/GP2C-551j) of *Dasypus* sp. Arrows indicate cut marks on bones. Scale bar = 20 mm.

(1907) was mentioned by Wetzel (1980) as having 72 mm in maximum length in contrast to 66 mm for *C. tatouay*. The humerus of *Cabassous tatouay* MZUSP-7665 (Figures 3–B) used for comparison in the present study presented the maximum length of 66.7 mm, being larger than the specimen mentioned by Wetzel (1980), but smaller than the specimen found by Ameghino (1907) in Ribeira de Iguape Valley. The only specimen of the Abismo Ponta de Flecha Cave in which it was possible to obtain the maximum length was the right femur PF-654/GP2C-552, 91.5 mm, and it was compared with an adult male *Cabassous tatouay* femur of 71.7 mm in maximum length (Figures 3C–D).

For the present study, we adopted the name suggested by Wetzel (1980), cf. *Cabassous antiquus*, because we agree with the author when he states that more specimens and more anatomical information are needed to characterize the

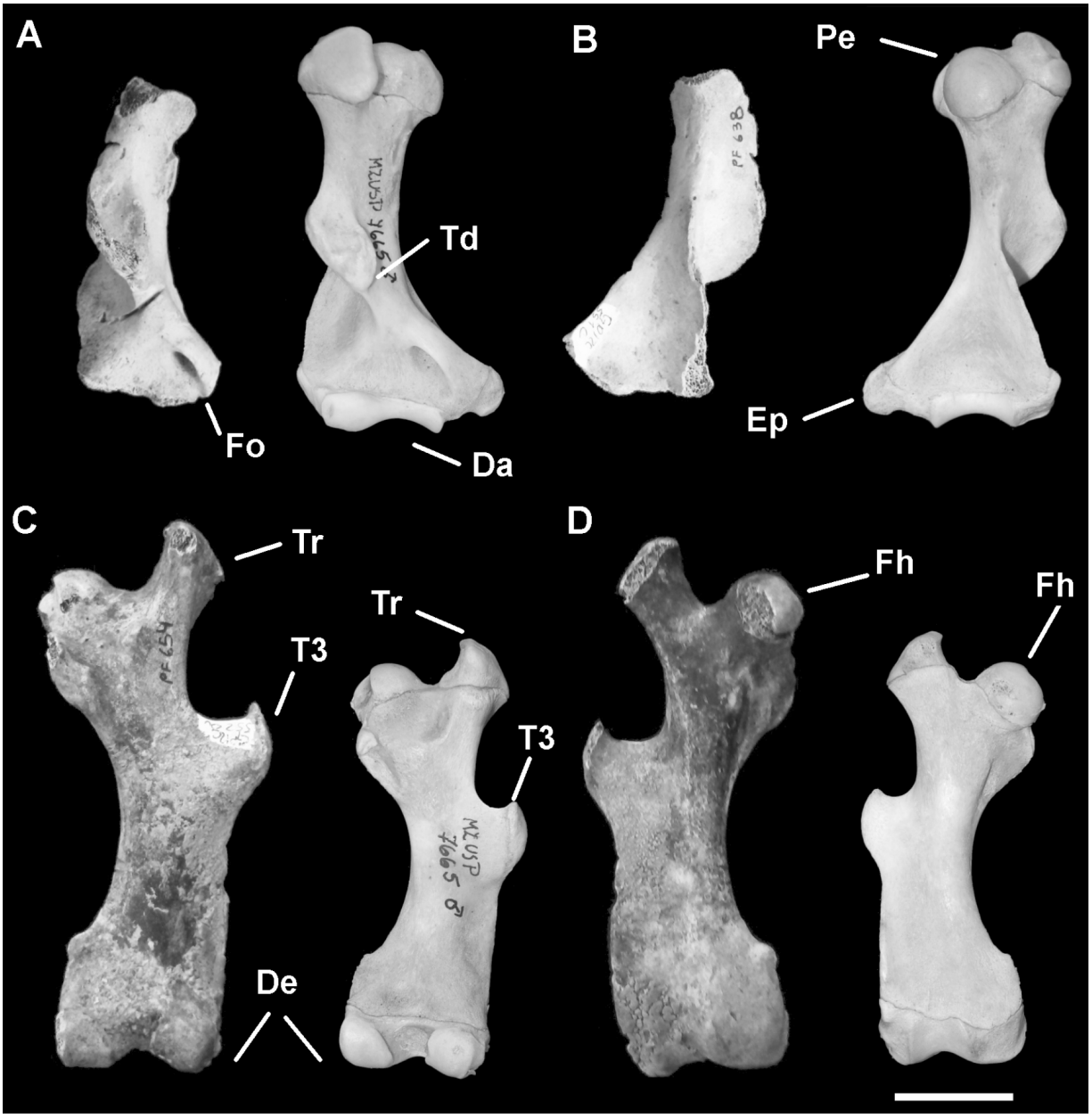

Figure 3. *Cabassous* found in the Abismo Ponta de Flecha Cave compared with the specimen of *Cabassous tatouay* (MZUSP-7665). **A-B**, Right humerus (PF-638/GP2C-551c), **A**, cranial view and **B**, caudal view; **C–D**, Right femur (PF-654/GP2C-552), **C**, caudal view and **D**, cranial view. **Abbreviations: Fo**, entepicondyloid foramen; **Td**, pectoral deltoid tuberosity; **Pe**, proximal epiphysis; **Da**, distal joint; **Ep**, epitrochlea; **Tr**, greater trochanter; **T3**, third trochanter; **Fh**, femoral head; **De**, distal epiphysis. Scale bar = 20 mm.

