Pleistocene EQUUS (Equidae: Mammalia) from Northern Brazil: Evidence of Scavenger Behavior by Ursids on South American Horses

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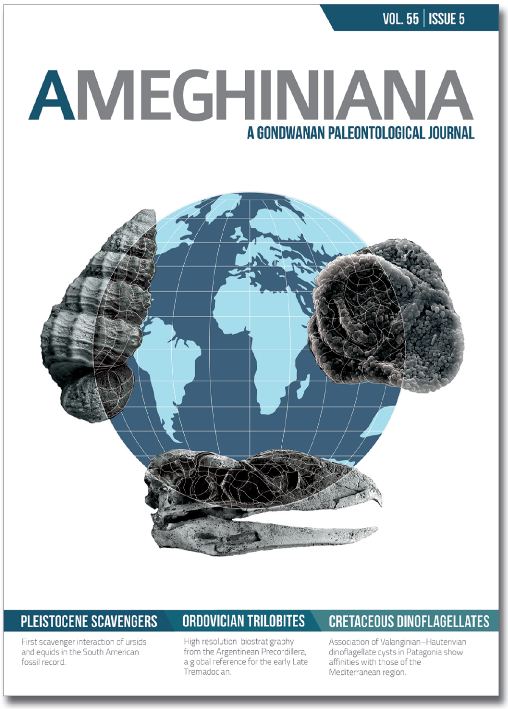

PLEISTOCENE *EQUUS* (EQUIDAE: MAMMALIA) FROM NORTHERN BRAZIL: EVIDENCE OF SCAVENGER BEHAVIOR BY URSIDS ON SOUTH AMERICAN HORSES

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Abstract. During paleontological surveys conducted in 2013 and 2014 in Quaternary deposits from the Gruta do Urso cave, Tocantins State, nine isolated teeth and five postcranial elements of *Equus neogeus* were recovered. Absolute datings indicate that *E. neogeus* inhabited the surroundings of Gruta do Urso cave during the Last Glacial Maximum. The specimens probably represent very young individuals that died outside the cave, were weathered prior to the final burial, with ontogenetic and taphonomic similarities. Herein, we report the first scavenger interaction of ursids and equids in the South American fossil record.

Key words. Megafauna. Quaternary. New record. Biodiversity. Taphonomy. Paleoecology. Scavenger.

Resumen. LOS *EQUUS* (EQUIDAE: MAMMALIA) PLEISTOCÉNICOS DEL NORTE DE BRASIL: PRIMERA EVIDENCIA DEL COMPORTAMIENTO CARROÑERO DE URSIDEOS EN CABALLOS SUDAMERICANOS. Durante levantamientos realizados en 2013 y 2014 en el depósito Cuaternario de la cueva Gruta do Urso, Tocantins, se recuperaron nueve dientes aislados y cinco elementos fósiles del postcráneo de *Equus neogeus*. Las dataciones absolutas indican que *E. neogeus* habitó los alrededores de la cueva de Gruta do Urso durante el Último Máximo Glacial. Los especímenes probablemente representan individuos muy jóvenes que murieron fuera de la cueva, erosionados antes del entierro final, con similitudes ontogenéticas y tafonómicas. También se reconoció el primer registro de interacción necrófaga de úrsidos en équidos para el registro fósil de América del Sur.

Palabras clave. Megafauna. Cuaternario. Nuevo registro. Biodiversidad. Tafonomía. Paleoecología. Necrofagia.

Horses, asses, and zebras are extant members of the genus *Equus*, today restricted to Africa and Asia. Nevertheless, this diversity and geographic distribution is only a remnant of *Equus* evolutionary history, which also includes Europe and the Americas. Although it is recognized that *Equus* arrived in South America from North/Central America during the Great American Biotic Interchange (**GABI**), there is no consensus as to how many migratory pulses occurred during its dispersion (Woodburne, 2010; MacFadden, 2013). Subsequently, a very rapid diversification was experienced by *Equus* in South America and five species can be recognized: *E. santaeelenae*, *E. insulatus*, *E. lasallei*, *E. andium*, and *E. neogeus* (Prado and Alberdi, 1994; Alberdi *et al.*, 2003). However, Machado *et al.* (2017) demonstrated that there is no taxonomic support for the validity of all five species for South American *Equus*. These authors recognized a continuum of gradual linear morphological variations among those *Equus* species, interpreted as a cline (Machado *et al.*, 2017). Thus, the only valid species of *Equus* in South America is *E. neogeus* (Machado *et al.*, 2017). Additionally, this species is considered a fossil index for the Lujanian South American Land Mammal Age (**SALMA**)—from the Late Pleistocene to the early Holocene (Cione and Tonni, 1995, 2005). The Brazilian records are among the latest *Equus* in the Americas, from the Pleistocene/Holocene transition.

Due to adaptations on the distal portion of its locomotory apparatus, such as the elongation of autopods and the monodactylia, *Equus* can be used as a direct paleoenviromental indicator of open lowland areas (MacFadden, 1992; Alberdi and Prado, 2004). Furthermore, the presence of *Equus* might be an indirect indicative of semi-arid and arid biomes, since open environments are usually associated with dry climates (Costa, 2017).

Paleoecological studies supported by high resolution taphonomic studies for South American Pleistocene mammals are very rare. Taphonomy is a very important tool in the recognition of paleoecological and paleoenvironmental aspects (Behrensmeyer *et al.*, 2000; Rogers *et al.*, 2007). Thus, a taphonomic analysis was conducted to recognize predator/scavengers and prey relations by the study of marks on fossilized bones (Dominato *et al.*, 2009, 2011; Araújo-Júnior *et al.*, 2011; Reyes *et al.*, 2013).

This is the first contribution that performed an analysis gathering studies on taxonomy, taphonomy, paleoecology, paleoenvironment, and paleoclimate to understand the paleobiological aspects of an association of Quaternary *Equus* from low latitudes of South America.

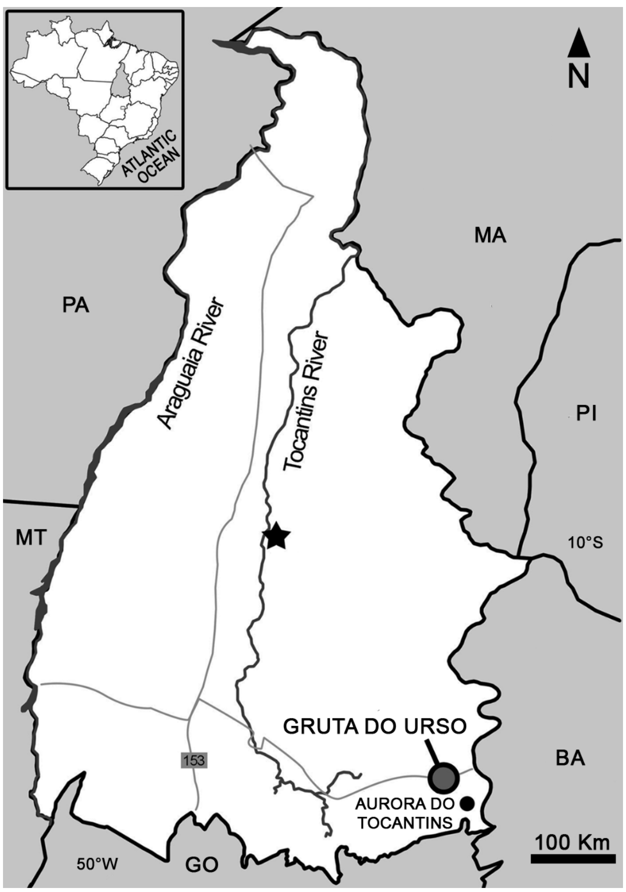

Figure 1. Location map of the Gruta do Urso cave, at Aurora do Tocantins (state of Tocantins, Brazil). On top left, the map of Brazil with Tocantins state in grey. The study area is represented by the large grey dot, and it is located at the Southeast region of the State of Tocantins (12° 35′ 0.08″ S; 46° 30′ 58.39″ W). The black star indicates the Tocantins state capital, the city of Palmas. **BA,** Bahia State; **GO,** Goiás State; **MA,** Maranhão State; **MT,** Mato Grosso State; **PA,** Pará State; **PI,** Piauí State.

GEOLOGICAL SETTING

The fossils described herein were collected between 2013 and 2014 from a Quaternary deposit from the Gruta do Urso limestone cave, at Aurora do Tocantins (12° 35′ 0.08″ S; 46° 30′ 58.39″ W), Tocantins State, Northern Brazil (Fig. 1). Online notes of Companhia de Pesquisa de Recursos Minerais (**CPRM**) on the geology of this region reported carbonate and terrigenous deposits of the Bambuí Group, which is Neoproterozoic in age (CPRM, 2006). A controlled excavation procedure was conducted in the cave, and a deposit with three levels was recognized: (i) the lower layer consists of an unfossiliferous yellowish coarse sand presenting a thickness of 50 mm that may vary according to different sections of the cave; (ii) the intermediary layer, a fossiliferous laminated reddish-grey loess-like sand of a thickness varying from 180 to 220 mm; and (iii) the upper layer, an unfossiliferous carbonate-cemented sandy layer of 10 to 20 mm of thickness (Rodrigues *et al.*, 2014; Maldonado *et al.*, 2016).

