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# First record of a complete humerus of *Agriotherium* (mammalia-ursidae) from the early-late Hemphillian of Zacatecas, Mexico

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## ABSTRACT

A complete humerus referred to *Agriotherium* is described, collected from early-late Hemphillian deposits from Zacatecas. *Agriotherium* is widely represented by isolated molars, mandibles, and maxillae in early-late Hemphillian faunas of Eurasia and North America. In the literature, postcranial elements are scarce and briefly described with little detail. The greatest diversity is known from the Langebaanweg quarry in South Africa; however, the only complete specimen is from Mexico. The proximal end is described, and the humerus shares similarities with the description of the distal end from South Africa, in which the medial epicondyle and crest of the lateral epicondyle are reduced, which can be considered as a limitation in the hunting of larger prey for food. This implies that *Agriotherium* was not strictly carnivorous but was a predator-scavenger with an omnivorous diet that included plants and fruits.

Key words: Ursidae; *Agriotherium*; carnivore, humerus; early-late Hemphillian; Juchipila basin; Zacatecas; Mexico.

## RESUMEN

*Se describe un húmero completo referido a Agriotherium, recolectado en depósitos de edad lo más tardío del Henfiliano temprano de Zacatecas. Agriotherium está ampliamente representado por molares, mandíbulas y maxilares aislados en las faunas de edad Henfiliano temprano-tardío de África, Eurasia y América del Norte. En la literatura, los elementos poscraneales son escasos y descritos someramente con poco detalle. La mayor diversidad se conoce de la cantera de Langebaanweg en Sudáfrica, sin embargo, el espécimen de México es el único completo. Se describe el extremo proximal de Agriotherium que era desconocido; comparte similitudes con la descripción del extremo distal del espécimen de Sudáfrica, en el cual el epicóndilo medial y la cresta lateral del epicóndilo lateral están reducidos, esto se considera una limitación durante la caza de presas grandes para conseguir alimento. Esto implica que Agriotherium no era estrictamente carnívoro, sino también un depredador carroñero con una dieta omnívora que incluía plantas y frutas.*

*Palabras clave: Agriotherium; carnívoro; húmero; Henfiliano temprano-tardío; cuenca de Juchipila; Zacatecas; México.*

## INTRODUCTION

The extinct giant bear *Agriotherium* in the late Miocene and Pliocene was well dispersed with a nearly worldwide distribution in Africa, Eurasia, and North America except for the island continents of Australia and South America (Jiangzuo and Flynn, 2020). Yet, its fossils are quite rare, often consisting of fragmentary dental remains. Rarely documented are its postcranial skeletons, and a complete humerus has never been reported. For an ursid reaching to a body size of 400 kg and with controversial diet (Sorkin 2006a; Oldfield *et al.*, 2012), its limb bones contain much-needed information about its locomotion as well as predatory behaviors.

The faunas of North America have had different displacement episodes to the south during the Barstovian - Clarendonian - Hemphillian ages, probably influenced by climatic changes, and arrival of new invaders from Euro-Asia or due to greater competition for food during these ages in the faunas of North America (Jiangzuo and Wang, 2022).

The continuous research in the Juchipila basin, state of Zacatecas, has demonstrated these southern mammalian movements in early Hemphillian age in central Mexico, with its importance and diversity of mammals contained in the sedimentary sequence described in previous works (Carranza-Castañeda *et al.*, 2013; Tseng *et al.*, 2017; Carranza-Castañeda, 2022; Carranza-Castañeda *et al.*, 2022). This work presents the latest discovery, a humerus, the only complete element known in the early Hemphillian deposits that has been referred to *Agriotherium*, in deposits dated to 6.35±0.38 Ma (U/Pb method). This Mexican specimen possibly represents an individual of the first migration of ursids from Asia to North America in the late Miocene Hh3 age (Jiangzuo and Wang, 2022).

### Records of *Agriotherium* in Mexican faunas

The oldest record in North America was described from an m1 collected in Tehuichila deposits, state of Hidalgo (Freudenberg, 1910, p.205) named *Hyaenarctus* (=*Agriotherium*, Stock, 1950). According to Frick (1926), Freudenberg considered it an ancestral to the arctotheres of South America, in his interpretation "to have had unreduced premolars". Dalquest (1986), only mentioned the records of *Agriotherium* in Mexican faunas. The Yepomera fauna in the northwestern Chihuahua is the most important Hemphillian-Blancan fauna because of its diversity, *Agriotherium* cf. *schneideri* is part of the

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associated fauna (Merriam *et al.* 1916; Stock 1950). A further record of *Agriotherium* cf. *A. schneideri* has been found from the late Hemphillian fauna of Matachic, state of Chihuahua (Lindsay *et al.*, 2006).

During a new research supported by Universidad Autónoma del Estado de Hidalgo, in the Zacualtipan basin, state of Hidalgo, lower molars and other fragments referred to *Agriotherium,* plus horse teeth of *Calippus* and the peccary *Prosthennops* sp., were discovered in the Zietla deposits of early-late Hemphillian age (Carranza-Castañeda, 1991, 1994). Another report, of Tecolotlán basin state of Jalisco, isolated molars of *Agriotherium* that were collected in San José deposits, referred to late Hemphillian (Carranza-Castañeda and Miller, 2004). In San Miguel Allende basin a complete jaw and maxillary, that surely belong to the same individual, were collected in the Rinconada locality in the same stratigraphic level (Carranza-Castañeda, 1992; Miller and Carranza-Castañeda, 1996; Carranza-Castañeda, 2006), Figure 1a.

