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Damaged glyptodontid skulls from Late Pleistocene sites of northwestern Venezuela: evidence of hunting by humans?

Alfredo A. Carlini¹, Jorge D. Carrillo-Briceño² , Arturo Jaimes³, Orangel Aguilera⁴ , Alfredo E. Zurita⁵, José Iriarte⁶  and Marcelo R. Sánchez-Villagra^{2*} 

Abstract

The Muaco and Taima-Taima sites, in Falcón State of northwestern Venezuela, are among the earliest sites of human occupation in South America containing artifacts associated with preserved megafaunal remains and dating between 19,810 and 15,780 calybp. Here we report novel visual and CT scanning analysis of six glyptodont skulls of *Glyptotherium* cf. *cylindricum* from these sites, of which four exhibit distinct and similar patterns of breakages in the fronto-parietal region that suggest intentional blows by direct percussion by humans, with fractures not being diagenetic but instead antemortem or transmortem. This hypothesized and unreported hunting technique focused in an area of the skull where the cephalic shield becomes thin, thus increasing the effectiveness of the blow. From Taima-Taima other glyptodont remains included an inverted carapace, also previously reported as probable evidence of human–glyptodont interaction during the latest Pleistocene. We estimated that roughly 150–170 Kg of potentially accessible muscles and fat of an adult *Glyptotherium cylindricum* could be used as food sources.

Keywords: Hunting, Glyptodonts, Megafauna, Extinction, South America

Introduction

The role of humans in the Late Quaternary Megafaunal Extinction (LQME) is a matter of continuous controversy (e.g., Martin, 1973; Gill et al., 2009; Rozas-Davila et al., 2016; Prates & Pérez, 2021). Despite the fact that the LQME accounts for the loss of over 80% of large mammal species in South America (Barnosky & Lindsey, 2010), archaeological evidence for the interaction of humans and late Pleistocene megafauna is scarce, in contrast to the number of North American megafauna kill sites. In South America, the predatory nature of human–megafauna interaction and its role in the LQME is a matter of debate (e.g., Borrero, 2009; Raczka et al., 2017). The

great majority of archaeological sites evidencing interactions of humans with extinct megafauna mostly come from the Pampean and Patagonian regions of Argentina and Chile in southern South America (Chichkoyan et al., 2017; Labarca et al., 2020; Politis & Gutiérrez, 1998; Politis et al., 2019; Prates & Pérez, 2021, and references therein). This general biased geographic location of findings is the case also for glyptodonts, the largest armored herbivores among cingulates and one of the most abundant and iconic megafauna species (Zurita et al., 2016). Notwithstanding ample evidence of coexistence between the so-called megafauna and humans in several areas of South America since ca. 12 ka (see, among others Correal Urrego, 1981; Cione et al., 2003, 2009; Borrero, 2009; Barnosky & Lindsey, 2010; Fariña et al., 2014; Pires et al., 2015; Politis et al., 2019; Mothé et al., 2020; Morcote-Ríos et al., 2021; Prates & Pérez, 2021), almost nothing is known about the interaction between glyptodonts and early humans beyond the Pampean–Patagonian region

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*Correspondence: m.sanchez@pim.uzh.ch

² Palaeontological Institute and Museum, University of Zurich, Karl-Schmid-Strasse 4, 8006 Zurich, Switzerland

Full list of author information is available at the end of the article



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of Argentina (Politis & Gutiérrez, 1998). Apart from the Pampas, evidence is limited to the existence of a few glyptodont osteoderms at Late Pleistocene archaeological sites, making it difficult to determine the nature of interaction between humans and these megafaunal forms. Some of the sites with relevant remains were reported more than a century ago (Vogt, 1881), with taxa that included diverse body masses ranging from the small *Neosclerocalyptus* (ca. 300 kg) (Quiñones et al., 2020) to the giant *Doedicurus* weighing almost two tons (Soibelzon et al., 2012). Here we report novel evidence of human–glyptodont interactions from the Late Pleistocene sites of Muaco and Taima-Taima in Venezuela, northern South America. We hypothesize that the unique breakage pattern found on four archaeological glyptodont specimens at these sites represent an unreported human hunting technique involving slamming heavy instruments like stone choppers or wooden clubs on the head. Our interpretation is aided by consideration of taphonomic processes, comparison with skulls on non-archaeological settings (e.g., Carlini et al., 2008; Gillette & Ray, 1981), and a thorough examination of potential signs of human vs natural influence that may result in the breakage patterns observed (Behrensmeyer, 1978). Likewise, we estimated the body mass of the glyptodonts studied (see Fariña et al., 2013) and present an informed discussion on northern neotropical glyptodonts as potential food source for humans.

Overall, the new evidence improved our understanding of human–glyptodont interactions in a region where cingulates show a different taxonomic diversity compared to that of other regions from South America from which such interaction has been reported (Carlini et al., 2008; Cuadrelli et al., 2019).