MATERIALS AND METHODS

The anatomy and morphology of all fossil elements were directly compared with South American Equidae specimens, housed in several scientific collections from the Americas and Europe.

An Electron Spin Resonance absolute dating analysis (Avilla *et al.*, 2013) was conducted for the molar UNIRIO-PM 1004. Unfortunately, this specimen was destroyed for the dating procedures.

The specimens were submitted to a macroscopical taphonomic analysis, where the following taphonomic aspects were evaluated: (i) degree of disarticulation; (ii) weathering stages; (iii) abrasion marks; (iv) scavenging traces; (v) transport aspects; and (vi) sedimentological features. All these features were interpreted according to the literature (Behrensmeyer, 1978; Haynes, 1980, 1982, 1983; Shipman, 1981; Shipman *et al.*, 1981; Fiorillo, 1988; Rogers *et al.*, 2007). The survey of the carnivore fossil assemblage from the Gruta do Urso cave was based on Rodrigues *et al.* (2014), and the scavenger marks were also interpreted according to the literature (Behrensmeyer, 1975; Haynes, 1980, 1983; Garshelis, 2009; Dominguez-Rodrigo and Pickering, 2010; Saladié *et al.*, 2011; Reyes *et al.*, 2013; Sala and Arsuaga, 2013; Sauqué *et al.*, 2014). The dentary and postcranial anatomical nomenclature followed Alberdi and Prado (2004), and Getty (2008).

Figure 2. Geographic distribution of ***Equus neogeus*** in South America (hachured area), following Machado *et al.* (2017). The black star represents the locality of the Gruta do Urso cave, in the State of Tocantins, Brazil, a new record for ***Equus neogeus***. Only the countries within the geographic distribution of ***Equus neogeus*** are named in the map.

RESULTS AND DISCUSSION

Two taxa of Equidae, *Equus* and *Hippidion,* are recognized for the Pleistocene/Holocene of South America. The Equidae fossils from Gruta do Urso are *Equus* because of the following characters: 1) all upper premolars and molars (except for dP2 and P2) have a triangular protocone in occlusal view, while in *Hippidion* this cusp is elliptical or rounded; 2) the presence of a circular protocone in occlusal view in the dP2 ensures the identification of *E. neogeus* because this cusp is comparatively more oval in other species of *Equus* from outside South America; 3) the ectoflexid never invades the isthmus on the lower teeth of *Equus*; and 4) all postcranial elements are more slender in *Equus* than in *Hippidion*. We recognize it as *E. neogeus* because we are following the arguments of Machado *et al.* (2017), by which this is the only valid species for *Equus* in South America.

SYSTEMATIC PALEONTOLOGY

PERISSODACTYLA Owen, 1848
EQUIDAE Gray, 1821
EQUINAE Gray, 1821

Genus ***Equus*** Linnaeus, 1758

Type species. *Equus caballus* Linnaeus, 1758.

Equus neogeus Lund, 1840
Figures 3–11

Distribution. Records of *Equus neogeus* Lund, 1840 are from Argentina, Uruguay, Chile, Paraguay, Bolivia, Peru, Ecuador, Colombia, Venezuela, and Brazil (Fig. 2). This species is restricted to the Lujanian SALMA, Late Pleistocene to earliest Holocene (Prado and Alberdi, 1994).
Locality and age. Gruta do Urso, Tocantins. See the Geological Setting section.
Material. We recognized nine Equidae teeth at the Gruta do Urso cave. From those, five are lower teeth—two left incisors (di1, UNIRIO-PM 1313; i1, UNIRIO-PM 1308), one third left deciduous premolar (UNIRIO-PM 1317), one third left molar (UNIRIO-PM 1312)—one upper right P3 (UNIRIO-PM 1315), one fragment of a non-identified left tooth (UNIRIO-PM 1336), and two are upper right deciduous premolars—

Figure 3. Incisors of ***Equus neogeus*** from the Gruta do Urso cave. **1–3,** lower first right incisor (**UNIRIO-PM** 1313); **1,** occlusal view; **2,** vestibular view; **3,** lingual view. **4–5,** first lower left incisor (**UNIRIO-PM** 1308); **4,** vestibular view; **5,** lingual view. Scale bar= 1 cm.

dP1 (UNIRIO-PM 1314), dP2 (UNIRIO-PM 1316). The molar UNIRIO-PM 1004 was used as a sample to conduct the absolute dating analysis by Electron Spin Resonance. Moreover, some postcranial materials, represented by one right humerus (UNIRIO-PM 1309), two pelvic bones (UNIRIO-PM 1338, UNIRIO-PM 5877), one right metatarsal (UNIRIO-PM 1335), one right metacarpus (UNIRIO-PM 2758), one right calcaneus (UNIRIO-PM 1337), one left calcaneus (UNIRIO-PM 2859), and a right proximal phalanx (UNIRIO-PM 1311), were also recognized.

Right first lower incisor (i1) (UNIRIO-PM 1313). This lower incisor (i1) preserved only its dental crown, without wear and infundibulum (Figs. 3.1–3). A mesial portion of the crown, on the occlusal surface, higher than the distal region, indicates that this is a right incisor (Figs. 3.2–3).

Left first lower incisor (i1) (UNIRIO-PM 1308). This permanent incisor is very fragmented and only preserved its labial portion (i1; Figs. 3.4–5). We recognized this specimen as a lower incisor because it has a coronal angulation lower than the upper incisors. In addition, its mesial portion is slightly higher than most of its apical surface. This specimen is at the same wear level than the incisor UNIRIO-PM 1313, so it was recognized that both are complementary first lower incisors. As the first lower incisors erupt as early as 2.5 years old (Fraústo da Silva *et al*., 2003) and both UNIRIO-PM 1313 and UNIRIO-PM 1308 have no wear, the individual represented by these incisors probably died before this age.

Left third lower premolar (dp3) (UNIRIO-PM 1317). This lower premolar is very fragmented, missing its entire labio-medial portion (Figs. 4.1–3). The UNIRIO-PM 1317 has no wear (Fig. 4.1), and it was probably not yet erupted. The permanent p3 usually erupts as from 2.5 to 3 years old (Fraústo da Silva *et al*., 2003). Thus, the individual represented by UNIRIO-PM 1317 was under 2.5 years old at the moment of death.

Left third lower molar (m3) (UNIRIO-PM 1312). This molar is fragmented, without wear, missing the entire labio-medial portion (Figs. 4.4–6). Moreover, the root is missing, although a detailed analysis indicated that, possibly, it had not been completely formed. The m3 erupts from 3.5 to 4 years old (Fraústo da Silva *et al*., 2003) so the individual represented by UNIRIO-PM 1312 was under 3.5 years old when it died.

Unidentified left lower tooth (UNIRIO-PM 1336). It was not possible to identify the specimen UNIRIO-PM 1336 because of its very fragmentary condition (Figs. 4.7–9). This specimen preserved only the metastilid and its anterior cusp, which have no wear.

Right second upper premolar (dP2) (UNIRIO-PM 1314). This specimen is fragmented, missing only part of its lingual portion (Figs. 5.1–3). Note the circular protocone in occlusal view (Fig. 5.1), attesting its identification as *E. neogeus*. Contrary to the wear pattern described previously, this equid tooth is worn. Considering that the P2 erupts from 2.5 to 3 years old (Fraústo da Silva *et al*., 2003), this individual represented by UNIRIO-PM 1314 was around 2.5 years old when it died. Still, the presence of other morphological features, such as a less evident pli-caballin and a well-defined hypoconal groove, may indicate that this individual was at an initial wear stage of P2 when it died (Fig. 5.1).