### ***Agriotherium*** **in faunas of North America**

*Agriotherium i*s widely represented in the late Miocene faunas at ages ranging from 7 to 3.6 Ma (Tedford *et al*., 2004). The only middle-Blancan record is known from Hagerman fauna, Idaho (Samuels *et al*., 2009). Most records of *Agriotherium* are described based on isolated upper and lower molars, plus maxillae, and mandibles (Sellars, 1916; Dalquest, 1986; Everhart and Hawkins, 2020). Almost all these reports do not mention postcranial elements. Schultz and Martin (1975) described and illustrated a complete radius (UNSM 6013) from the late Hemphillian, Ash Hollow Formation in Ogallala Group (Hunt, 1998). From the Edson Quarry, Kansas, Harrison (1983) described *Agriotherium* based on an upper canine, including the so far widest representation of postcranial elements, such as radius, ulna, metacarpus III and IV as well as part of a metapodial; however, she only describes a distal fragment of a humerus with part of the lateral epicondylar crest, that according to the brief description matches with the Mexican specimen.

Hendey (1976, 1980), mentions a collection of postcranial elements known, all referred to *Agriotherium africanum* including from Langebaanweg Quarry in South Africa: skull, jaws, upper and lower molars, and different postcranial elements, also scapula and humerus fragments that correspond to different individuals. However, the comparisons with the humerus presented in this work, are made with a fragment of humerus illustrated in Hendey (1980, p. 32, fig. 15), and with information provided from Samuels *et al*., (2013). The main objective of this paper is to describe this new specimen (MPG 5676) from the Zac Juch 47 El Resbalón locality (Figure 1a), which is the only complete known humerus in the early-late Hemphillian faunas.

## ABBREVIATIONS

Jal: Jalpa; Juch: Juchipila; Tab: Tabasco; LACM: Los Angeles County Museum of Natural History; MPGJ: Museo de Paleontología Geociencias Juriquilla, Querétaro, México; TMM: Texas Memorial Museum, University of Texas at Austin, Jackson School of Geosciences; Zac: Zacatecas; FMNH: Field Museum Of Natural History, Chicago; MLP: Museo de la Plata; USNM: United States National Museum; UCMP: University of California Museum of Paleontology; UNAM: Universidad Nacional Autonoma de Mexico; USA: United States of America; km: kilometer; m: meter; cm: centimeter; mm: millimeter.

## METHODS

The humerus described in this work was prepared in Laboratory of Paleontology of Centro de Geociencias, Juriquillla, UNAM, Querétaro, and is cataloged and housed in the Paleontological collections of the same Institution. According to different authors (Hendey, 1980; Wolff *et al*., 1973; Sorkin, 2006a) no complete humerus of *Agriotherium* is known. In general, it is represented by fragmented material from different individuals. The Mexican specimen was compared with the illustration of Hendey (1980, fig. 15 L45063), and fragmented humerus of *Arctodus* from La Brea Tar Pits and Museum, Los Angeles. Other comparisons were made with TMM M-3773 *Ursus arctos*, TMM M-137 *Ursus americanus* and recent material of TMM M-7503 *Ursus maritimus* specimens catalogued in Vertebrate Paleontology collections of Jackson School of Geosciences, University of Texas and UCMP 22362 type specimen of *Indarctos oregonensis*. The measurements mentioned were taken according to the illustrations of Crouch (1969). Illustrations of other consulted publications were considered (Sorkin, 2006b); Davis, 1964; Torres Perez-Hidalgo, 1988; Samuels *et al*., 2013). The measurements mentioned are in millimeters, as defined in Figure 2 of this paper. Numbers between square brackets are identifications of the measurements shown in Table 1.

## BIOSTRATIGRAPHY OF JUCHIPILA BASIN

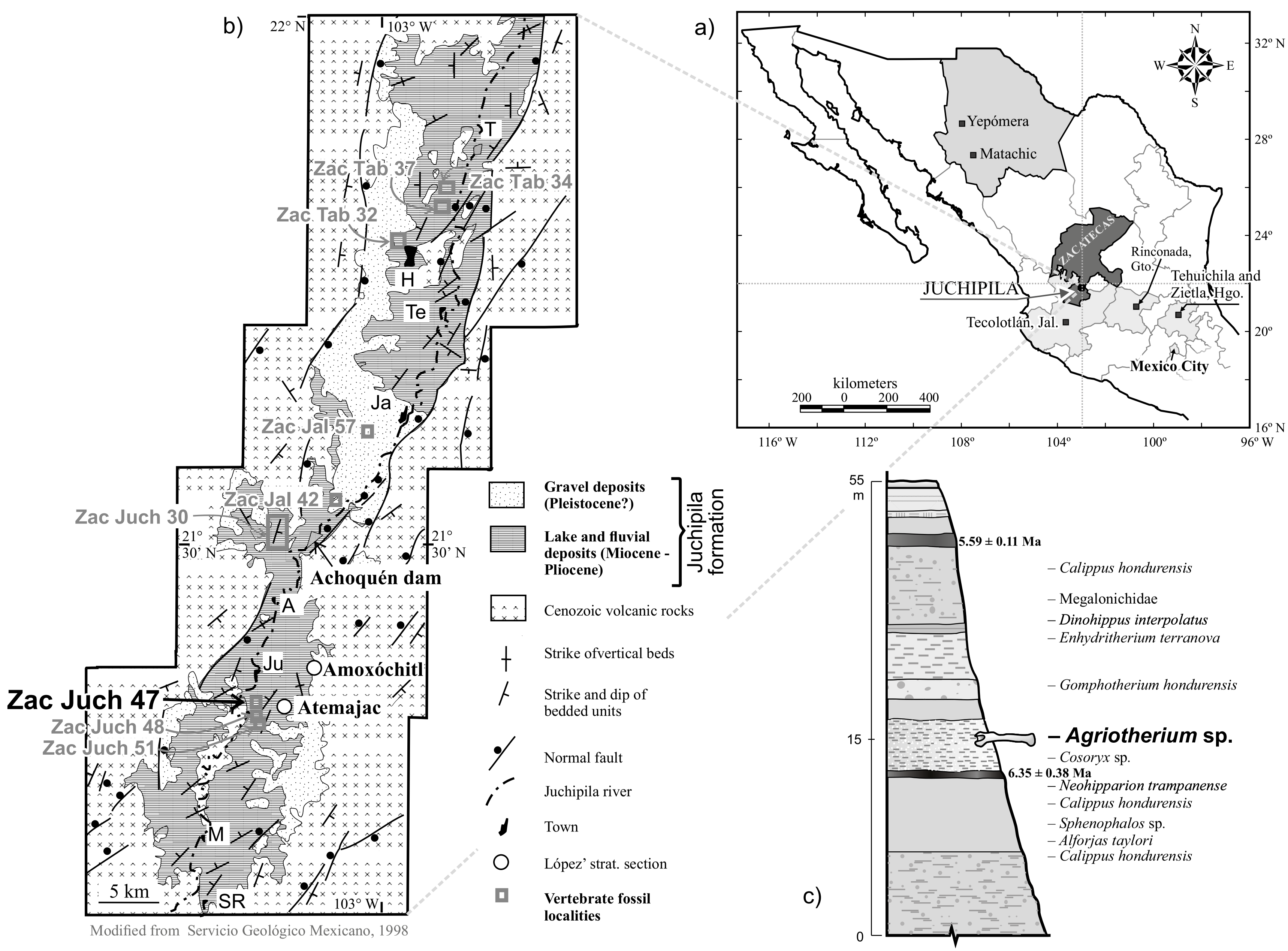
The stratigraphy of the Juchipila basin has been logged by Aranda-Gómez (described in Carranza-Castañeda *et al*., 2013), in selected areas where the greatest diversity and number of fossil mammals from the early Hemphillian have been recovered.