Study sites and brief archaeological background

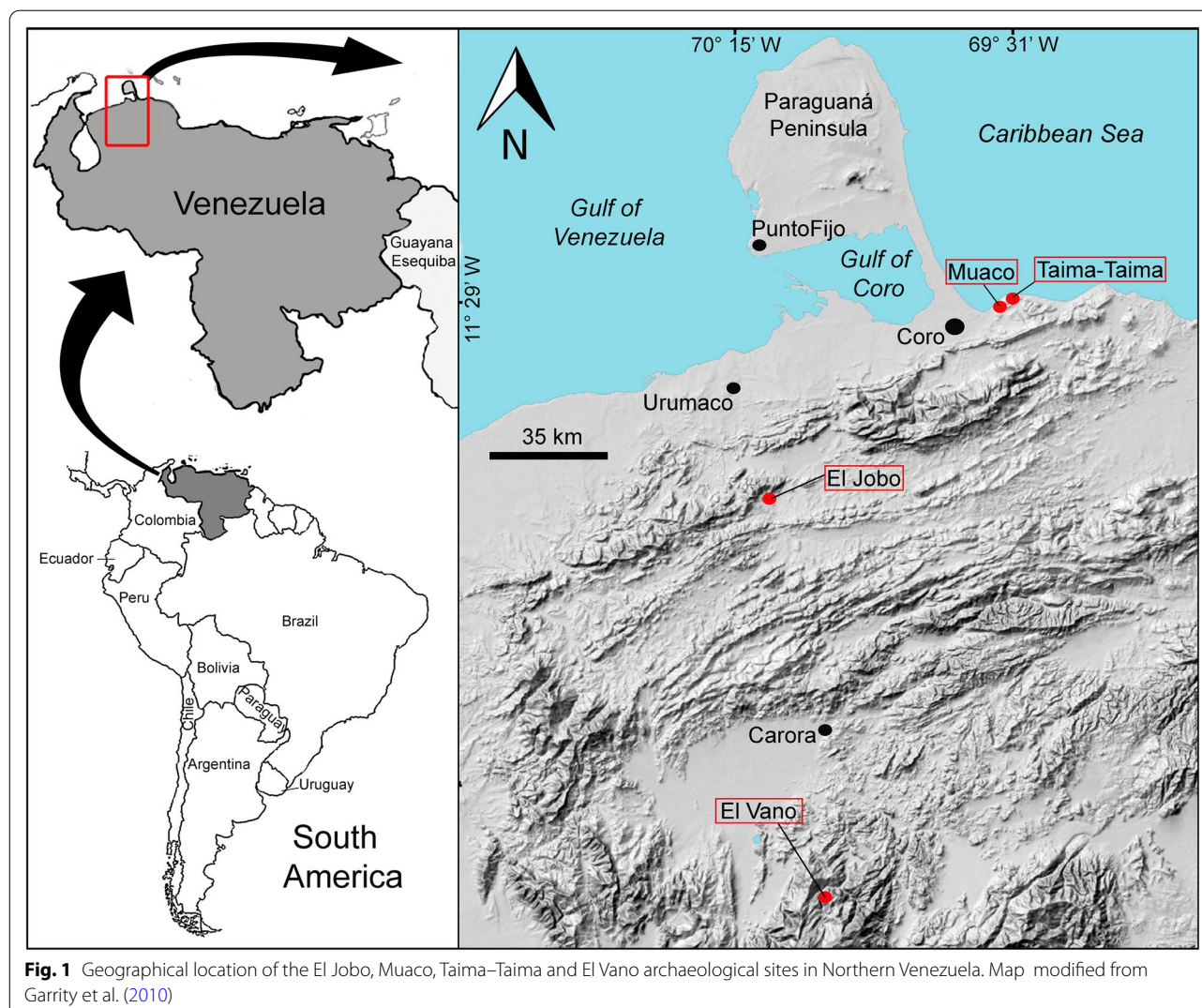
Located in the vicinity of the Caribbean coast of Venezuela in northern South America, which nowadays is a semi-arid region characterized by xerophytic associations (Ochsenius, 1980), the Muaco (11° 28' 50" N, 69° 32' 41" W) and the Taima-Taima (11° 29' 57" N, 69° 31' 20" W) sites are of crucial importance to understand the arrival of humans in South America and their interactions with the South American megafauna. Due to its location at the gateway of South America, this region was central to the interchanges between both American subcontinents, as exemplified by xenarthran megamammals (Carlini & Zurita, 2010), and human dispersal during the Late Pleistocene (Politis et al., 2009).

Beginning in the 1950s, substantial Neogene and Quaternary palaeontological and archaeological discoveries were made in this region of northern South America (Cruxent & Rouse, 1956; Royo y Gómez, 1959, 1960;

Cruxent, 1967, 1970; Bryan et al., 1978; Ochsenius & Gruhn, 1979; Aguilera, 2006; Sánchez-Villagra et al., 2010; Carrillo-Briceño, 2015). The Late Pleistocene sites of Muaco, Taima-Taima and El Jobo (Falcón State, Venezuela) have proven of historical importance in studies of early human occupation in the Americas (Politis et al., 2009) since they were among the first to document pre-Clovis occupations, exhibiting distinct lithic technologies and shedding light on human–megafauna interactions (Cruxent, 1961; Cruxent & Rouse, 1956; Moore, 2014).

The Muaco site is situated on a spring-fed pond (Royo y Gómez, 1959, 1960), still active, which was hypothesized to attract animals and humans during the drier conditions of the Late Pleistocene (Ochsenius, 1980). This site is in a coastal plain, approximately one kilometer from the coast and 17 km northeast of the city of Coro, near the towns of Carrizal and Muaco, Colina municipality (Fig. 1). It corresponds to a continental accumulation characterized largely by muddy sequence preserving a sedimentary environment influenced by a spring-fed pond (Royo y Gómez, 1959, 1960; Cadena & Carrillo-Briceño, 2019). Excavations in Muaco revealed large quantities of well-preserved remains, including tortoises Testudinidae, Podocnemididae and Geoemydidae turtles, snakes, birds, marsupials, rodents, rabbits, proboscideans, ground sloths and glyptodonts (*Xenarthra*), notoungulates, artiodactyls, perissodactyls, and carnivorans (Royo y Gómez, 1959, 1960; Ochsenius, 1980; Aguilera, 2006; Rincón et al., 2006; Soibelzon & Rincón, 2007; Carlini & Zurita, 2010; Carlini et al., 2008; Chávez-Aponte et al., 2008a, 2008b; Carrillo-Briceño, 2015; Cadena & Carrillo-Briceño, 2019). Among the recovered remains, some of which were burned, one bone piece showed parallel-pattern traces of human cutting (see Oliver & Alexander, 2003, fig. 17; Aguilera, 2006, p. 28; Fariña et al., 2014). A fragment of the El Jobo type point and other stone elements such as scraper, a possible knife, and a hammerstones were found also in situ in the same archaeological strata (Rouse & Cruxent, 1963). Chronology ranges between ~19,810 calybp [calibrated years before the present using IntCal20 (Ramsey, 2009)] (16,375 ± 400 ybp) and ~17,420 calybp (14,300 ± 500 ybp) were reported for the Muaco site based on radiocarbon essays on a glyptodont osteoderm and burned bones, respectively (Cruxent, 1961; Rouse & Cruxent, 1963).

In 1961, Cruxent discovered the site of Taima-Taima (Fig. 1), about 3 km northeast of Muaco (Carrillo-Briceño, 2015). Descending springs with permanent water are common in this area, that is why the site of Taima-Taima was initially named “Los Pozos de Royo y Gómez” (Ardila, 1987; Bryan et al., 1978; Cruxent, 1967). Cruxent began excavations of Taima-Taima in



March 1962 (Fig. 2), performing at least four different seasons up to the beginning of the decade of 1970, were some lithic artifacts and abundant remains of megafauna were exhumed (Cruxent, 1967; Carrillo-Briceño, 2015). In 1976, Alan Bryan, Ruth Gruhn and Cruxent excavated the site of Taima-Taima, and four stratigraphic units were identified (Ochsenius & Gruhn, 1979) (Fig. 3), as well as evidence of human action in the oldest (lowest level), represented by several fragmented “El Jobo points” associated with proboscidean bones (Cruxent, 1970; Ochsenius & Gruhn, 1979; Gruhn, 2005). In addition, a distal fragment of a projectile point was recovered from the pelvic cavity of a young gomphotheriid the same year, as well as scattered bone remains from various extinct animals, confirming past interaction between megafauna and humans (Bryan et al., 1978). This whole

assemblage was dated based on several C14 analyses to between $\sim 17,300$ calybp ($14,200 \pm 300$ ybp) and $\sim 15,780$ calybp ($12,980 \pm 85$ ybp) (Bryan & Gruhn, 1979; Bryan et al., 1978), about two millennia younger than the Muaco site (Cruxent, 1961). In sum, the evidence from Taima-Taima demonstrated that a big-game hunting complex tied to the El Jobo technological tradition existed in northern Venezuela at the end of the Pleistocene.