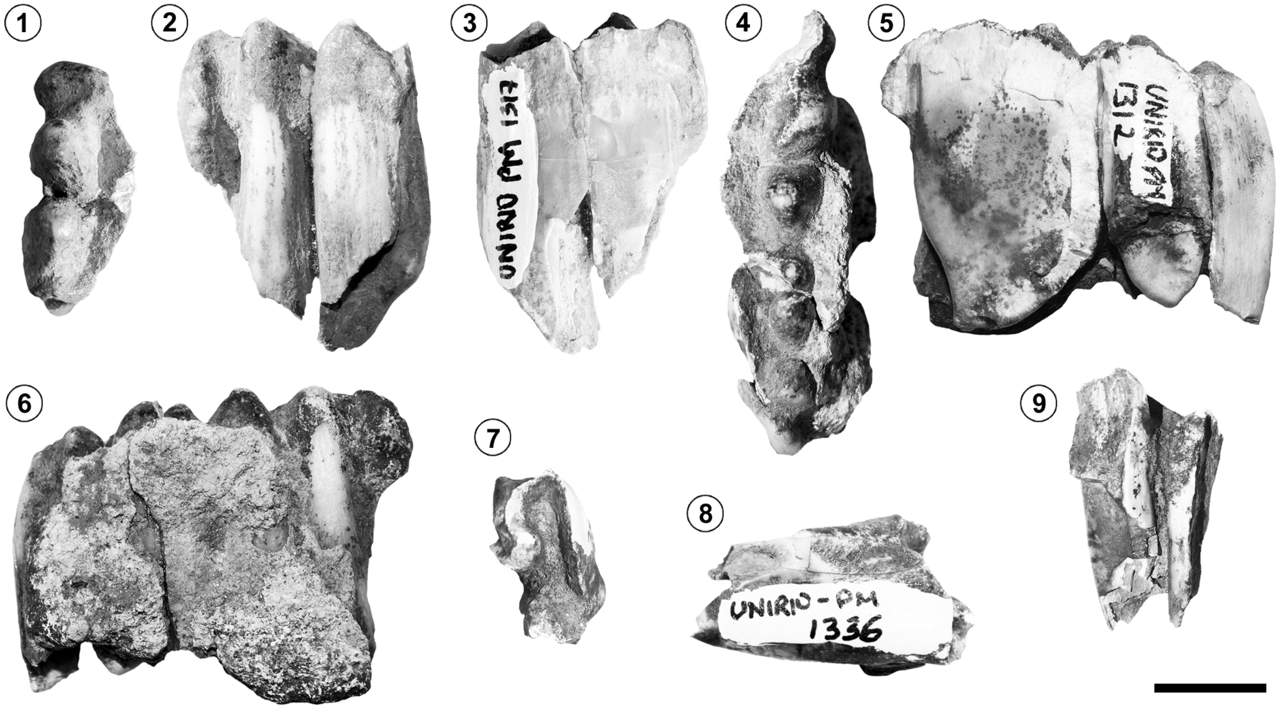

Figure 4. Lower teeth of ***Equus neogeus*** recovered from the Gruta do Urso cave. **1–3,** third lower left premolar (**UNIRIO-PM** 1317); **1,** occlusal view; **2,** lingual view; **3,** labial view. **4–6,** third lower left molar (**UNIRIO-PM** 1312); **4,** occlusal view—note that this tooth has no wear and exhibits all cusps; **5,** lingual view; **6,** labial view. **7–9,** unidentified lower left tooth (**UNIRIO-PM** 1336); **7,** occlusal view; **8,** distal; **9,** medial view. Scale bar= 1 cm.

Right upper premolar (UNIRIO-PM 1316). This specimen has only the labial portion of the crown preserved (Figs. 5.4–6) and, because of its poor preservation, it was not possible to deeply identify this teeth.

Right third upper premolar (P3) (UNIRIO-PM 1315). This is the best well-preserved dental specimen of *Equus* recovered from the Gruta do Urso cave (Figs. 5.7–9). A very triangular protocone in the P3 assures that this specimen is *Equus* and not *Hippidion* (the latter has an oval or rounded protocone). This tooth is longer mesio-distally than linguo-labially, which is characteristic of P3 (compared to P4 and molars). The P3 erupts from 2.5 to 3 years old (Fraústo da Silva *et al.*, 2003). The UNIRIO-PM 1315 is slightly worn and, compared to UNIRIO-PM 1314 (the other upper premolar recovered from Gruta do Urso), it is even less worn. These two specimens might be from the same individual because the P2 distal part fits well the P3 mesial portion. Additionally, it is expected that the P2 would be a little more worn than the P3, because the former erupts earlier (Fraústo da Silva *et al.*, 2003). Moreover, this tooth did not erupt a long time before the death of the individual, because some structures, such as the pli-caballin, the parastyle, and the mesostyle, are still well-defined, not very worn out, and the prefossette and postfossette are not very open.

Proximal epiphysis of right humerus (UNIRIO-PM 1309). This specimen is represented by a fragmented humeral head (Figs. 6.1–4) with a wide fossa and an intertuberal sulcus; the intermediate tubercle is worn out (Figs. 6.2–3). The great tubercle and lateral tubercle present a smooth fragmentation on their caudal portion (Fig. 6.2). It is possible to observe that the humerus epiphysis was not completely fused with the diaphysis. Additionally, the internal spongy portion of the humerus is still very incomplete, which could be an indicative of an uncompleted fusion of the proximal epiphysis. The fusion of proximal epiphysis of horses is very late and this process is completed as from 3 to 3.5 years old (Bennett, 2008).

Pelvis (UNIRIO-PM 1338). The UNIRIO-PM 1338 is a right pelvic bone including a complete acetabular region, with fragmentations at the ischium and ilium articulations (Figs.

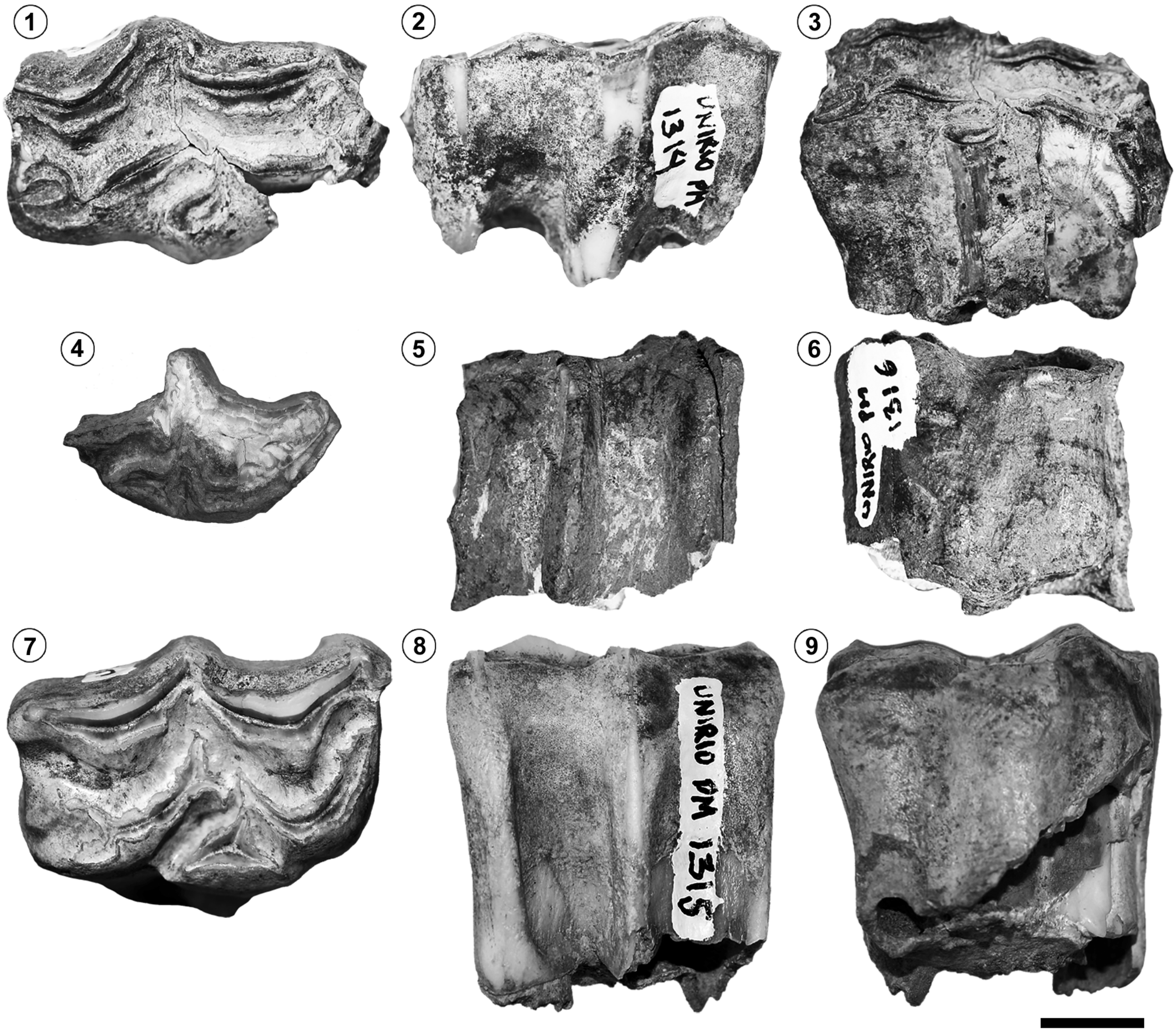

Figure 5. Upper teeth of ***Equus neogeus*** recovered from the Gruta do Urso cave; **1–4,** second upper right deciduous premolar (**UNIRIO-PM** 1314); **1,** occlusal view; **2,** labial view; **3,** lingual view; **4,** occlusal view. **5** and **6,** right upper premolar (**UNIRIO-PM** 1316); **5,** lingual view; **6,** labial view; **7–9,** third upper right premolar (**UNIRIO-PM** 1315); **7,** occlusal view. Note the triangular protocone, one of the diagnostic features for ***Equus***; **8,** lingual view; **9,** labial view. Scale bar= 1 cm.