The Juchipila basin (Figure 1) has an extension of 165 km long and 15 km wide, with its long axis trending NNE. The Miocene-early Pliocene continental deposits that fill the basin were informally described as Juchipila Formation by Lahiere (1992) and López (1991). The deposits that fill the basin are from lacustrine, alluvial, floodplain, and pyroclastic origin. The fossil mammals are found in these deposits throughout the basin, although important localities are around the town of Huanusco (Zac Tab 32 and Zac Tab 37, Figure 1b). In the central part of the basin, El Mixtón deposits are found (Zac Juch 30, Figure 1b), which contains the greatest diversity of mammals. South of Jalpa city is Cofradía (Zac Jal 42, Figure 1b), where records of *Cosoryx* sp. and *Gomphotherium hondurensis* were recovered.

The stratigraphic sequence that contains the greatest diversity of early late Hemphillian mammals is found south of Juchipila city. The most important localities of this stratigraphic sequence are: El Resbalón (Zac Juch 47), La Copa (Zac Juch 48) and El Epazote (Zac Juch 51), due to the diversity of recovered mammals: *Sphenophalos*, *Gomphotherium hondurensis*, *Neohipparion trampanense*, *Dinohippus interpolatus*, *Calippus hondurensis*, *Enhydritherium terranovae*, *Alforjas taylori*, Megalonichid? Teeth (Carranza-Castañeda *et al*., 2013; Tseng *et al*., 2017). Recently, in El Resbalón locality, we collected the southernmost record of *Agriotherium* of the early-late Hemphillian age known outside of the USA faunas.

The stratigraphic sequence of El Resbalón is 45–55 m thick. The strata lie horizontal without evidence of folding, however, laterally the strata have significant changes in lithology. The base of the sequence is a layer of clayey sand with a thickness of 10 m, a layer of dark gray volcanic ash laterally interrupts the sequence. Towards the top, the sequence is an alternation of clay strata with different degrees of compaction and thickness. The *Agriotherium* humerus was recovered at 15 m from the bottom of the section (Figure 1c).

The ash below the strata, bearing *Agriotherium* fossil, was analyzed by $^{207}$Pb/$^{235}$U method, and gave an age of 6.35 ± 0.38 Ma. In the last 22 m towards the top, the sequence is an alternation of clay, sandy-gravel, and clay layers, with different degrees of compaction and thickness.



Modified from Servicio Geológico Mexicano, 1998

Figure 1. a) Map of Mexico, showing the states with records of *Agriotherium*. b) Geologic map of the Juchipila basin, with the location of the most important localities by their diversity of mammals (modified from Aranda-Gomez in Carranza-Castañeda *et al*., 2013). c) Composite biostratigraphic column in El Resbalón section, showing the approximate position of *Agriotherium* and associate fauna.