After the excavation of 1976, there was a period of inactivity in the Taima-Taima site. It was not until the late 1980s when Cruxent resumed excavations, especially in the southern section of the area excavated in 1976, performing these until approximately 1992–1993 (Oliver & Alexander, 2003; Carrillo-Briceño, 2015). However, there are no published data from these excavations. Subsequent excavations 1994 and 1996 were carried out to condition

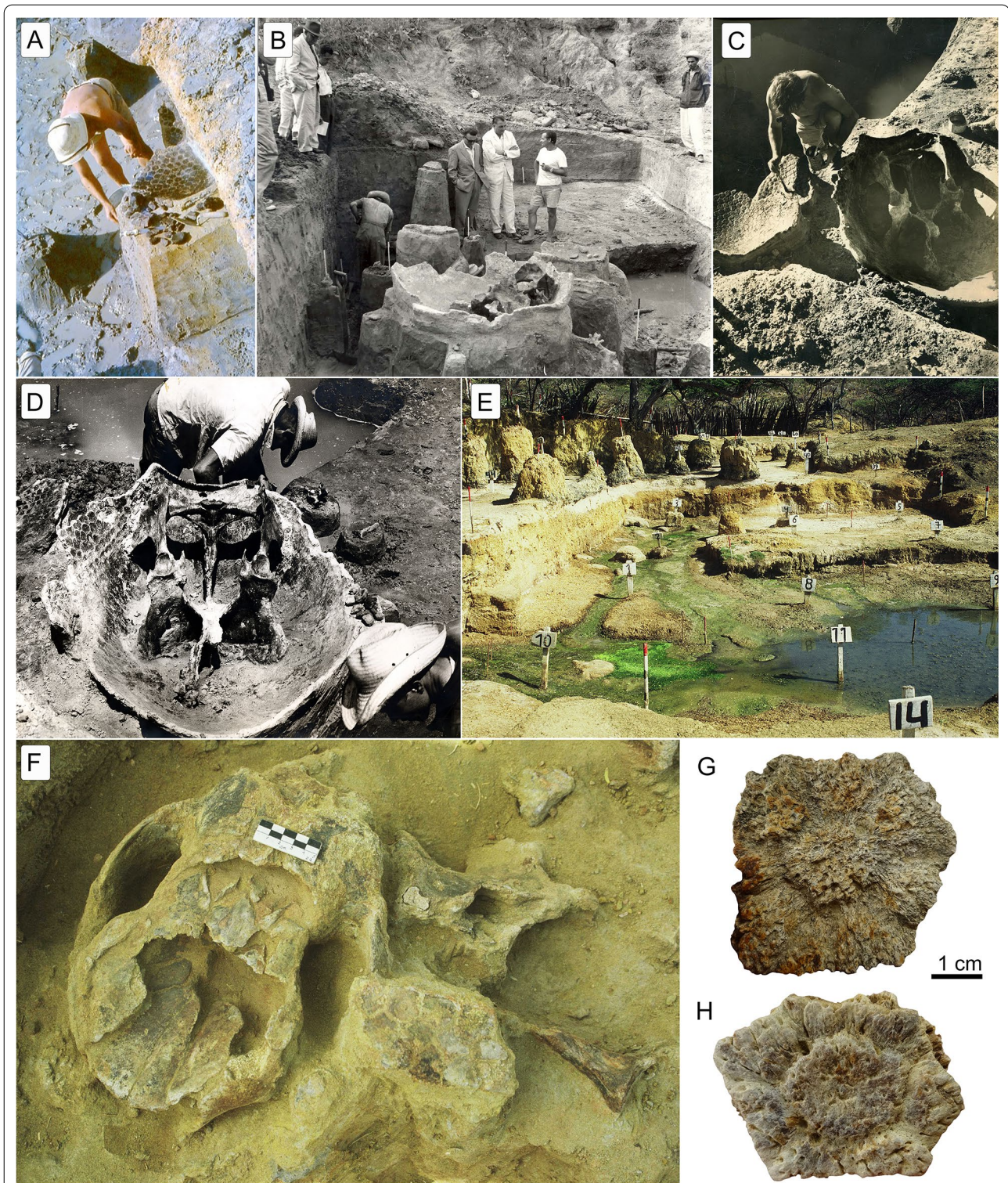
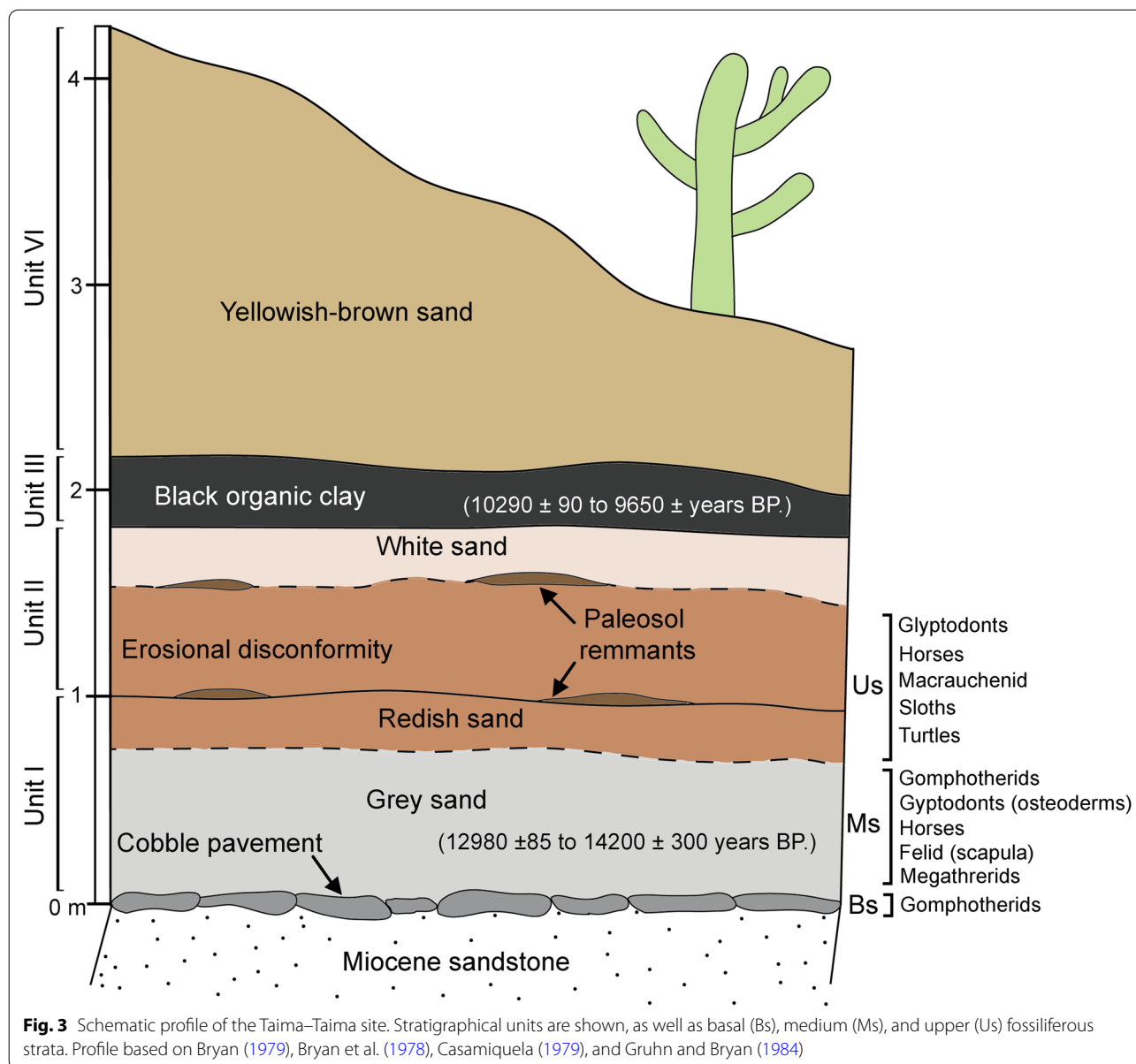