6.5–6). Medially, the iliopubic eminence articulation is preserved but covered by sediment. The articular face of the acetabulum and the acetabular fossa are deep and the former presents all its borders preserved. The anterolateral portion of the obturator foramen was recognized at the posteromedial region of the acetabulum (Fig. 6.5). In a dorsal view, the ischiatic spine is well-marked and runs anteroposteriorly (Fig. 6.4).

Right third metatarsus (UNIRIO-PM 1335). Only the proximal epiphysis and part of the diaphysis are preserved in this specimen, recognized as a right third metatarsus (Figs. 7.1–3). The proximal epiphysis is fused to the diaphysis and, according to Bennett (2008), this fusion occurs at a very early age, from before birth to six months old. While the palmar surface of the diaphysis is well-preserved, presenting the articulation for the second and fourth metatarsi (Fig. 7.2), the lateral surface is very fragmented (Fig. 7.3). The proximal articulation facets are all very worn, but the facet for the fourth tarsial is missing.

Right calcaneus (UNIRIO-PM 1337). The right calcaneus is lacking the tuber calcis and the region of the sustentacular facet (Figs. 7.4–7)—the former was probably not fused. The

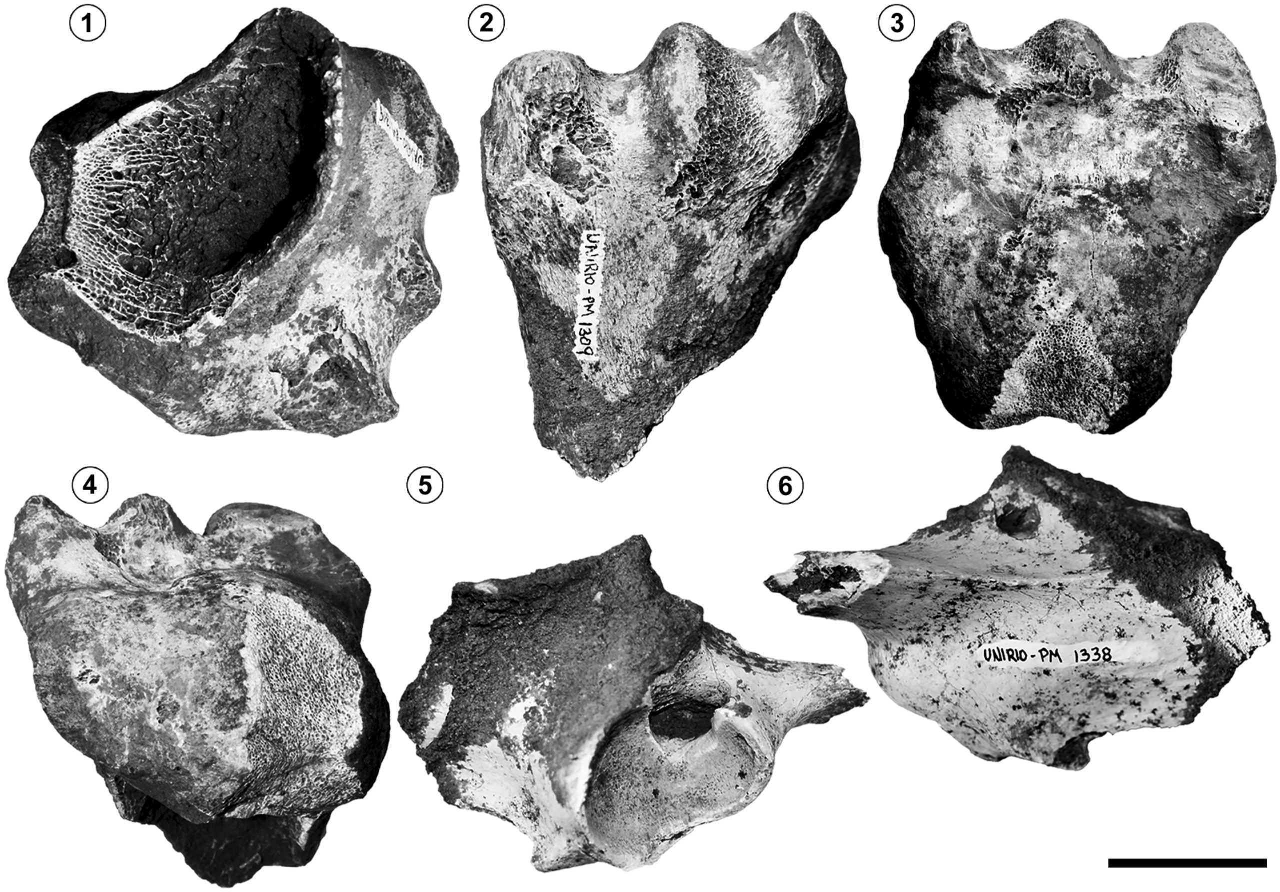

Figure 6. Postcranial bones of ***Equus neogeus*** recovered from the Gruta do Urso cave; **1–4,** proximal epiphysis of right humerus (**UNIRIO-PM 1**309); **1,** distal view. Note the large bite mark at the base of its proximal epiphysis, exposing the medullar tissue; **2,** anterior view; **3,** proximal view**; 4,** posterior view; **5** and **6,** pelvis (**UNIRIO-PM** 1338); **5,** medial view; **6,** dorsal view. Scale bar= 3 cm.

tuber calcis fusion occurs in individuals of around 3 years old (Bennett, 2008). Consequently, the individual represented by the calcaneus UNIRIO-PM 1337 was probably younger than 3 years old at the time of death. The lateral surface is very worn, exposing its spongy internal portion (probably due to transportation; Fig. 7.7). The medial surface bears a great sediment incrustation (Fig. 7.6). The ectal, cuboid and fibular facets are preserved, but the latter is incrustrated by sediments (Fig. 7.4).

Right first phalanx III (UNIRIO-PM 1311). The specimen UNIRIO-PM 1311 is a right first phalanx of the third metapodium, missing both the proximal and the distal epiphyses (Fig. 8). All surfaces of the diaphysis are very worn, probably because of transportation during the deposition process, which prevented the preservation of anatomical features of this phalanx. Possibly, this resulted in very fragile borders of the diaphysis and, after the specimen was photographed, part of its palmar wall eroded, exposing its internal spongy structure. This exposed that the phalanx was not completely ossified internally. The complete internal ossification of the first phalanx in horses occurs before birth, as well as the fusion of its distal epiphysis (Bennett, 2008). The fusion of the proximal epiphysis of this bone occurs later, between 1 to 1.5 years old (Bennett, 2008). However, UNIRIO-PM 1311 has the size expected for an almost adult individual. Consequently, the absence of ossification and the non-fusion of both epiphyses in an almost adult individual could be related with a case of osteopathology.

Pelvis (UNIRIO-PM 5877). The UNIRIO-PM 5877 is a right pelvic bone with a complete acetabular region (Figs. 9.1–3). The articular face of the acetabulum is deep, as well as the acetabular fossa, and its borders are covered by sediment, as well as the pubic groove (Fig. 9.1). The specimen is fragmented in the iliopubic eminence, in the acetabular branch and where it articulates with the body of the ilium. The fragmented portion where it articulates with the acetabular branch is completely covered by a depositional matrix (Fig. 9.2). The anterolateral portion of obturator foramen was recognized at the posteromedial region of the acetabulum. In dorsal view (Fig. 9.3), the specimen is fragmented, and only a part of the ischiatic spine, is observable because it is covered by sediment.

Third metacarpus (UNIRIO-PM 2758). The UNIRIO-PM 2758 is a little right metacarpus, diagonally fragmented from the distal supra-articular portion to the diaphysis, revealing its spongy internal structure (Figs. 9.4–5). The proximal epiphysis and a great part of the diaphysis are not present. In dorsal view, the lateral and medial condyles are separated by a well-marked sagittal crest (Fig. 9.6).