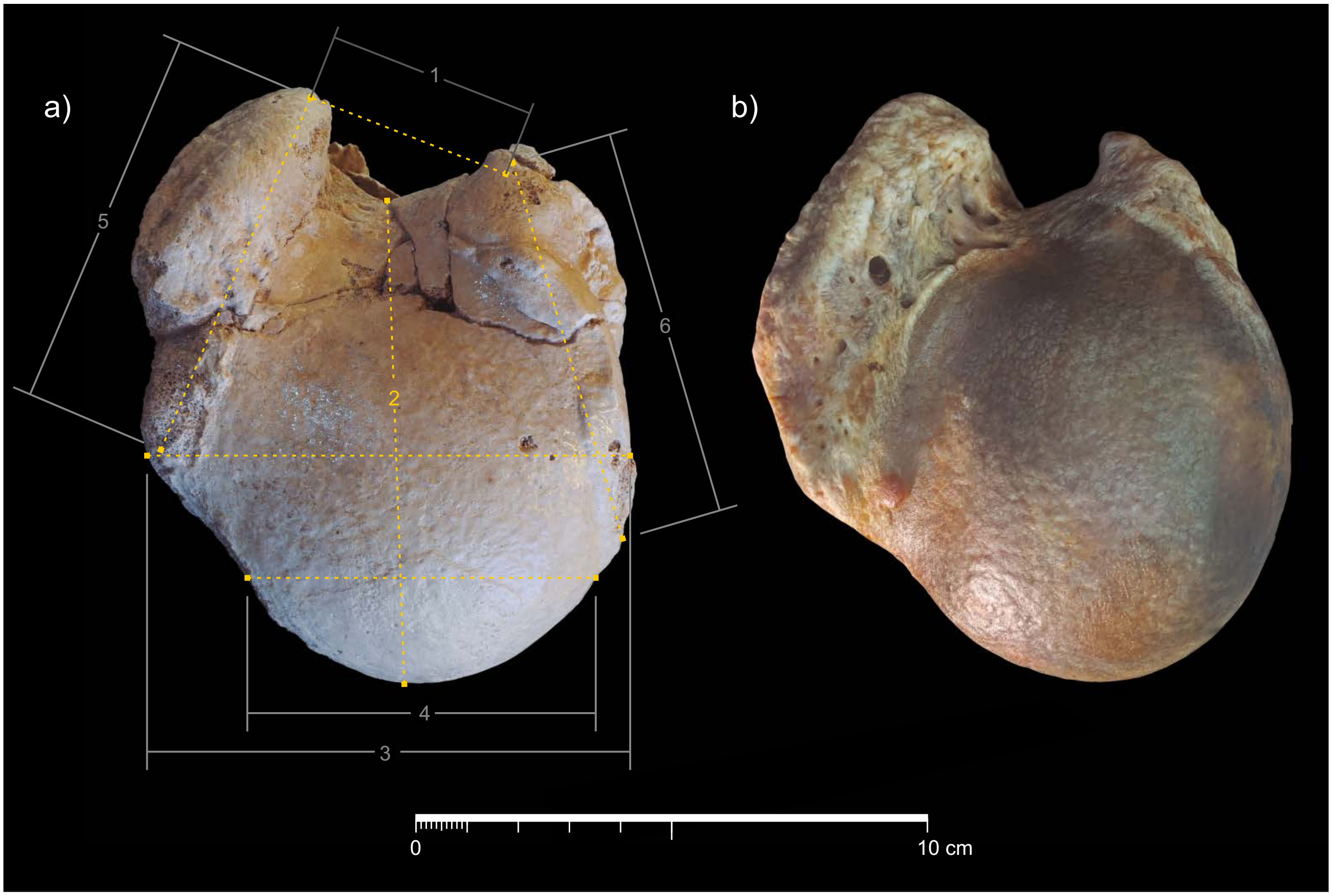


Figure 2. a) MPGJ 5676, *Agriotherium* left humerus, proximal view. The bicipital groove is wide, a fossa separates the tuberosities. It is remarkable the large size of the medial tuberosity that continues by a thin projection around the margin of the head. Note the differences in the hemispherical shape of the head. b) Recent *Ursus maritimus* humerus, with the lateral tuberosity larger and higher, the medial tuberosity greatly reduced. The head is more ovoid and there is no fossa between the tuberosities. All measurements are in Table 1.

The highest ash in the sequence, analyzed by the U/Pb method, gave an age of 5.59 ± 0.11 Ma. The stratigraphic sequence ends in a caliche layer less than 50 cm thick. It is important to point out that *Calippus* molars are found throughout the entire sequence (Carranza-Castañeda *et al*., 2013), Figure 1c.

Order Carnivora
Family Ursidae Fischer von Waldheim, 1817
Genus *Agriotherium* Wagner, 1837
***Agriotherium* sp.**

Figures 2a, 3, 4 and 5a, 6 and Table 1.

**Material.** MPGJ 5676 left humerus, in good condition without distortion.

**Locality and Age.** Locality El Resbalón (Zac Juch 47, Figure 1), of Juchipila basin, state of Zacatecas, Mexico. Age early-late Hemphillian.

**Description.** MPGJ 5676. The humerus is a long, stout and almost straight bone. The head, that occupies all the proximal end, is distinctly large and rounded. The part that articulates with the scapula is slightly convex with rounded shape projecting posteriorly to the shaft.

The anterior part the bicipital groove is limited by a shallow fossa between the tuberosities; which are offset to the internal side (Figure 2a measurement [1], and Figure S1a of the Supplementary Material).

The anteroposterior axis (Figure 2a and S1a) from the middle of the bicipital groove to the posterior edge is long ([2] in Figure 2a), and the transverse axis including the posterior extension of the tuberosities almost have the same dimension ([3] in Figure 2a).

The lateral tuberosity is not completely ossified (Figure 2a, and S1a), forming an elongated-convex and robust structure; it protrudes slightly from the articular surface, and is partially incomplete although it is possible to visualize the continuity through the posterior middle part of the articular surface of the head ([5] in Figure 2a).

The medial tuberosity is a smaller and low structure that project slightly from the surface of the head, continues toward posterior part by a thin projection around the margin of the head ([6] in Figure 2a).

The upper lateral side of the proximal end is not complete (Figure 3a and 3b, and S1d); however, it is possible to observe a deep concave depression surface for insertion of the infraspinatus muscle. The medial side of the proximal end has a wide, concave, and elongate impression (Figure 3b and S1d2) with multiple foramina and scars, for insertion of the subscapularis muscle.

The diaphysis is long, almost straight, and robust (Figure 4, and Figure S2 of the Supplementary Material). The anterior side has a flat triangular shape arrangement by the cephalo-humeral surface, which originates from the base of the lateral tuberosity ([10] in Figure 4), and the widest part is in the middle ([9] in Figure 4); it is a long, rough, and flat structure bounded in the inner side throughout by the prominent

Table 1. Measurement and comparisons between *Agriotherium* (MPGJ 5676) from El Resbalón locality and bears cited; Samuels *et al.*, 2013*, Sorkin 2006a°, Soibelzon *et al.*, 2011+. Square braquets apply only for the measurements of *Agriotherium.* Measurements in mm.