Fig. 2 Glyptodont remains from the Late Pleistocene Taima-Taima and the El Vano sites, Venezuela. Glyptodont carapaces found in Taima-Taima in 1962 ("Los Pozos de Royo y Gómez") (A–D). E Excavation of Taima–Taima in 1996. F Lost *Glyptotherium* cf. *cylindricum* skull in situ showing the fractured area of the hypothesized location of impact; articulated cephalic shield osteoderms are seen on the right side of the skull. G, H. Isolated osteoderms of *Glyptotherium* cf. *cylindricum* from the Late Pleistocene El Vano site. Photographs courtesy of Fundación José María Cruxent (A, C), Archivo de la Universidad Experimental Francisco de Miranda, UNEFM (B, D), and Arturo Jaimes (E, F)



the area for the construction of the in situ archeological and paleontological museum of Taima-Taima that opened in 2000 (Carrillo-Briceño, 2015 fig. 156).

It should be noted that both Muaco and Taima-Taima sites have few dating data, run in the 1970s, with large confidence intervals, which raises issues over the precision and comparability with more recently obtained dates run with state-of-the-art pre-treatment protocols. More work in these sites in the future will refine their chronology.

Additional evidence of animal consumption by humans was reported by Jaimes (1998, 1999, 2003, 2005) from El Vano site (Fig. 1), located in Morán municipality, Lara

State (Venezuela), based on three fragments of projectile points and other artifacts associated with remains of the ground sloth *Eremotherium rusconi* (= *E. laurillardii*, but see Faure et al., 2014), dated to ~12,709 calybp ($10,710 \pm 60$ ybp). The site was considered by Jaimes (1998, 1999, 2003, 2005) as a hunting area similar, broadly speaking, to Taima-Taima.

Materials and methods

Fossil specimens and identification/taxonomy

We carried out anatomical and comparative studies of six skulls and conducted non-invasive imaging analyses of one skull [AMU-CURS-1287 (MTT-V)]

using CT scanning. All specimens from the Muaco and Taima-Taima sites were housed at the Palaeontological collection of the Alcaldía Bolivariana de Urumaco (AMU-CURS/Museum of Taratara (MTT-V-), and Museo de Ciencias Naturales de Caracas, Caracas (MCNC). As described below, some specimens were collected by us and others were discovered upon the study of museum collections from the sites.

AMU-CURS-1287 (MTT-V) is a complete skull assigned to *Glyptotherium cf. cylindricum* (Figs. 4A, B, 5A–G) based on some diagnostic features and comparisons with other Pleistocene glyptodonts (see Zurita et al., 2018). A diagnostic feature is a lateral profile with a more open angle of the palatal plane and the dorsal skull line compared to the Southern South America *Glyptodon* spp. In frontal view, the nostrils are cordiform-like, with the upper margin wider than the lower one, and different to those of *Glyptodon* spp. in which the nasal opening has an inverted truncated sub-pyramidal outline (Cuadrelli et al., 2019, 2020). The descending processes of the maxillary bone are markedly divergent ventrally and their internal margins are almost completely straight, a shape distinct from that of *Glyptodon* spp., in which they are concave to the sagittal plane (Carlini et al., 2008).

In dorsal view, the nuchal ridges at both sides of the supraoccipital bone are transversally aligned, there is no defined sagittal ridge on the parietals, and the parieto-frontal area is expanded transversally. The frontal bone profile is somewhat convex and not flat as in *Glyptodon reticulatus* and *G. munizi* (Cuadrelli et al., 2019; Soibelzon et al., 2006). In occlusal view, the palate is wide and the premaxillae are longer than in *Glyptodon*; the molariform series diverge posteriorly. The infraorbital foramina are at Mf2/Mf3 level.

All the preserved molariforms (or the alveoli as indicated by their outlines) are lobed and with secondary osteodentine ramifications. One of the most specific characters is the clear lobation of the Mf1 (but without deep furrows between lobes in contrast to that observed in *Glyptodon* spp.), even more marked than in the remaining *Glyptotherium* species (with the exception of *G. reticulatus*). The Mf2 is evidently trilobated as the rest of the molariforms (for more detailed see Carlini et al., 2008; Zurita et al., 2018).

AMU-CURS-1287 (MTT-V) was collected in Pleistocene sediments adjacent to the ancient excavation of the Muaco site. The rescue paleontological activity took place in 2006 by three of the authors (OA, AAC and AEZ) to avoid the total loss of the specimen due to the erosion of outcrop. The specimen was prepared at UNEFM by AAC and AEZ, and posteriorly housed with the Paleontological collections of the Alcaldía Bolivariana de Urumaco, Urumaco, Falcón State, where it remains temporarily, to

later be returned to the local museum of Taratara (MTT-V-). Unfortunately, no stratigraphic information about the site was ever published from the Muaco site by Royo y Gómez (1959, 1960) or Cruxent (1961).