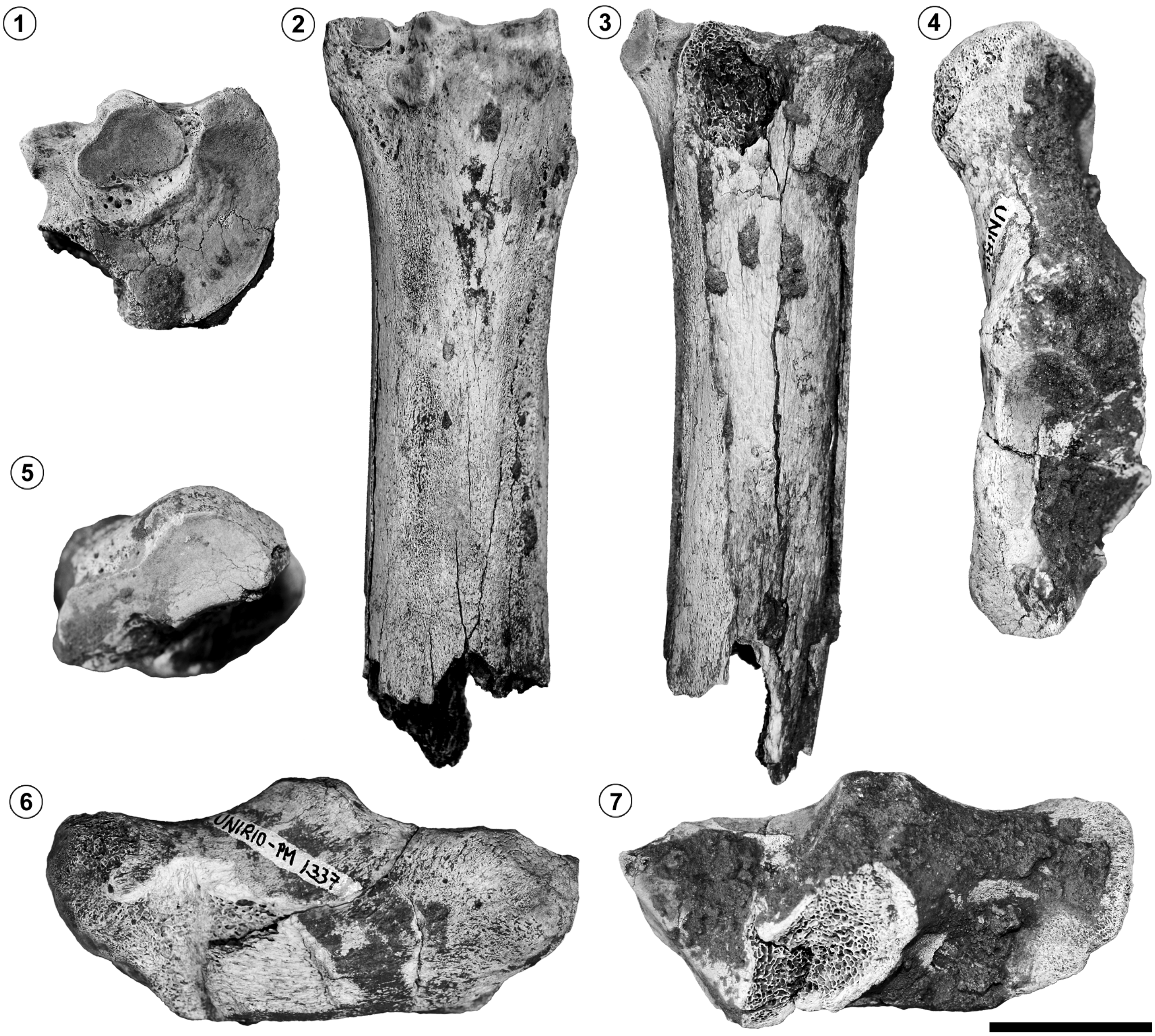

Figure 7. Postcranial bones of ***Equus neogeus*** recovered from the Gruta do Urso cave; **1–3,** right third metatarsus (**UNIRIO-PM** 1335); **1,** proximal view; **2,** palmar view; **3,** lateral view; **4–7,** right calcaneous (**UNIRIO-PM** 1337); **4,** anterodorsal view; **5,** proximal view; **6,** medial view**; 7,** lateral view. Scale bar= 3 cm.

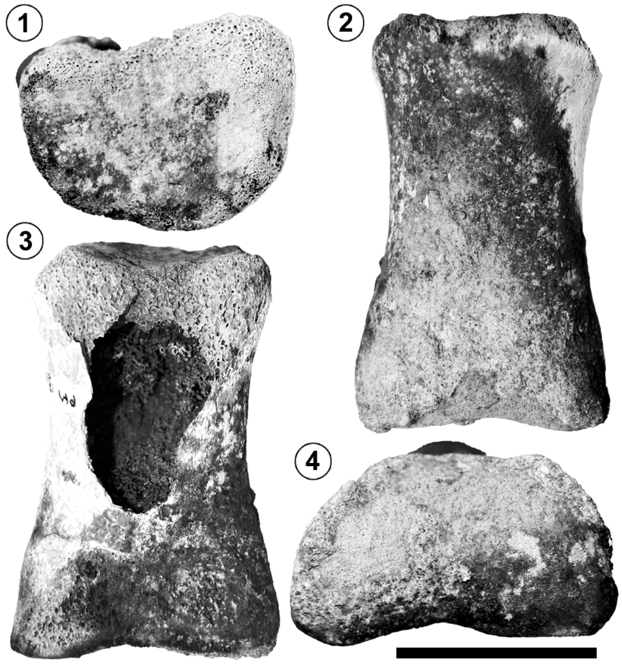

Figure 8. Postcranial bones of ***Equus neogeus*** recovered from the Gruta do Urso cave; **1–4,** first phalanx III (**UNIRIO-PM** 1311); **1,** proximal view; **2,** dorsal view; **3,** palmar view**; 4,** distal view. Scale bar= 3 cm.

Left calcaneus (UNIRIO-PM 2759). The UNIRIO-PM 2759 is a little left calcaneus lacking the tuber calcis and the sustentacular facet region, representing an immature individual (Fig. 9.7–8). The specimen presents the coracoid process but is fragmented in the fossa and in the portion that articulates with the talus, presenting only the posterior articular surface (Fig. 9.8). The lateral surface is covered by a sedimentary matrix.

PALEOBIOLOGY, PALEOECOLOGY, DATINGS AND TAPHONOMIC ASPECTS

The molar UNIRIO-PM 1004 was used as sample to conduct the absolute dating analysis by Electron Spin Resonance, which resulted in 23.7 ky BP (late Pleistocene). This indicates that *Equus neogeus* from the Gruta do Urso cave inhabited its surroundings during the Last Glacial Maximum. Before this study, the fossiliferous deposit of Gruta do Urso had some other absolute datings for its base and top, which ranged from 22 kyBP to 3.8 kyBP (Rodrigues *et al.*, 2014; Maldonado *et al.*, 2016). The *Equus* fossils herein

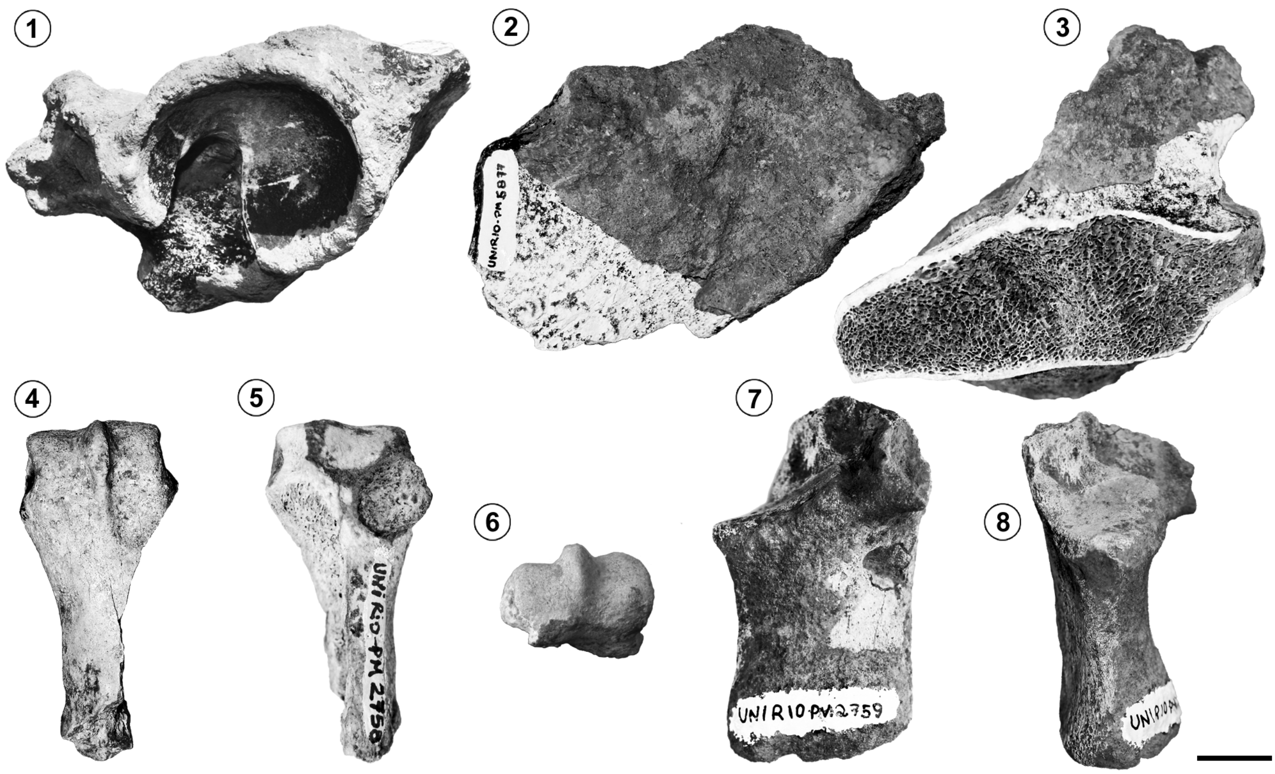

Figure 9. Postcranial bones of ***Equus neogeus*** recovered from the Gruta do Urso cave; **1–3,** pelvis (**UNIRIO-PM** 5877); **1,** medial view; **2,** dorsal view**; 3,** lateral view**; 4–6,** right third metacarpus (**UNIRIO-PM** 2758); **4,** proximal view; **5,** palmar view**; 6,** distal view; **7** and **8,** left calcaneus (**UNIRIO-PM** 2759); **7,** medial view; **8,** anterodorsal view. Scale bar= 5 cm

described are the oldest elements known from the Gruta do Urso deposit, increasing the early range limits for this deposit 1.7 kyBP, from 22 kyBP to 23.7 kyBP. Thus, the mammalian fossils assemblage of Gruta do Urso was deposited from the SALMA Lujanian (Late Pleistocene/early Holocene; Cione and Tonni, 1999) until the middle Holocene.