| Numbers in Figures | | ***Agriotherium*** MPGJ 5676 | ***Ursus maritimus*** TMM M-7503 | ***Ursus maritimus**** USNM 218230 | ***Ursus americanus**** USNM 275184 | ***Ursus arctos**** LACM 30466 | ***Ursus arctos**** LACM 30586 | ***Ursus arctos°*** FMNH 27268 | ***Arctodus simus°*** FMNH-M 24880 | ***Actotherium angustidens +*** MLP 35-IX.26 |
|---|---|---|---|---|---|---|---|---|---|---|
| [1] | Maximum distance between the posterior part of the tuberosities. | 90 | 85 | | | | | | | |
| [2] | Maximum anteroposterior axis of the head. | 98 | 91 | | | | | | | 156 |
| [3] | Transversal axis including the extensions of tuberosities. | 96 | 87 | | | | | | | 130 |
| [4] | Maximum transversal axis of articulation of the head. | 84 | 77 | | | | | | | |
| [5] | Anteroposterior length of the lateral tuberosity. | 86 | 85 | | | | | | | |
| [6] | Length of the medial tuberosity including the rim. | 86 | 45 | | | | | | | |
| [7] | Greatest anteroposterior width of the shaft. | 74 | | 5043 | 43.33 | 30.82 | 35.06 | | | 91 |
| [8] | Maximum length of the humerus including the proximal and distal ends. | 507 | 428 | 418.96 | 350.9 | 284.81 | 301.45 | 383 | 580 | 620 |
| [9] | Maximum transversal width of the shaft in the middle of the deltoid surface. | -63 | 66 | | | | | | | 84 |
| [10] | Maximum length of the delto-pectoral ridge including the tuberosity. | 334 | 245 | 288.81 | 230.33 | 191.35 | 209.95 | 291 | 370 | |
| [11] | Maximum high of the external epicondylar crest. | 142 | 158 | | | | | | | |
| [12] | Greatest distal width between the epicondyles. | 126 | 144 | 95.38 | 73.73 | 62.48 | 63.27 | | | |
| [13] | Height of the nutritive foramen. | 225 | 151 | | | | | | | |
| [14] | Transversal width of the lateral epicondylar crest. | 85 | - | | | | | | | |
| [15] | Maximum width of distal end between the epicondyles. | 125 | 123 | 144.41 | 104.67 | 85.4 | 89.4 | | | 185 |

MPGJ: Museo de Paleontología Geociencias Juriquilla, Querétaro, México; TMM: Texas Memorial Museum, University of Texas at Austin; USNM- United States National Museum; LACM: Los Angeles County Museum of Natural History; FMNH- Field Museum of Natural History, Chicago; MLP- Museo de la Plata.

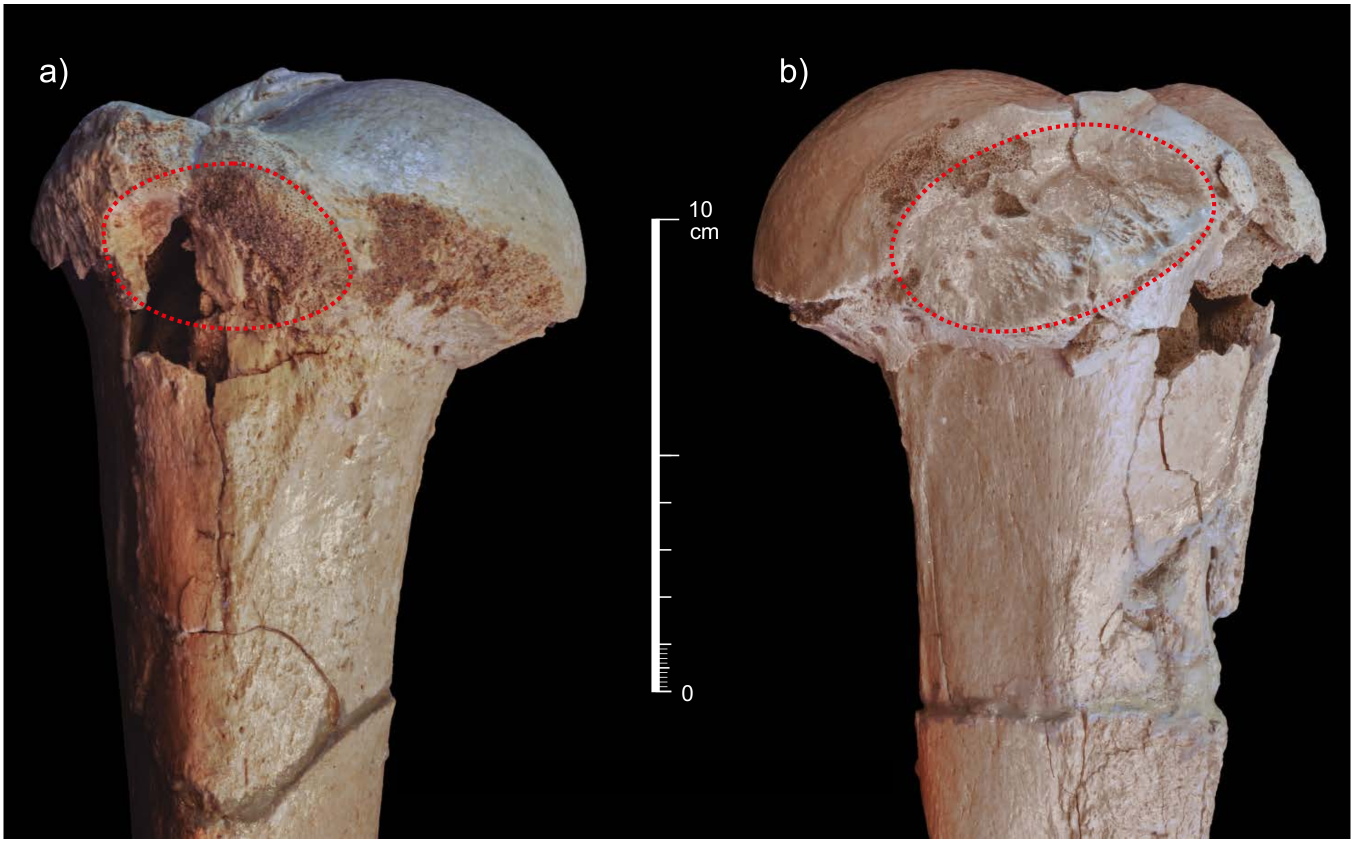


Figure 3. MPGJ 5676 *Agriotherium* left humerus. a) Upper lateral side with depression surface for insertion of infraspinatus muscle. b) Medial side with attachment for subscapularis muscle.

and robust deltoid crest that ends in the delto-pectoral tuberosity. The pectoral ridge merges in external border of the lateral tuberosity and between them is a flat surface for the insertion of the cephalo-humeral muscle (= clavotrapecius + clavodeltoid). The upper part is slightly wider and more convex outwards, because the origin of the pectoral crest denotes that the surface is broader and lightly convex (Figure 4a and S2).