The other specimens (Fig. 4C–I) correspond to two relatively complete skulls (MCNC-Pal-1839 and MCNC-Pal-1840) (Fig. 4C–F), and two fragmented skulls (MCNC-Pal-1837 and MCNC-Pal-1838) (Fig. 4H, I) coming from the Taima-Taima site, all housed in the paleontological collection of the Museo de Ciencias Naturales de Caracas (MCNC), Venezuela. MCNC-Pal-1840 was previously reported as *Glyptotherium cf. cylindricum* without catalog number (MCN n/n) by Carlini et al., (2008, fig. 2A–D). Here MCNC-Pal-1839 and MCNC-Pal-1840 are taxonomically allocated to *Glyptotherium cf. cylindricum* (Fig. 4C–F), skulls that are almost identical in morphology to that of AMU-CURS-1287(MTT-V). Given the completeness of the skull, the lack of definitive species allocation may seem peculiar—this uncertainty is due to the difficulties in glyptodont taxonomy derived from the rareness of the association of carapace shield and skulls for most taxa (see Zurita et al., 2009, 2016). This particular situation is evident with the North American species *Glyptotherium cylindricum*, mostly recognized on the basis of the dorsal carapace (see Gillette et al., 2016; Zurita et al., 2018) The fragmented skulls MCNC-Pal-1837 and MCNC-Pal-1838 are assigned also to *Glyptotherium cf. cylindricum* on the basis of morphological evidence. The provenance of these four skulls is presumably from the first excavation campaigns in Taima-Taima, known as the “Los Pozos de Royo y Gómez” during the 60s and early 70s (see Cruxent, 1967, 1970; Ardila, 1987; Carrillo-Briceño, 2015), prior to the 1976 excavation (Ochsenius & Gruhn, 1979). This is supported by the absence of glyptodont skulls in the 1976 excavation report (Casamiquela, 1979; Bocquentin-Villanueva, 1982). Bocquentin-Villanueva (1982, p. 482) briefly mentioned the presence of an unstudied glyptodont skull from Taima-Taima (pre-1976 excavation) housed at the MCNC. The stratigraphic provenance of these skulls from Taima-Taima remains unknown. However, based on the fact that the faunal assemblage of the Unit I/II disconformity (Fig. 3) represent the last evidence of megafauna in the Taima-Taima section (Bryan, 1979; Casamiquela, 1979; Gruhn & Bryan, 1984), it could be assumed that these specimens are not younger than this fossiliferous stratum.

The stratigraphic provenance of an inverted carapace from Taima-Taima probably eviscerated by humans (Bryan, 1979; Casamiquela, 1979), the lost skull (Fig. 2F), as well as other mammalian remains correspond to the upper stratum, specifically with the disconformity between units II and I (Bryan, 1979, p. 49; Casamiquela,

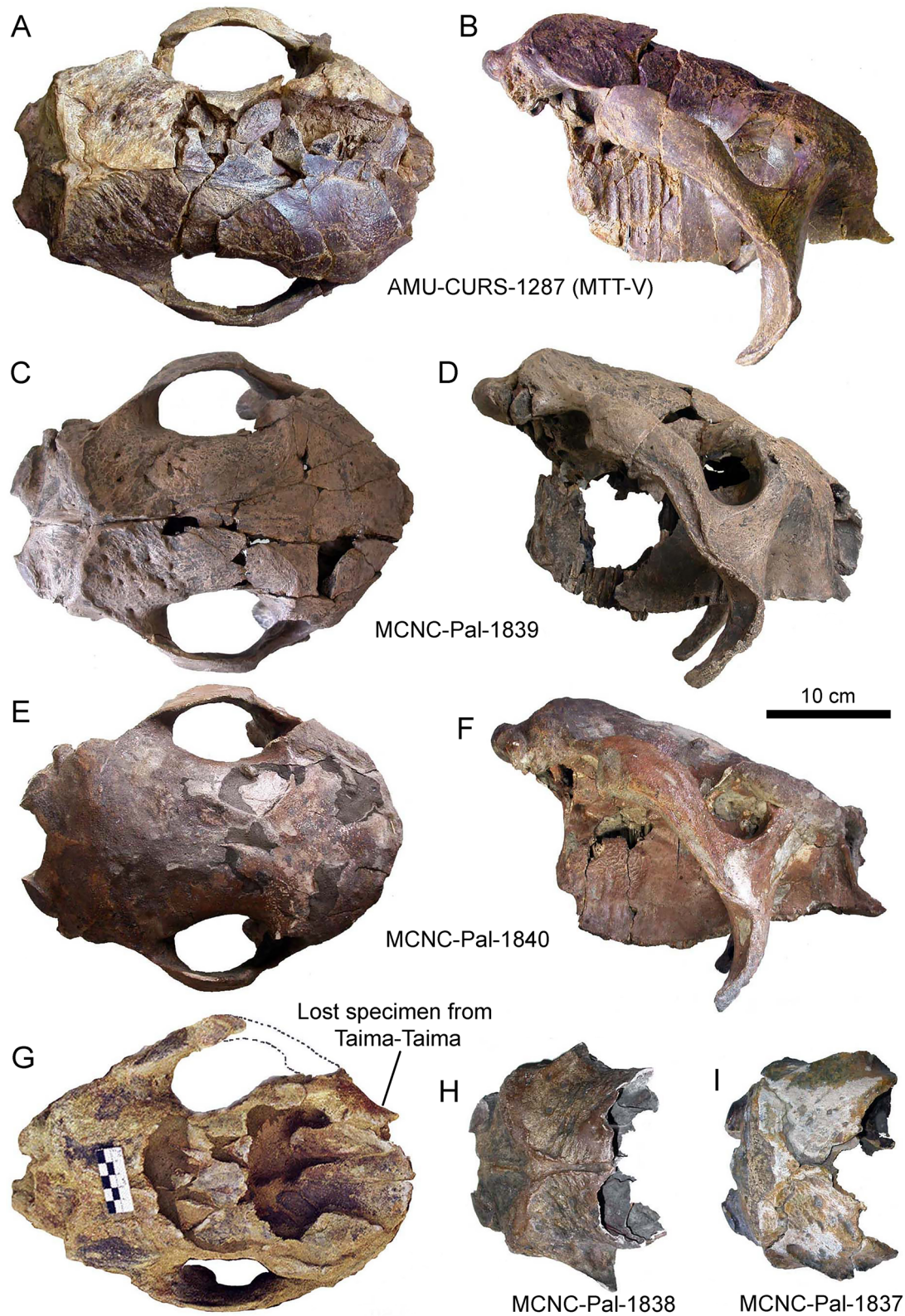


Fig. 4 *Glyptotherium* cf. *cylindricum* skulls. Specimens from the Muaco (A, B) and Taima-Taima sites (C–I) are shown. Specimens A–G show the fractured area of the hypothesized location of impact. Views: dorsal (A, C, E, G–I) and lateral view, left side (B, D, F)

1979, p. 63; Fig. 3). The faunal assemblage of the Unit I/II disconformity represents the last evidence of megafauna in the Taima-Taima section (Casamiquela, 1979; Gruhn & Bryan, 1984). Although this horizon was never dated, Gruhn and Bryan (1984, p.131) speculated that an anomalous date of $\sim 13,730$ calybp ($11,860 \pm 130$ ybp) may be derived from a waterlogged root of a tree that grows on the Unit I/II surface.