The Equidae teeth recovered from Gruta do Urso have little wear or no wear (Figs. 3–5). The eruption pattern (Fraústo da Silva *et al.*, 2003; Bennett, 2008) of each tooth was analyzed, and it was possible to infer that the *Equus neogeus* from the Gruta do Urso cave were between 2 and 3.5 years old when they died (Tab. 1). Additionally, a similar age group was estimated when analyzing the epiphysis fusion pattern of each of the preserved postcranial bones (Tab. 1). Nevertheless, the first phalanx fossil from the same site (UNIRIO-PM 1311, Fig. 8) does not follow the estimated age of the other fossils of *E. neogeus*. In accordance to Bennett (2008), the UNIRIO-PM 1311 individual was probably a fetus because it has both epiphyses of the first phalanx unfused (Fig. 8; Tab. 1).

The *Equus* sample analyzed from the Gruta do Urso cave is composed of several isolated specimens, which present taphonomic features such as biogenic traces, weathering, abrasion, and staining.

All *Equus neogeus* specimens recovered from the Gruta do Urso cave were collected between the entrance of the secondary conduct and the second curve of the same conduct. However, a size sorting of bioclasts was recognized: all postcranial elements (Figs. 6–9), the complete teeth (Figs. 3, 5) and the denser elements were recovered in the entrance of the secondary conduct while the partially fragmented teeth (Fig. 4) were collected only between the entrance of the secondary conduct and the first curve; as for the lighter specimens, the incisors (Fig. 3) and the very fragmented premolar UNIRIO-PM 1312 (Fig. 4.5–6), were collected at the second curve. No Equidae fossil was collected in the second curve of the secondary conduct.

Desiccation marks were observed on metacarpus III (UNIRIO-PM 2758, Figs. 10–11), metatarsus III (UNIRIO-PM 1335, Figs. 10–11), the calcaneus (UNIRIO-PM 1337, Fig. 9), the calcaneus (UNIRIO-PM 2759, Fig. 9) and the acetabulum (UNIRIO-PM 1338, Fig. 10). All marks were assigned to the stage 1 of Behrensmeyer's Weathering Scale (Behrensmeyer, 1978) but one (recognized on metatarsus III), which was identified as stage 3 (Fig. 10.4). The presence of desiccation marks in the equid specimens suggests that the death occurred outside the Gruta do Urso cave, and the carcasses were exposed during a time span between one to five years until they were transported and buried into the cave (Behrensmeyer, 1978).

Additionally, three incrustation stages were recognized (*sensu* Maldonado *et al.*, 2016): (i) stage 0, bony surface not

***Table 1** – Estimative of ontogenetic age of equid fossils recovered from Gruta do Urso cave, using Fraústo da Silva* et al. *(2003) and Bennett (2008) age groups estimations. BB means Before Birth.*

Ontogenetic Events	*Age (in years)*									
	BB	*0.5*	*1*	*1.5*	*2*	*2.5*	*3*	*3.5*	*4*	*4.5*
First lower incisor eruption						■	■			
Third lower premolar eruption						■	■			
Third lower molar eruption								■	■	
Second upper premolar eruption						■	■			
Third upper premolar eruption						■	■			
Humerus Proximal epiphysis fusion							■	■		
Metatarsus Proximal epiphysis fusion	■									
Tuber Calcis fusion							■			
First Phalanx Proximal epiphysis fusion			■	■						
First Phalanx Distal epiphysis fusion	■									

covered by concretions; (ii) stage 1, until 50% of the bony surface covered by concretions; and (iii) stage 2, up to 50% of the bony surface covered by concretions. Considering this classification, two specimens were assigned to stage 0 (UNIRIO-PM 1335 and UNIRIO-PM 2758), only one element was attributed to stage 2 (UNIRIO-PM 5877), and all the remaining fossils were classified in stage 1 of incrustation.

The presence of sharp edges in the fragmented portions of the humerus (UNIRIO-PM 1309, Fig. 6), the acetabulum (UNIRIO-PM 1338, Figs. 9–10) and metatarsus III (UNIRIO-PM 1335) suggests a minor degree of transport from the death site to the Gruta do Urso cave (Shipman *et al.*, 1981; Fiorillo, 1988). On the other hand, some specimens—although not fragmented—are hydraulically abraded (*e.g.*, calcaneus and phalanx), thus indicating some degree of transport. In addition, the preservation of the fossils in fine sediments and the minor bioclastic sorting are indicative of low-energy transport.

Some specimens have punctures, pits, and bony erosions, interpreted as the result of predation or scavenging activity by other vertebrates (Figs. 10–11). In cranial view, the humerus (UNIRIO-PM 1309, Fig. 11) has a set of pits associated with a bony erosion below the great tubercle. Besides, in the same view, there are pits, also related to bony erosions, which extend from the cranial base of the lateral tubercle to its apex. In caudal view, there are scratches also related to continuous bony erosions from the cervical region to the humeral head (Fig. 11). In proximal view, there is a shallow pit associated with a scratch, which extends from the caudal base of the intertuberal sulcus, between the lateral tubercle and the intermediate tubercle (Figs. 6, 11). In the same view, there are three parallel scratches in the great tubercle apex (Figure 11.7). The pelvis (UNIRIO-PM 1338, Fig. 10) presents, in dorsal view, a well-marked pit (length= 7.37 mm; width= 7.61 mm) on the base of the ischiatic spine. The third metatarsus (UNIRIO-PM 1335, Fig. 11) presents, in lateral view, a big puncture (length= 16.73 mm; width= 15.32 mm) associated with a removal of the articular surface in the proximal epiphysis (Figure 11.4). The left calcaneus (UNIRIO-PM 2759) presents a puncture (length= 15.42 mm; width= 13.76 mm), also suggesting predatory/scavenging activity.

Besides the tooth marks, the physical integrity of all postcranial specimens varies from partial to fragmented and, apparently, the bony erosions are also associated with large bites assigned to scavengers. A large bite was observed in the base of the proximal epiphysis of the humerus (UNIRIO-PM 1309, Figs. 6, 11), causing the exposition of the medullar tissue. Generally, scavengers break bones to access the marrow tissue, which has a high nutritional value (Behrensmeyer, 1975; Haynes, 1980). Such bite is continuous toward the neck and head of the humerus. The articulation of the acetabulum with the ilium and ischium (acetabulum, UNIRIO-PM 1338, Fig. 10) presents a fragmentation that resembles tooth marks. These regions absent in the haunch bone are near larger concentrations of muscles of the axial skeleton. The metatarsus III (UNIRIO-PM 1335, Figs. 10–11) is distally fragmented and with a spiral fracture resembling that of a bone broken during scavenging (see Haynes, 1983).