Halfway down the diaphysis, the cephalo-humeral crest begins to reduce (Figure 4a [10]) and becomes narrower due to the convergence of deltoid and pectoral crests, which join a little more than halfway up the diaphysis and form the delto-pectoral tuberosity, ending below the pointed border at the upper external lateral epicondylar ridge.

The distal end is wider, the articular surface is the most developed part, the transverse axis across the epicondyles is 75 % narrower (Figure 4a [15]).

The medial epicondyle is a prominently marked convex structure that projects out of the shaft (Figure 4a, 5a, S1c and S2a), with several concave scars for the muscle insertion of the wrist and digits. Its separation from the lateral epicondylar ridge is the widest part of the distal end. The lateral epicondylar ridge is distinctly thin and triangular in outline. It is located above the radial fossa. The external border of this structure is curved and thick with two deep grooves in the middle for the extensor muscles of the hand. It joints with the shaft a little above where the delto-pectoral tuberosity ends. This structure occupies about 32 % of total length of the shaft (Figure 4a [11], and the total distance between the epicondyles represents the widest part of the distal end (Figure 4a [15], 5a, S1c and S2a).

The internal condyle in the Mexican specimen is a concave surface where the ulna articulates; above is the larger and deep coronoid fossa separated from the radial fossa by a convexity, which is small and shallow, the lateral epicondylar ridge begin in the border of the radial fossa.

In the posterior side, the olecranon fossa is deep and moderately wide, and oriented towards the lateral epicondyle (Figure 6).

The nutrient foramen is a little higher in the posterior face (Figure 4b [13]), and there is no evidence of a scar of entepicondylar foramen (Figure 4b).

**Taxonomic remarks.** While describing a new species, *Agriotherium hendeyi*, from the late Hemphillian Quiburis Formation of Arizona, Jiangzuo and Flynn (2020) provided the most recent taxonomic treatment of North American *Agriotherium*, largely based on a hypothesized transformation series in the metaconid-entoconid complex in the lower molars. Although they did not treat in detail all previously named species of *Agriotherium* from North America, they concluded that there are only two valid species, *A. hendeyi* and *A. schneideri*, with the former confined to Arizona only and the latter including the rest of North American records. Furthermore, *A. hendeyi* is a small species, substantially smaller than *A. schneideri*. By these criteria, our Zacatecas humerus likely belongs to *A. schneideri*, as all known dental materials from Mexico were referred to the latter (Carranza-Castañeda and Miller, 2004).

From the early Hemphillian (Hh2) of North America, Jiangzuo and Hulbert (2021) also recognized another large ursid, *Indarctos*, including humeri from the Rattlesnake Formation of Oregon (Merriam *et al.*, 1916), Hi Level Quarry of Nevada, and Withlacoochee River 4A of Florida. Relationships between *Indarctos* and *Agriotherium* are not clear, but in general, *Indarctos* tends to be more hypocarnivorous with a distinct M2 talon and may belong to a distant relative of the

Figure 4. MPGJ 5676 *Agriotherium* left humerus. a) Anterior view: the cephalo-humeral surface, form the delto-pectoral tuberosity. The medial epicondyle is convex and prominent, and the lateral epicondylar ridge is wider and occupied the 32 % height of the diaphysis. b) Posterior view: olecranon fossa reduced, and straight. c) Lateral view: the head is hemispherical in shape, protrudes posteriorly. All measurements are in Table 1.

giant panda clade Ailuropodinae (Abella *et al.*, 2012; Qiu *et al.*, 2014), whereas others regarded *Agriotherium* to be descended from *Indarctos* (Hendey, 1980). Dentally, *A. schneideri* may also have mixed characters of both *Agriotherium* and *Indarctos* (Hunt, 1998; Jiangzuo *et al.*, 2019). Regardless the relationship (or lack thereof) of North American *Agriotherium* and *Indarctos*, based on dental morphology, all known Mexican late Miocene ursids are clearly identifiable as belonging to *A. schneideri*.

## COMPARISON

The main objective of this work is to describe the humerus of *Agriotherium* collected in El Resbalón locality, the only complete specimen known in faunas of the early-late Hemphillian and equivalent beds in Mexico, Africa, and Eurasia. Records of humerus of *Agriotherium* are very scarce, an also the proximal end is always missing. We made comparisons with humeri from recent bears housed