The sixth skull reported here (Figs. 2F, 4G), also assigned to *Glyptotherium cf. cylindricum*, comes from the upper fossiliferous stratum of the Taima-Taima site (AJ pers. ob.; Fig. 3), and the specimen is known exclusively from photographs and an unpublished drawing (Figs. 2F, 4G). This skull disappeared from the set of fossil elements left in situ during the excavation of 1996 (AJ pers. ob.). Small fragments were extracted in 1996 from this now lost specimen, and these fragments were used for radiometric dating.

Scanning analysis (CT)

One skull, AMU-CURS-1287 (MTT-V), was CT scanned (348 cuts/0.80 mm) in 2012 using a General Electric High Speed Dual Helicoidal Scanner from the Instituto Falcóniano de Emergencias Médicas (IFEM), in Coro City, Falcón State. The 3D model was created using 3D-Slicer (v. 4.8.1 r26813) free software.

Body mass estimates

We estimated the body mass of two *Glyptotherium* species using linear measurements of specimens available to us based on a calculation of the volume of half a sphere simulating the carapace, to which the volume of the head approximated as sphere and that of the tail simulate as a cone, assuming an average density for mammals of 1000 kg/m^3 (Fariña et al., 1998). This estimate based on geometric forms was compared to that resulting from one based on the molar series (Janis, 1990), using this formula for our study: lower molar row length (Lmrl): $\log \text{mass} = \log \text{LMRL} \times 3.265 - 0.536$.

Results

Glyptodont skulls with signs of potential human interaction

Visual and CT scanning analyses of the skulls showed that four glyptodont skulls of *Glyptotherium cf. cylindricum* exhibited breakages in the fronto-parietal region showing a similar pattern in all of them. Evidence

suggests that these were likely caused by a mechanical effect by direct percussion, most likely a blow with a stone chopper or club, which resulted in a restricted area of broken and falling bones pieces into what must have been the internal soft tissue. Below follows a description of the breakage patterns in each skull.

Description of specimens

AMU-CURS-1287 (MTT-V). It represents a *Glyptotherium cf. cylindricum* from the Muaco locality. The skull exhibits fractures and breakages characteristic of the effects of the strike with a large object in the frontal and parietal (Figs. 4A, B; 5A–G).

MCNC-Pal-1837, 1838, 1839, 1840, and an uncatalogued and lost specimen (only known by photograph) are from the Taima-Taima site and referred here to *Glyptotherium cf. cylindricum* (Figs. 2F, 4G). In MCNC-Pal-1839 and MCNC-Pal-1840, the fronto-nasal region is fully preserved but very cracked (supposedly preferred area of impact during the hunting process), and both specimens show the same vertical–diagonal fractures that run through the maxillary bones from front to back, with an inclination of about 75° with respect to the palatal plane (Fig. 4C, E), such as those observed in the Muaco specimens (AMU-CURS 1287 (MTT-V); Figs. 4A, B; 5A). In these specimens, the fronto-nasal region is then fragmented and submerged, whereas the zygomatic arches are not. Specimens MCNC-Pal-1837 and 1838 are represented only by the posterior part of the braincase (Fig. 4H, I), the portion homologous to the undisrupted areas of the more complete skulls (AMU-CURS-1287 (MTT-V); MCNC-Pal-1839, 1840).

The same inferred pattern of human-induced breakage could have happened in the lost specimen from Taima-Taima, of which there is only a photograph at the moment of extraction during the original works at the site in 1996 (Figs. 2F, 4G). Some articulate osteoderms from the cephalic shield were also preserved next to the skull.

All the reported broken skulls do not present breaks in equally fragile spindles (e.g., zygomatic arches or their descending processes; posterior palatal laminar area of the pterygoids; anterior region of the base of the nasal chamber), which would typically be affected by post-mortem mechanical effects and during the fossilization process. The skulls consistently show vertical–diagonal fractures in the high maxillary walls that house the

(See figure on next page.)

Fig. 5 Imaging of *Glyptotherium cf. cylindricum* skull AMU-CURS-1287(MTT-V) from the Muaco site. A photograph (A) and computer tomography images (B–G) of *Glyptotherium cf. cylindricum* skull AMU-CURS-1287(MTT-V) from the Muaco site, Falcón state, Venezuela are shown. Views: Dorsal view, anterior to left (A). Fronto-dorsal view, inclined (B), blue arrows point to the hypothesized location of impact and red arrows the direction of sliding of the bone fragments. Dorsal view, inclined (C). Lateral view, left side (D) and its cross section (E). Plane of cut (F) and its longitudinal section (G) (anterior to left)