species. Still, we emphasize that the femora found are larger than those of a *C. tatouay*. It is possible to affirm that there were specimens of the genus *Cabassous* larger than known specimens that occur nowadays in the region of Ribeira de Iguape Valley.

Osteoderms that have not been abraded or polished by physical transport have a quadrangular, rectangular, pentagonal or hexagonal shape (Figure 4A). Although we only found specimens of the genus *Cabassous*, the characteristics of these osteoderms are similar to those of other species of Chlamyphoridae. Therefore, we associate the osteoderms with this family and not only with the genus *Cabassous*. The characteristics of osteoderms are the presence of a flat-convex dorsal surface and a concave ventral surface, it has several foramina and the central region of the osteoderms of the mobile region of the armor is marked by grooves that extend to the sides of each osteoderm.

Family DASYPODIDAE Gray, 1821

Dasypus Linnaeus, 1758

Dasypus sp.
(Figures 2F–H, 4B)

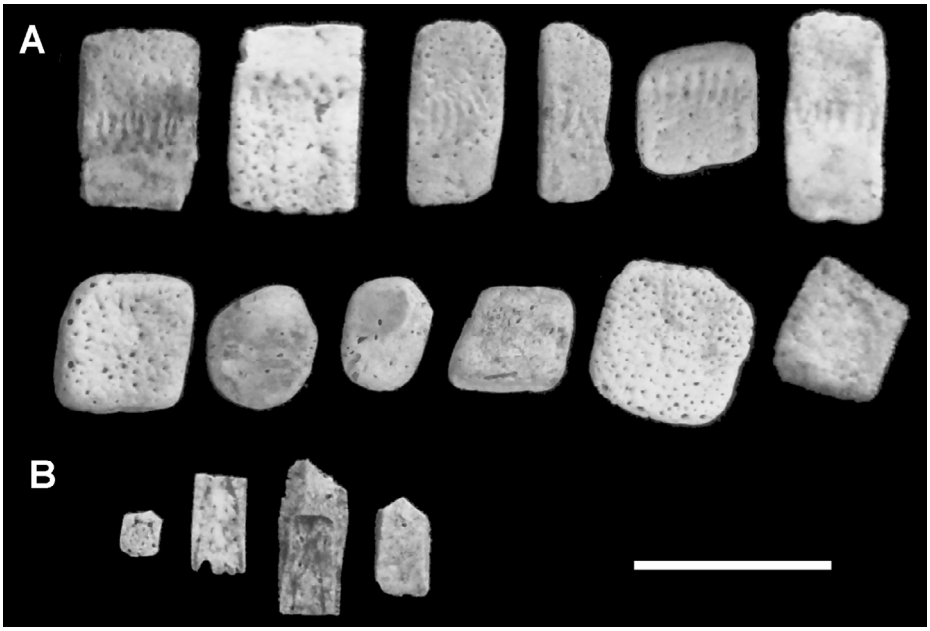

Figure 4. Cingulata osteoderms found in the Abismo Ponta de Flecha Cave. **A**, Chlamyphoridae, above moveable osteoderms with little abrasion and below indeterminate osteoderms with extensive remobilization; **B**, *Dasypus*. Left to right, first fixed osteoderm and moveable osteoderms. Scale bar = 20 mm.