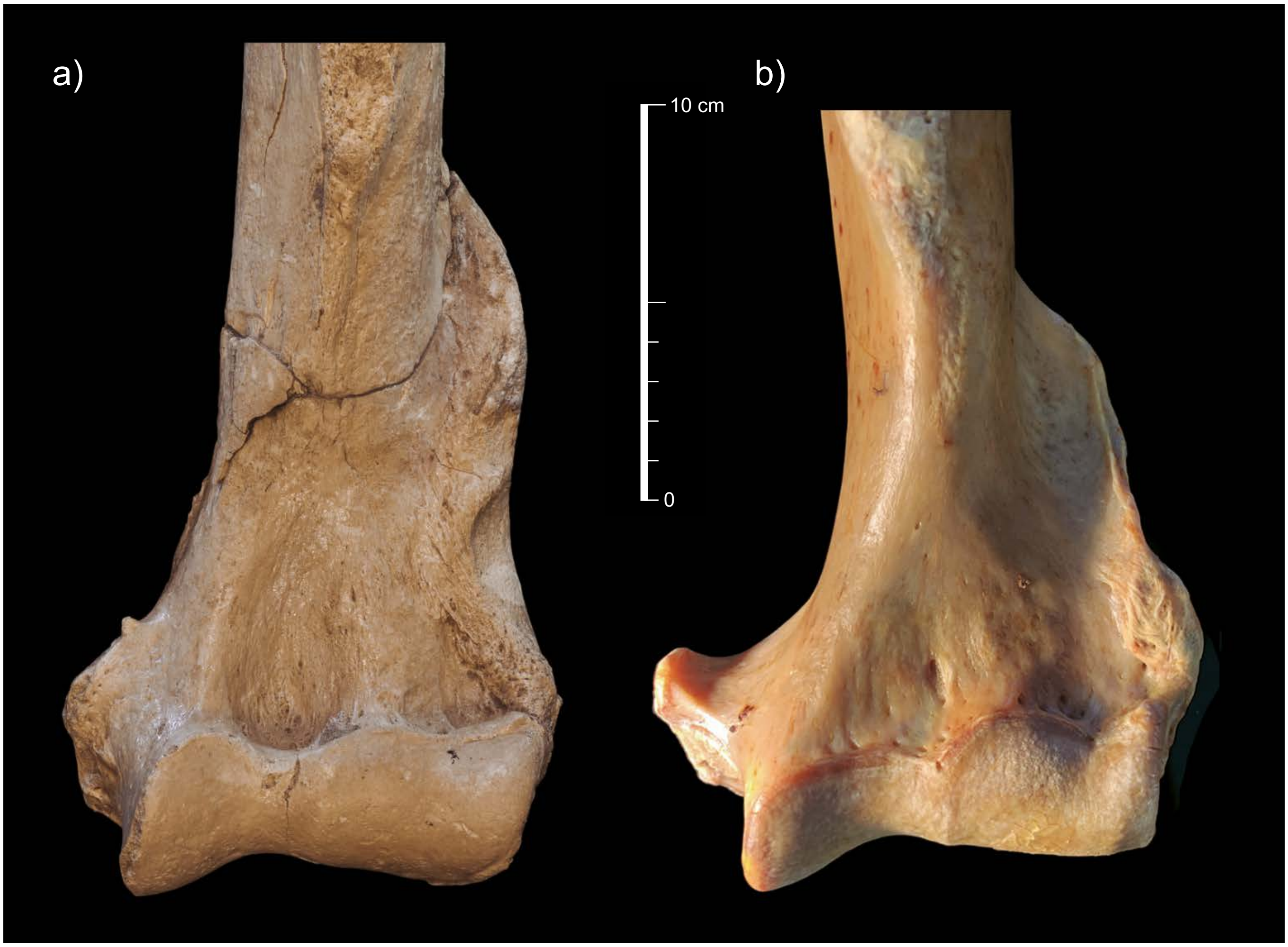


Figure 5. a) MPGJ 5676 left humerus of *Agriotherium* anterior view: the medial epicondyle is convex and protrude from the shaft. The condyloid fossa is large and deep; two grooves meet in the middle, the shaft end little above the deltoid tuberosity. b) TMM M-7503, Ursus *maritimus* anterior view: the medial epicondyle is large and hooked; the lateral epicondylar crest is concave in all the extension; no grooves are present along the edge.

in the collection of the Jackson School of Geosciences, University of Texas. In *Ursus americanus* (TMM M-137, Figure 7) from Alaska, the medial condyle is long and ends in a notable hook. In *Ursus arctos* (TMM M-3773), a young animal, the proximal epiphysis is still separated from the diaphysis, and the medial condyle is prominent. In an adult individual (LACM 625, collection of the Los Angeles Museum), the medial condyle is long and ends in a hook. The same structure is well developed and is pointed in *Indarctos oregonensis* (UCMP 22362, Figure 8).

When compared the proximal end in both specimens, *Ursus arctos* and *Ursus americanus*, its medial tuberosity is small and the lateral tuberosity is larger, the bicipital groove is narrower in the anterior part; these are the main differences with the Mexican specimen. In *Ursus maritimus*, the lateral tuberosity is larger and slightly higher, is wide and form a rounded-concave depression with multiple foramina, ending in the middle of the head. The bicipital groove is narrower and relatively deep. The medial tuberosity is smaller and narrower in *Ursus maritimus*, and the lateral tuberosity is larger than in the Mexican specimen (Figure 2).

In the upper lateral side in *Ursus maritimus* the impression for the infraspinatus muscle is wide and deep, occupying all the lateral side. In *Agriotherium* from México, this structure is incomplete, but it is possible to see that it is rounded and deep (Figure 3a dotted line). In the proximal medial side, the fossa for the subscapularis muscle is wide and directed toward the posterior part of the shaft and is larger, in contrast to the Mexican specimen. The head of the humerus that articulates with the scapula is more rounded in the specimen from Mexico (Figure 3b and S1d2).

Hendey (1980) describes a humerus fragment of *Agriotherium* from the Langebaanweg quarry in South Africa. It is important to point out that the form and structures are like those mentioned in this work for the complete humerus of Zac Juch 47 from El Resbalón, including measurements provided for the two specimens, they are within the range of measurements of the Mexican specimen and the differences are not greater than 10 %.

In the Hendey illustration (Hendey, 1980), the medial epicondyle where the insertions for the phalangeal and metacarpal muscles of the hand are found, is comparable in shape and size with the Mexican specimen (Figure 4a and S2a).