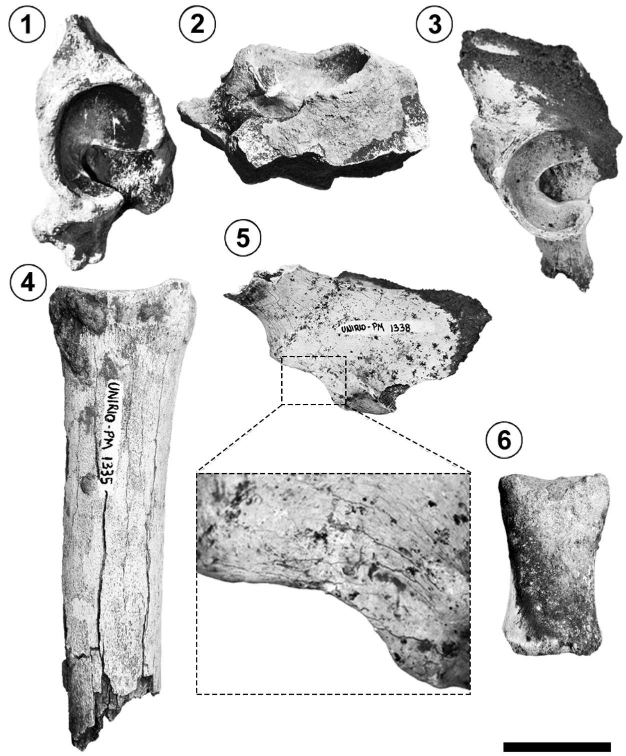

Figure 10. Taphonomic features observed in the ***Equus neogeus*** remains from the Gruta do Urso cave; **1, UNIRIO-PM** 5877 right pelvic bone with stage 2 of incrustation; **2, UNIRIO-PM** 5877 right pelvic bone with different coloration marks and incrustation; **3, UNIRIO-PM** 1338 right pelvic bone with stage 1 of incrustation; **4, UNIRIO-PM** 1335 right third metatarsus with stage 3 of desiccation and spiral fracture; **5, UNIRIO-PM** 1338 right pelvic bone with stage 1 of desiccation; **6, UNIRIO-PM** 1311 right first phalanx III with dark olive brown staining and stage 1 of incrustation. Scale bar= 4 cm.

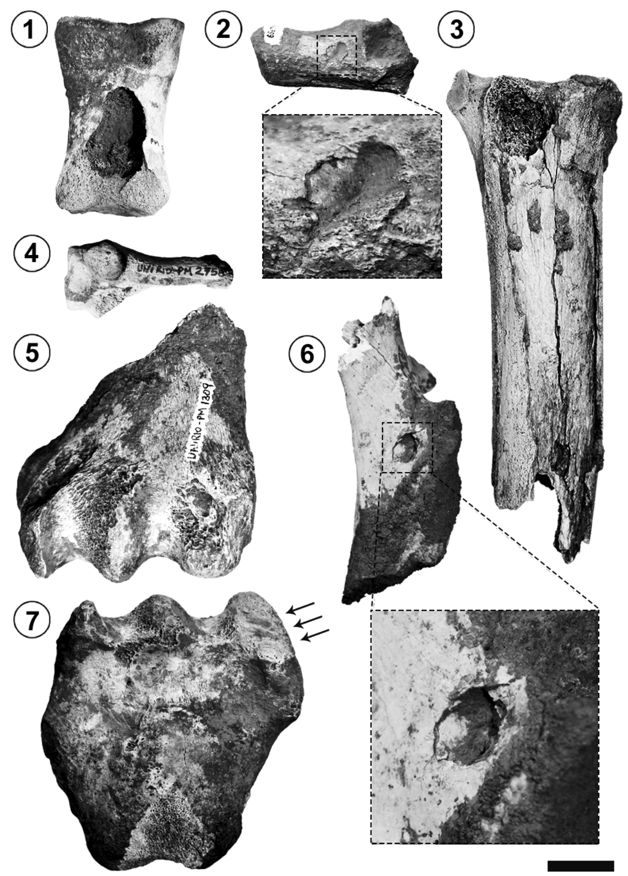

Figure 11. Taphonomic features observed in the ***Equus neogeus*** remains from the Gruta do Urso cave: **1, UNIRIO-PM** 1311 right first phalanx III with bone removal caused by scavengers; **2, UNIRIO-PM** 2759 left calcaneus with a puncture caused by predator activity; **3,** Big puncture highlight of **UNIRIO-PM** 1335 right third metatarsus, caused by predator activity; **4, UNIRIO-PM** 2758 right third metatarsus with a big puncture; **5, UNIRIO-PM** 1309 proximal epiphysis of right humerus with three tooth marks (scratches); **6, UNIRIO-PM** 1338 right pelvic bone with a well-marked pit in dorsal view; and, **7**, three tooth marks (scratches) highlight in proximal epiphysis of right humerus of **UNIRIO-PM** 1309. Scale bar= 2 cm.

We excluded the possibility of these features having been produced during the collection or preparation of the specimens because all the regions affected by such features are filled by sediments or with a color pattern similar to that of the non-affected surface. The association between these features with desiccation marks suggests that all these signatures were produced during the biostratinomic phase rather than during the fossil diagenetic one. We exclude the hypothesis of trampling because we have not observed other diagnostic signatures such as non-oriented scratches (see Araújo-Júnior *et al.*, 2011).

Through the exclusion of other processes and due to the resemblance with bite marks, we interpret the features discussed herein as generated during events of scavenging (Haynes, 1983). Although evidence of scavenging has been interpreted, we have not enough evidence to conclude whether the scavengers were responsible by the death of the horses or only consumed their carcasses. Among the taxa recorded in the fossil assemblage of Gruta do Urso (Rodriguez *et al.*, 2013; Rodrigues *et al.*, 2014, 2016), the following carnivores can be erected as the possible scavengers: (i) the felid *Panthera onca* Linnaeus, 1758; and (ii) the ursid *Arctotherium wingei* Ameghino, 1902.

According to Haynes (1983), large felids, such as *P. onca*, do not fragment and consume large bones, such as the humerus. Besides, according to Burke (2013), felids leave only furrows and pits on bones, and do not produce scratches. Furthermore, bone concentrations produced by felids have large amounts of complete long bones with little signs of fragmentation/bone removals (Dominguez-Rodrigo and Pickering, 2010), which is not observed in the specimens from Gruta do Urso (*i.e.*, all specimens show evidence of fragmentation and/or bone removal).

According to Burke (2013), taphonomic modifications produced by ursids include prominent furrowing on the greater trochanter with punctures surrounding the epiphyses between the trochanter and the remainder of the diaphyses. Furthermore, scratches may occur associated with punctures and pits in the cases of scavenging by ursids (Saladié *et al.*, 2011: fig. 8; Burke, 2013; Arilla *et al.*, 2014: fig. 6). Thus, considering the patterns of punctures, pits, scratches, bone removals and fragmentation observed in the equid specimens (Figs. 10–11) match with those described as produced in events of scavenging by ursids (Haynes, 1983; Saladié *et al.*, 2011; Burke, 2013; Sala and Arsuaga, 2013; Arilla *et al.*, 2014). Thus, in the case of the Gruta do Urso cave, *Arctotherium wingei* can be erected as the possible scavenger of the horses. It is noteworthy that ursids scavenger habit occurs only during periods of nutritional stress (Garshelis, 2009).

Additionally, through actualistic studies, Sala and Arsuaga (2013) and Arilla *et al.* (2014) revealed that ursids do not transport skeletal elements from their place of consumption, *i.e.*, they consume carcasses outside the caves, differing from felids, which can consume it inside the caves

(Sauqué *et al*., 2014). The presence of scavenging evidence and wear marks—indicating hydraulic transport—suggests that the scavengers consumed the carcass outside the cave and, then, the bones were transported by some kind of hydraulic flow into the cave.

Evidence of ecological interaction among extinct mammals of the Quaternary of Brazil have been observed in deposits of the states of Minas Gerais (Dominato *et al*., 2011) and Ceará (Araújo-Júnior *et al*., 2011), however, they are related to the interaction canids-proboscideans and canids-xenarthrans, respectively. Recently, Reyes *et al.* (2013) observed evidence of interaction between canids and glyptodonts in Argentina. This work reports the first record of interaction between ursids and equids from the Quaternary of South America.

CONCLUSIONS

The fourteen *Equus neogeus* specimens described herein from the Gruta do Urso cave, a new locality for fossil horses in Brazil, were assigned to young individuals of between 2 to 3.5 years old. They possibly died outside the cave and experienced weathering prior to final burial inside the cave. Furthermore, in accordance with the taphonomic signature on the horse elements, we identified the scavenging activity by a nutritionally-stressed individual of *Arctotherium wingei*, an unprecedented feeding behavior for ursids in South America.

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REFERENCES

Alberdi, M.T., Cartelle, C., and Prado, J.L. 2003. El registro de Pleistoceno de *Equus* (*Amerhippus*) e *Hippidion* (Mammalia, Perissodactyla) de Brasil. Consideraciones paleoecológicas y bio- geográficas. *Ameghiniana* 4: 173–196.

Alberdi, M.T., and Prado, J.L. 2004. *Caballos fósiles de America del Sur: Una historia de tres millones de años.* Universidad Nacional del Centro de la Provincia de Buenos Aires. INCUAPA, Buenos Aires, 269 p.

Ameghino, F. 1902. Notas sobre algunos mamíferos fósiles nuevos o poco conocidos del valle de Tarija. *Anales del Museo Nacional Buenos de Aires* 3: 225–261.

Araújo-Júnior, H.I., Porpino, K.O., and Bergqvist, L.P. 2011. Marcas de dentes de carnívoros/carniceiros em mamíferos pleistocênicos do Nordeste do Brasil. *Revista Brasileira de Paleontologia* 14: 292–296.

Arilla, M., Rosell, J., Blasco, R., Domínguez-Rodrigo, M., and Pickering, T.R. 2014. The "Bear" Essentials: Actualistic research on *Ursus arctos arctos* in the Spanish Pyrenees and its implications for Paleontology and Archaeology. *PLoS ONE* 9: e102457.