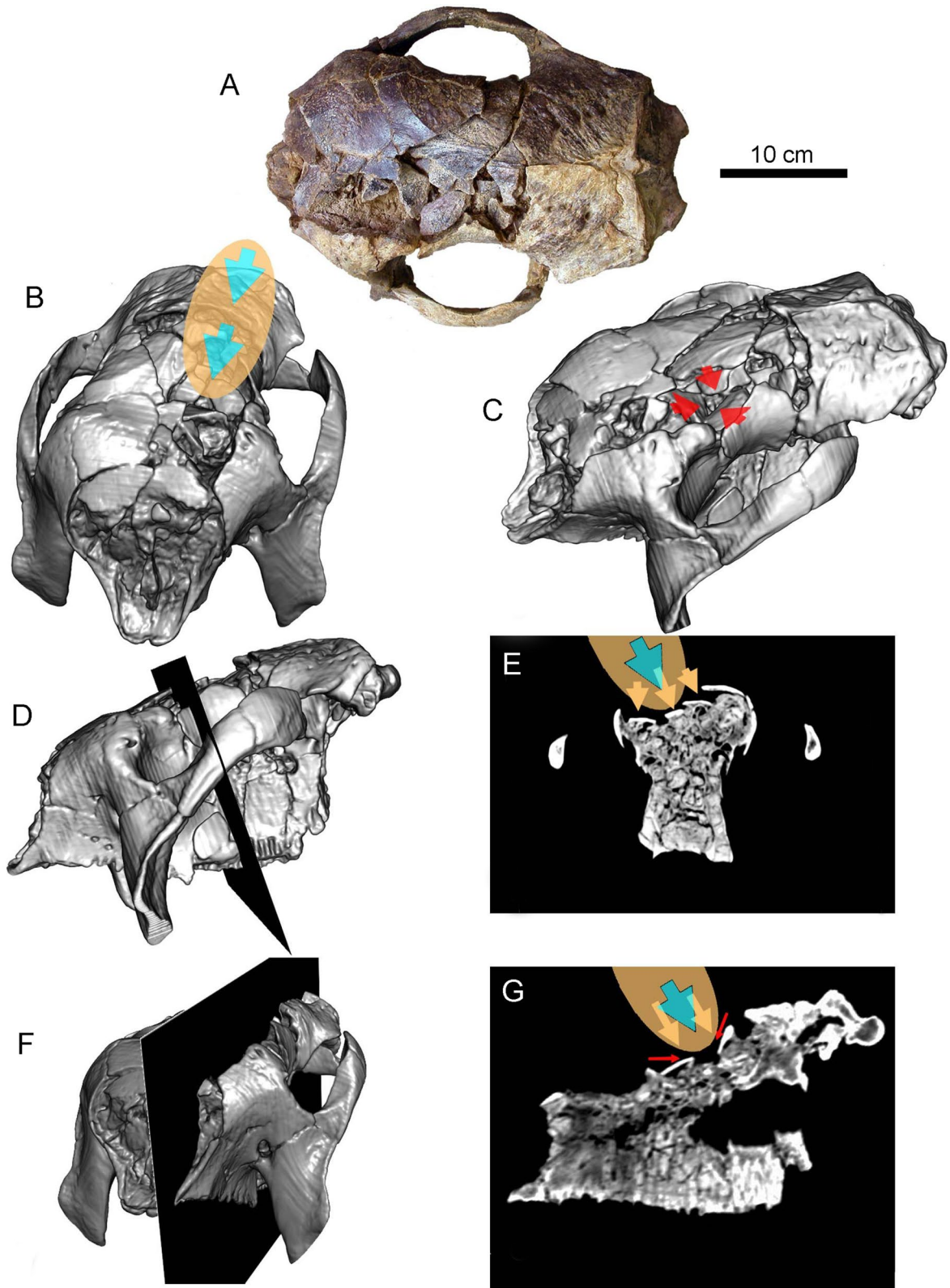


Fig. 5 (See legend on previous page.)

intra-alveolar part of the molariforms, mainly under the sunken area of the cranial roof.

Despite the fact that several skulls were complete and showed no signs of post-mortem transport, they often lacked their jaws. These may have been removed during the process, and the “hunters” may have consumed masticatory muscles and tongue.

A final observation concerning the reported broken skulls is that there are signs of the fractures being ante-mortem or trans-mortem as opposed to post-mortem, i.e., the fractures present other signs of being true traumas leading to death. The fractured margins of the bones have the same color as the adjacent external surface of the bones, because they were in contact with the sediment for the same lapse of time. Also relevant is that at the time of death the periosteum was still present and intact, as some of the loose fragments are not displaced but still in contact with the adjacent unfractured areas.

From the El Vano site in the Andes of Venezuela (see Jaimes, 2003, 2005), one of the authors (AJ) recovered some isolated glyptodont osteoderms; however, there is not clear evidence to support interaction between humans and glyptodonts or their consumption. These osteoderms are reported here for the first time, being identified as *Glyptotherium* cf. *cylindricum* (Fig. 2G–H).

Body mass estimates resulted in a total of 350/380 kg for *Glyptotherium* cf. *cylindricum* based on geometric forms, similar to that resulting from an estimated based on the molar series (Janis, 1990), based on this formula: lower molar row length (lmrl): $\log \text{mass} = \log \text{LMRL} \times 3.265 - 0.536$ (see Janis, 1990). For *Glyptotherium* cf. *cylindricum*, with molar row length (lmrl) of 7.8 cm, the estimated body mass was 375 kg. The same calculation for *Glyptodon reticulatus*, molar row length (lmrl) of 9.5 cm, results in a body mass of 457 kg.

Discussion

The coexistence of early hunter–gatherers and glyptodonts in South America was first hypothesized based on findings from the Pampean region of Argentina more than a century ago (Vogt, 1881). Since then, several reliable records of exploitation of faunal resources during the latest Pleistocene and early Holocene (ca. 12,000–7000 ybp) in the Pampean region have been accumulating (e.g., Borrero, 2008, 2009; Politis et al., 2019; Prates & Pérez, 2021). Among armored xenarthrans, the “armadillo” *Eutatus seguini* was exploited, and in this group and in particular within Glyptodontidae, this has been recorded for *Doedicurus clavicaudatus*, one of the largest and last survivors of the South American megafauna (Politis & Gutiérrez, 1998; Politis et al., 2019). Associations with *Glyptodon* sp. also existed, and direct utilization of the resource may have occurred according

to the evidence, but this is not conclusive (Gutiérrez & Martínez, 2008). This set of glyptodonts includes very different forms ranging from the relatively small *Neosclerocalyptus* (300–450 kg; see Quiñones et al., 2020) to the giant *Doedicurus*, achieving a mass of about 2 tons (Soibelzon et al., 2012).

The only reference of probable interaction between human and glyptodonts outside the Pampean region, beyond the findings of glyptodont osteoderms at archaeological sites, was reported from Taima-Taima by Casamiquela (1979) and Bryan (1979), who noticed an inverted carapace that was probably eviscerated by humans. No other evidence was known about the potential interaction with humans in northern South America, where the late Pleistocene taxonomic composition and diversity of glyptodonts was very different compared to that of southern South America (see Carlini et al., 2008; Carlini & Zurita, 2010). From North America little evidence of possible consumption based on glyptodont osteoderms has been reported from the Clovis site Lewisville in Texas (Crook & Harris, 1958; Waguespack & Surovell, 2003).

Our report here from Muaco and Taima-Taima significantly expands the geographic reports of potential active exploitation for glyptodonts in an area completely different from the Pampean region (Politis et al., 2019). An evident difference when compared to the Pampean region of Argentina (where most of the evidence comes from the appendicular skeleton and carapace remains, see Politis & Gutiérrez, 1998) is that here we report, for the first time, the potential signal of human predatory behavior at skull level in several specimens. Another difference involves the body mass of the glyptodonts and, according to that, probably the strategy followed by hunting them. While *Doedicurus* was the largest glyptodont ever existed (ca. 2 tons) and having evident defensive weapon at level of the caudal tube (see Blanco et al., 2009), *Glyptotherium* was a very smaller glyptodont (ca. 500 kg) lacking evident “defensive weapons” (Carlini et al., 2008).

Both the Muaco and Taima-Taima skulls are rare cases of fractured thin bones that were preserved as such during the burial and fossilization process, practically without displacement and in a three-dimensional condition. This particularity was surely favored by the presence in life of a cephalic shield above the skull. We hypothesize that the fractures in the AMU-CURS-1287 skulls are ante-mortem or trans-mortem given the fractured margins of the bones having the same color as the adjacent external surface and the preservation of the periosteum, as explained above. The cephalic shield is formed by numerous osteoderms covering and protecting it, being this character a synapomorphy of the cingulates that is preserved in the lost skull from Taima-Taima (see Figs. 2F, 4G), and another unstudied

specimen (IVIC-VF-5) from the same locality (see Aguilera, 2006, p. 43). These osteoderms are of greater size and thickness in the middle of the shield, coinciding with the posterior frontal and parietal region of the skull roof, and providing an important passive protection. This protection though thins peripherally corresponding to the detected area of impact on the skull. None of the specimens presented secondary blows that would have produced more cranial indentations (neither dorsal nor lateral). This is relevant, as indicate that the blows may have been very effective, if not to direct death at least disorientate the animal.