Material. The specimens are represented by two femora, right (PF-957/GP2C-551j) and left (PF-1285/GP2C-551d), a left humerus (PF-1150/GP2C-551h) and eight osteoderms (PF-915/GP2C-236).

Remarks. The few osteoderms found are either fixed or belong to the mobile belt and when compared to those of Chlamyphoridae, these are smaller and thinner (Figure 4B). Fixed osteoderms are quadrangular or pentagonal, but those belonging to the mobile part are rectangular and thin. All are ornamented by sulci and foramina on their surface, and in the osteoderms of the mobile part there are two prominent lateral sulci that form a "V-shaped" figure.

The observed bones include two femora of opposite sides, but slightly different in size (representing two individuals) and without the epiphyses and extremities preserved. The morphological characteristics of the diaphysis, thinner than those of *Euphractus* and *Cabassous*, are typical of representatives of current species of the Dasypodidae, in shape and robustness (Chahud, 2022), and may be associated with the genus *Dasypus*. The specimen PF-957/GP2C-551j, which is in a better state of preservation (Figure 2H), presents most of the third trochanter preserved, suggesting that only the edges were worn, and that the specimen did not have articulated epiphyses when it started to be transported. The humerus PF-1150/GP2C-551h did not preserve its proximal part, but its external morphology concurs with a that of *Dasypus* and may also be associated with this genus.

The bones have an approximate size of the femora and humeri of *Dasypus novemcinctus* Linnaeus, 1758 and *Dasypus septemcinctus* Linnaeus, 1758, both extant species found in the region. However, due to the state of preservation and considering the possibility that both femora are from subadult specimens it is not possible to define the species.

TAPHONOMY AND HUMAN ACTIVITY

The estimation of the number of identified specimens (**NISP**) resulted in 119 specimens of Chlamyphoridae and 11 of Dasypodidae (Table 1). The Minimum Number of Individuals (**MNI**), considering the length, age class, and laterality of the appendicular bones, is of four individuals of Chlamyphoridae and two of Dasypodidae in the deposits of the Abismo Ponta de Flecha Cave (Table 1). Despite being more abundant, it is not possible to say that Chlamyphoridae was more common than Dasypodidae in the region, given the small number of individuals collected. Moreover, the greater robustness and thickness of the Chlamyphoridae osteoderms probably imply that they are more resistant to remobilization, abrasion, and breakage.

The osteoderms found have rounded edges and, in some cases, the specimens are almost completely rounded (Figures 4A–B). The breaks at the ends of the appendicular bones (Figures 2A–H) are suggestive of intense remobilization

Table 1. Number of identified specimens (**NISP**) and minimal number of individuals (**MNI**) of Cingulata from the Abismo Ponta de Flecha inferred from osteoderms and appendicular bones.

	Osteoderms	Appendicular bones	NISP	MNI
Chlamyphoridae	104	5	119	4
Dasypodidae	8	3	11	2
Total	112	8	120	6

of the material in the cave deposits. This statement can be confirmed if compared with specimens found in similar cave deposits that had suffered less remobilization, as observed in the specimen of *Euphractus sexcinctus* from Cuvieri Cave, a Holocene deposit in the state of Minas Gerais, in which most of the osteoderms, appendicular bones, and the skull were recovered with little wear or polishing (Chahud, 2021).

The broken ends found in the femora are also suggestive of physical transport, because if there were breaks during the preparation for consumption by the activity of human communities, this would be uneven and much more accentuated at a certain end of the bone, as observed in the specimens discarded by the Awá-Guajá community in the state of Maranhão, in which there were extremities without breakage and wear and others very damaged on the same bone due to preparation for consumption by the local community (Chahud, 2022).

Only three appendicular bones and few osteoderms of *Dasypus* were recovered. Apparently, there are no bite or cut marks or breaks from preparation for consumption by the human communities (Chahud, 2022).

It was possible to identify incisions in three bones (PF-638/GP2C-551c, PF-654/GP2C-552, and PF-755/GP2C-551e). All of them had marks that were possibly caused by intense remobilization in the cave. Such marks, characterized as resulting from trampling, can be identified through their morphology (shallow marks parallel and close to each other, with a sinuous path, wide base, variable length, and width, and start and end at points not related to anatomical areas of the bones; Binford, 1981; Lyman, 1994; Domínguez-Rodrigo *et al*., 2009).