Avilla, L.S., Figueiredo, A.M.G., Kinoshita, A., Bertoni-Machado, C., Mothé, D., Asevedo, L., Baffa, O., and Dominato, V.H. 2013. Extinction of a gomphothere population from Southeastern Brazil: Taphonomic, paleoecological and chronological remarks. *Quaternary International* 305: 85–90.

Behrensmeyer, A.K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages of lake Rudolf, Kenia. *Bulletin of the Museum of Comparative Zoology* 46: 437–578.

Behrensmeyer, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150–162.

Behrensmeyer, A.K., Kidwell, S.M., and Gastaldo, R.A. 2000. Taphonomy and Paleobiology. *Paleobiology* 26: 103–147.

Bennett, D. 2008. *Timing and rate of skeletal maturation in horses, with comments on starting young horses and the state of the Industry*. World Wide Web: http://www.equinestudies.org/ranger_2008/ranger_piece_2008_pdf1.pdf

Burke, C.C. 2013. Neotaphonomic analysis of the feeding behaviors and modification marks produced by North American carnivores. *Journal of Taphonomy* 11: 1–20.

Cione, A.L., and Tonni, E.P. 1995. Chronostratigraphy and Land mammal ages: The Uquían problem. *Journal of Paleontology* 69: 135–159.

Cione, A.L., and Tonni, E.P. 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean area, Argentina. In: J. Rabassa, and M. Salemme (Eds.), *Quaternary of South America and Antarctic Peninsula*. CRC Press, Boca Raton, p. 23–51.

Cione, A.L., and Tonni, E.P. 2005. Bioestratigrafía basada en mamiferos del Cenozoico Superior de la Provincia de Buenos Aires, Argentina. In: R.E. de Barrio, R.O. Etcheverry, M.F. Caballé, and E. Llambias (Eds.), *Geología y Recursos Minerales de la Provincia de Buenos Aires. Relatorio del XVI Congreso Geológico Argentino*. La Plata, p. 183–200.

Companhia de Pesquisa de Recursos Minerais (CPRM). 2006. *Rochas Carbonáticas do Grupo Bambuí na região Nordeste do Estado de Goiás*. World Wide Web: http://www.cprm.gov.br/publique/cgi/cgilua.exe/sys/start.htm?infoid=261&sid=32.

Costa, T.S. 2017. [*O esqueleto pós-craniano de Hippidiformes (Equidae: Mammalia) e aspectos morfofuncionais e adaptativos*. Tesis, Graduação em Ciências Biológicas, Universidade Veiga de Almeida, Rio de Janeiro, 44 p. Unpublished.].

Dominato, V.H., Mothé, D., Avilla, L.S., and Bertoni-Machado, C. 2009. Ação de insetos em vértebras cervicais *Stegomastodon waringi* (Gomphotheriidae: Mammalia) do Pleistoceno de Águas de Araxá, Minas Gerais, Brasil. *Revista Brasileira de Paleontologia* 12: 77–82.

Dominato, V.H., Mothé, D., da Silva, R.C., and Avilla, L.S. 2011. Evidence of scavenging on remains of the gomphothere *Haplomastodon waringi* (Proboscidea: Mammalia) from the Pleistocene of Brazil: Taphonomic and paleoecological remarks. *Journal of South American Earth Sciences* 31: 171–177.

Dominguez-Rodrigo, M., and Pickering, T.R. 2010.A multivariate approach for discriminating bone accumulations created by spotted hyenas and leopards: harnessing actualistic data from East and Southern Africa. *Journal of Taphonomy* 8: 155–179.

Fraústo da Silva, M.F., Gomes, T., Dias, A.S., Aquino-Marques, J., Mendes Jorge, L., Cavaco Faísca, J., Alexandre Pires, G., and Caldeira, R.M. 2003. Estimativa da idade dos eqüinos através do exame dentário. *Revista Portuguesa de Ciências Veterinárias* 98: 103–110.

Fiorillo, A.R. 1988. Taphonomy of hazard homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. *Contributions to Geology* 26: 57–97.

Garshelis, D.L. 2009. Family Ursidae (Bears). In: D.E. Wilson, and R.A. Mittermeier (Eds.), *Handbook of the Mammals of the World 1—Carnivores*. Lynx, Barcelona, p. 448–492.

Getty, R. 2008. *Anatomia dos Animais Domésticos*. Guanabara Koogan, Rio de Janeiro, 2048 p.

Gray, J.E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository*15: 296–310.

Haynes, G. 1980. Evidence of carnivore gnawing on Pleistocene and recent mammalian bones. *Paleobiology* 6: 341–351.

Haynes, G. 1982. Utilization and skeletal disturbances of North American prey carcasses. *Arctic* 35: 266–281.

Haynes, G. 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology* 9: 164–172.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Holmiae, Stockholm, 847 p.

Lund, P.W. 1840. Nouvelles recherches sur la faune fossile du Brésil. *Annales des Sciences Naturelles* 13: 310–319.

MacFadden, B.J. 1992. *Fossil horses: systematics, paleobiology, and evolution of the family Equidae*. Cambridge University Press, Cambridge, 384 p.

MacFadden, B.J. 2013. Dispersal of Pleistocene *Equus* (Family Equidae) into South America and calibration of GABI 3 based on evidence from Tarija, Bolivia. *PLoS ONE* 8: e59277.

Machado, H., Grillo, O., Scott, E., and Avilla, L.S. 2017. Following the footsteps of the South American *Equus*: Are autopodia taxonomically informative? *Journal of Mammalian Evolution*. doi: 10.1007/s10914-017-9389-6

Maldonado, V., Monteiro, L.G.P.M., Rotti, A., Pereira, C., Araújo-Júnior, H.I., and Avilla, L.S. 2016. Taphonomic aspects of deer (Mammalia, Cetartiodactyla) remains from a Quaternary Cave Deposit in Northern Brazil. *Journal of Sedimentary Environments* 1: 234–248.

Owen, R. 1848. Description of teeth and portions of jaws in two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *H. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London* 4: 103–141.

Prado, J.L., and Alberdi, M.T. 1994. A quantitative review of the genus *Equus* from South America. *Paleontology* 37: 459–481.

Reyes, M., Pioré, D., Soibelzon, L.H., Zurita, A.E., and Arrouy, M.J. 2013. First evidence of scavenging of a Glyptodont (Mammalia, Glyptodontidae) from the Pliocene of the Pampa region (Argentina): taphonomic and paleoecological remarks. *Palaeontologia Electronica* 16: 1–13.

Rodrigues, S., Avilla, L., and Azevedo, S.A.K. 2016. Diversity and Paleoenviromental significance of Brazilian fossil *Galictis* (Carnivora: Mustelidae). *Historical Biology* 28: 907–912.

Rodrigues, S., Avilla, L.S., Soibelzon, L.H., and Bernardes, C. 2014. Late Pleistocene carnivores (Carnivora: Mammalia) from a cave sedimentary deposit in northern Brazil. *Anais da Academia Brasileira de Ciências* 86: 1641–1655.

Rodriguez, S.G., Soibelzon, L.H., Rodrigues, S., Morgan, C., Bernardes, C., Avilla, L.S., and Lynch, E. 2013. First record of *Procyon cancrivorus* (G. Cuvier, 1798) (Carnivora, Procyonidae) in stratigraphic context in the Late Pleistocene of Brazil. *Journal of South American Earth Sciences* 45: 1–5.

Rogers, R.R., Eberth, D.A., and Fiorillo, A.R. 2007. *Bonebeds: Genesis, analysis and paleobiological significance*. University of Chicago Press, Chicago, 399 p.

Sala, N., and Arsuaga, J.L. 2013.Taphonomic studies with wild brown bears (*Ursus arctos*) in the mountains of northern Spain. *Journal of Archaeological Science* 40: 1389–1396.

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., and Carbonell, E. 2011. Taphonomic modifications produced by modern brown bears (*Ursus arctos*). *International Journal of Osteoarchaeology* 23: 13–33.

Sauqué, V., Rabal-Garcés, R., Sola-Almagro, C., and Cuenca-Bescós, G. 2014. Bone accumulation by leopards in the Late Pleistocene in the Moncayo Massif (Zaragoza, NE Spain). *PLoS ONE* 9: e92144.

Shipman, P. 1981. *Life history of a fossil: an introduction to taphonomy and paleoecology*. Harvard University Press, Cambridge, Massachusetts and London, 222 p.

Shipman, P., Bosler, W., Davis, K.L., Behrensmeyer, A.K., Dunbar, R.I.M., Groves, C.P., Thackeray, F., Van Couvering, J.A.H., and Stucky, R.K. 1981. Butchering of Giant Geladas at an Acheulian Site [and Comments and Reply]. *Current Anthropology* 22: 257–268.

Woodburne, M.O. 2010. The Great American Biotic Interchange: Dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution* 17: 245–264.

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