The hypothesis presented here for Muaco and Taima-Taima skulls further builds on these as places of hunting rather than scavenging of glyptodonts, in agreement with previous evidence proposed for other megamammals (e.g., proboscideans) found at the same sites. Other glyptodont hunting evidence from the Taima-Taima site includes postcranial bones and incomplete carapaces (Bocquentin-Villanueva, 1982; Bryan, 1979; Casamiquela, 1979). During the “Los Pozos de Royo y Gómez” excavation campaigns in Taima-Taima, Crucent (1967, plate 1) excavated a glyptodont carapace with well-preserved elements of the pelvic and columnar region (Fig. 2A–D). This was the carapace that Bryan (1979, p. 49) referred to as he stated “it is possible that this animal had been eviscerated by man, but there were no artifacts or any other evidence of human intervention on this land surface or any later surfaces”.

The role of now extinct megamammals as food resources for humans during the Late Pleistocene in South America is difficult to estimate and may vary from site to site (Martínez & Gutiérrez, 2004). In studies of early hunter–gatherers of Pampas and Patagonia, the most systematically studied region of the continent, megafauna have been considered secondary for human subsistence, being opportunistic and non-crucial resources (Borrero, 2008, 2009). Little is known from Venezuelan sites as to discern any dietary strategy patterns for this region. In fact, evaluating the importance of megafauna in the diet of these early Americans is probably impossible with current data.

Our body mass estimate for *Glyptotherium cylindricum* is 375 kg, of which about 40% (after subtracting all bones and organs) or 150–170 kg suggest that it would offer potentially accessible muscles and fat as food sources. These animals would not have been fast, they would have a restricted field of vision and their limbs did not possess sufficient flexibility to offer protection. As such, they would have been a relatively easy prey if their point of weakness in their carapacial protections be identified and used. This point may have been precisely the head in front of the cephalic shield.

The proposed interaction of humans with glyptodonts in Muaco and Taima-Taima must have involved the use of heavy tools capable of producing the head breakage described above. The record of potential tools with that capacity such as choppers of relatively large size were identified and illustrated from the Taima-Taima site by Crucent (1967, plates 3–5), although these have not been associated with the fossils in question. According to Crucent (1967, pp. 7–8), these lithic materials come from a stratigraphic level below 1.6 m deep, in the same layer where he recovered megafaunal remains (see Crucent, 1967, plates 1), which would correspond to the sediments immediately overlying the Miocene rock found as basement. If Crucent’s assertions are correct, this fossil/lithic-bearing layer reported by him should correspond to the basal or medium fossiliferous strata shown in Fig. 1. Notwithstanding, in a comprehensive study of such stone tools, Szabadics (1997; figs. 29, 30, 53, 100, 101) illustrated several large hammer-like instruments that eventually could have been used to hit glyptodonts. Hunting tools such as clubs could also have been manufactured on perishable materials such as wood or bone.

It has not been possible to date the remains of *Glyptotherium cf. cylindricum* reported here—despite failed attempts of C14 dating that we have made from two of the specimens (AMU-CURS-1287 (MTT-V) and lost specimens from Taima-Taima). We do know though that this species is not recorded in any Quaternary deposit of South America prior to the Late Pleistocene, as is also the case of the giant ground sloth *Eremotherium laurillardii*. The two species would have differentiated in North/Central America and would have entered the South American continent during the late Pleistocene (ca. 15–20 ka), at the time of marked drops in sea level (approximately 120 m below sea level) during the more extended glaciations. This situation allowed the opening of wide lowland corridors (more than 60 km wide) along the current Isthmus of Panama (see Carlini et al., 2008; Carlini & Zurita, 2010), which may have been used by these species for enter South America, just as human beings might have entered.

Conclusions

We describe glyptodont skulls of *Glyptotherium cf. cylindricum* that suggest an active, direct and systematic hunting by humans. The skulls show a consistent pattern of rupture in the parieto-frontal and nasal area, with the sinking of bone fragments into the soft tissues and underlying skull cavities, and these same skulls do not present breaks in equally fragile areas that would typically be affected by postmortem mechanical effects and during the fossilization process. The lack of associated lower jaws in otherwise excellent preservation is also

consistent with hunting. The area of possible impacts evidenced by the breaks is precisely where the cephalic shield that covered the head of these animals was thinner or absent. Hunters may have recognized this vulnerability and hunted glyptodonts by inflicting a blow on these thinner parts of the skull. Glyptodonts may have been the slowest megamammals in the studied sites, with limited mobility in their anterior limbs, making them potential prey for humans. We estimated that roughly 150–170 kg of potentially accessible muscles and fat of an adult *Glyptotherium cylindricum* could be used as food sources. There is surely a degree of speculation in our hypothesis of active hunting of glyptodonts based on the repeated and peculiar breakage patterns of the skull, but the alternative explanation of natural occurrence of the features reported here due to taphonomy seems less likely. Future work in the important Venezuelan localities discussed in this paper could explore the revision of absolute dates and the search for further direct association of tools with faunal remains.

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Author contributions

AAC, AJ and MRSV conceived the study, AAC and AZ performed the taxonomic work. AAC and JDC-B prepared figures and/or tables. AAC, JDCB, AJ, OA, AEZ, and MRSV participated in field and laboratory work conducive to this research on Taima-Taima and Muaco, while AJ provided the samples and contextual information on El Vano. AAC, JDCB, AJ, JI and MRSV produced partial drafts of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All the fossil specimens described here are freely available for study at the Museums in question.

Declarations

Competing interests

The authors declare that they have no competing interests.

Author details

¹Laboratorio de Morfología Evolutiva y Desarrollo (Morphos), Facultad de Cs. Naturales y Museo, UNLP, CONICET (Consejo Nacional de Investigaciones

Científicas y Técnicas, Buenos Aires, Argentina. ²Palaeontological Institute and Museum, University of Zurich, Karl-Schmid-Strasse 4, 8006 Zurich, Switzerland. ³Centro de Antropología, Instituto Venezolano de Investigaciones Científicas, Km. 11 Altos de Pipe, Parroquia Macarao 1204, Miranda, Venezuela. ⁴Paleoecology and Global Changes Laboratory, Fluminense Federal University, Rua Marcos Waldemar de Freitas Reis, S/no, Campus Gragoatá, Bloco M, Lab. 110, Niterói, Rio de Janeiro CEP. 24210-201, Brazil. ⁵Laboratorio de Evolución de Vertebrados y Ambientes Cenozoicos, Centro de Ecología Aplicada del Litoral (CECOAL-UNNE-CONICET) y Universidad Nacional del Nordeste, 3400 Corrientes, Argentina. ⁶Department of Archaeology, College of Humanities, University of Exeter, Exeter, UK.

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