The humerus PF-638/GP2C-551c was the only one in which it was possible to identify marks of anthropic origin; the incisions are distributed along the entire diaphysis (Figure 2A). Its association with human activity can be attributed to the morphology of the cuts: elongated with a transverse orientation, with a V-shaped cross section (Binford, 1981; Lyman, 1994; Domínguez-Rodrigo *et al*., 2009). The morphology of these marks and their location suggests that their purpose was to extract consumable meat from bones.

The femur PF-755/GP2C-551e have three marks at the posterior end of its diaphysis (Figure 2C). The presence of sediment in the innermost part of the marks suggests that these incisions are not recent. The three are parallel to each other, curved, close to each other, and have a wide and shallow base. Its association with the action of carnivores is not certain, because the marks do not have a path as sinuous and irregular as those described in the work of Dominato *et al*. (2011) and Yravedra *et al*. (2019). Therefore, the most likely explanation for the origin of these marks is the action of physical transport.

The humerus of *Dasypus*, PF-1150/GP2C-551h (Figure 2F), has breakings in the proximal part and in the deltopectoral crest. The break in the crest is likely the result of remobilization and transport of the bone. Still, it is not possible to infer a single cause for the breaking of the proximal part, and it may also be the result of predatory or human activity.

ASSOCIATED FAUNA AND PALEOENVIRONMENTAL DISCUSSION

Cingulata of the genera *Dasypus* and *Cabassous* are common in the Brazilian territory, including the Ribeira de Iguape Valley (Wetzel, 1980; Anacleto *et al*., 2014; Gonzalez & Abba, 2014; Hayssen, 2014b; Chahud *et al*., 2021). The genus *Cabassous* can be found in very diverse environmental settings, while *Dasypus* is common in forests, also occurring in drier environments (Ubaid *et al*., 2010; Feijó & Cordeiro Estrela, 2016; Feijó *et al*., 2018). Both genera can be sympatric and, given the diversity of environments where they can be found, it is not possible to determine the paleoenvironment only by the presence of these genera.

The Ribeira de Iguape Valley suffered climatic and environmental changes at the end of the Pleistocene, and between 30,000 and 14,000 years BP the climate was drier than present one. After that period, climatic variations become smaller (Saia, 2006).

The Abismo Ponta de Flecha Cave has been a natural trap for the fauna (Chahud, 2003, 2012, 2021, 2022), being the material remobilizated and transported within the cave, suggesting that older bone pieces would be in a worse state of preservation.

Despite intense remobilization, specimens of extinct Pleistocene macrovertebrate fauna, such as *Toxodon platensis*, terrestrial sloths, and a small specimen of *Smilodon populator* (Chahud, 2005, 2022) were observed in the deposits of Abismo Ponte de Flecha Cave.

Studies regarding deposition and taphonomy of the osteological material suggest that small vertebrates with masses < 5 kg from the Abismo Ponta de Flecha Cave would be recent (Barros-Barreto *et al*., 1982; Chahud, 2001, 2003, 2012; Chahud *et al*., 2002). Part of this claim was based on the identification of only extant species, but the discovery of cf. *Cabassous antiquus*, an extinct species, suggests that some ancient small vertebrate specimens may have been preserved, and that the conditions for their preservation are more complex than previously considered. Alternatively, it is possible that cf. *Cabassous antiquus* has existed until recently.

CONCLUSIONS

The Cingulata found in the Abismo Ponta de Flecha Cave belongs to two families, Dasypodidae, represented by the genus *Dasypus*, and Chlamyphoridae, represented by the genus *Cabassous*. The genus *Cabassous* is represented by the living species *C. tatouay* and the extinct cf. *C. antiquus*.

The species *Cabassous antiquus* was described by Lund in the region of Lagoa Santa, Minas Gerais State, and identified by Ameghino (1907) in the Ribeira de Iguape Valley. The validity of this species has been discussed, since the only difference in relation to the extant *Cabassous* species is its larger size (Wetzel, 1980). However, observations showed that there are specimens of the genus *Cabassous* larger than the living species, which can be preliminarily attributed to *C. antiquus*.

In general, many materials showed physical transport marks, indicating that this is a striking feature of the Abismo Ponta de Flecha Cave. The humerus of *Cabassous tatouay* with several cut marks suggests the consumption of this species by past human groups in the Ribeira de Iguape Valley in the Holocene.

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