In *Ursus maritimus*, its large and tapered medial epicondyle suggests that the extensor muscles of the hand and fingers are more developed and efficient during hunting, as the metacarpal and phalangeal muscles are more important for prey retention (Sorkin, 2006a). This shows that these bears were more active predators and

Figure 6. Distal end of the humerus: the olecranon fossa is observed wide and straight located between the epicondyles.

had a specifically carnivorous diet. In *Agriotherium*, the same muscles may be reduced, which implies less efficiency in the retention of large prey and the diet could be not only carnivorous, but could also be supplemented with carrion, as well as some plants and fruits. In contrast, some authors suggest that *Arctodus simus* was more herbivorous (Emslie and Czaplewski, 1985). However, there are also views that *Arctodus simus* was predominantly carnivorous but obtained most of the animal material in its diet through scavenging (Matheus, 1995, 2003, Figures 4a, 7d, and S2a).

In *Agriotherium* from El Resbalón, the crest of the lateral epicondyle begins at the external condyle, and the external border limits the radial fossa. In the middle part, the humerus has a thick rim with two wide grooves, which are not described as part of the same structure in bears from the Pleistocene of North America or Europe, as illustrated in *Ursus maritimus* (Figure 5b and 7d). *In Ursus maritimus* (Figure 5b) the lateral epicondylar ridge is different from the Mexican *Agriotherium.* The crest begins in the external condyle as a concave structure throughout, which includes the radial fossa, continues towards the proximal region, and ends in a ridge that curves towards the shaft, ending in the same plane as the delto-pectoral tuberosity, and the grooves are not present. However, in *Ursus americanus* the crest is shorter, ending at the same height as the delto-pectoral tuberosity (Figure 7a).

In contrast, in *Ursus maritimus* and other ursids such as *Arctodus simus*, *Ursus americanus* and *Ursus arctos*, the medial epicondyle has a similar shape and size, and is highly developed and hook shaped. In *Ursus arctos*, the crest of the lateral epicondyle is slightly concave, ending just above the delto-pectoral tuberosity. In all these bears the grooves in the lateral epicondylar ridge are absent (Sorkin 2006a, fig. 11 B). Modern tremarctine bears (Vela-Vargas *et al.*, 2021) and their extinct relative *Arctodus* (such as a humerus from La Brea Tar Pits and Museum, we examined), preserve the entepicondylar foramen, which is not present in *Agriotherium* and has not been considered in this comparison (Figure 7).

When comparing *Indarctos orogenesis* (UCMP 22362) with the anatomical structures of *Agriotherium,* they have great similarity. The measurements illustrated in Figure 8 were calculated using the scale provided in the photograph. The most important thing is that the measurements obtained are none greater than 10%, which allows objectively considering the size of *Indarctos* and their comparison with *Agriotherium*. The biggest difference is the presence in *Indarctos* of an entepicondylar foramen which does not exist in *Agriotherium* (Jiangzuo and Hulbert, 2021). Also, this foramen is present in *Indarctos atticus* from Attica, Greece (Roussiakis, 2001). In general, all the anatomical characters of *Indarctos* match with the Mexican specimen, the differences fall in the individual variability on two populations of bears; however, the principal differences are the length the humerus, the medial epicondyle shape and the presence of entepicondylar foramen absent in the Mexican specimen, although in these specimens the sex is unknown.

According to the description of the Pleistocene bears of Spain (Torres Perez-Hidalgo, 1988), the lateral epicondylar ridge has a great

Figure 7. a) TMM M-3773, *Ursus arctos*; b) LACM 625, *Ursus arctos*. c) TMM M-137, *Ursus americanus*; d) TMM M-7503, *Ursus maritimus*. In a, c and d), the medial condyle is developed, forming a hook. The lateral epicondylar crest is concave throughout its length, and it does not have grooves. In d) the delto-pectoral tuberosity is longer than the epicondylar crest.

diversity of forms as observed in *Agriotherium* and its comparison with other bear materials. The crest has a similar shape but with different size and structures that, undoubtedly, have implications in the use of brachialis and brachioradialis muscles.

## REMARKS ON DIET AND LOCOMOTION

With an average body mass estimated at 700–800 kg (Christiansen, 1999), the Pleistocene short-faced bear, *Arctodus simus*, and it's even larger South American relative, *Arctotherium angustidens*, were the largest terrestrial carnivorans in the Americas (Soibelzon and Schubert, 2011) and were important predators during the Ice Ages. The late Miocene-Pliocene *Agriotherium* is similarly gigantic and may have served as top predators of their time. Its much wider distributions, from Africa through Eurasia to North America, also suggests that it may have played an important ecological role in a wide range of habitats.

Hannold *et al.* (2021) recently studied carbon isotope geochemistry of *Agriotherium schneideri* from the latest Hemphillian Yepómera site in Chihuahua, Mexico. It has a mean $\delta^{13}$C value of -5.7±0.3 ‰ from enamel samples (n=2). Correcting for a carnivorous lifestyle and associated +8 ‰ enrichment adjusting for body size, Hannold *et al.* (2021) arrived at a mena $\delta^{13}C$ diet of -13.7±0.3 ‰ and concluded that *Agriotherium* may have consumed preys of $C_4$ diet, although they cautioned that isotopic signatures of modern ursid analogues were not known well enough to be certain of the conclusion. Miller and Carranza-Castañeda (1996), on the other hand, suggested that *Agriotherium* was a cursorial predator-scavenger and an omnivore with a wide-ranging diet, as well as able to crush bones. Indeed, it is a safer assumption of an omnivore diet for *Agriotherium* given that living ursids are all omnivorous except for the polar bears and giant pandas. As the proportions of meat and plant consumptions are intensely debated for the Pleistocene big, short-faced bear *Arctodus simus*, with a mass estimated of 590–630 kg by Kurtén (1967) and of 700–800 kg by Christiansen (1999) for males, is considered an hypercarnivore. Figueirido *et al.* (2010) and Soibelzon and Schubert (2011) describe the largest bear from South America *Arctotherium angustidens*, with a body mass estimated between 1588–1749 kg, and suggest that it was the largest known bear and probably the most powerful terrestrial carnivoran of the late Cenozoic.

The diet of *Agriotherium* will likely remain controversial, partly for lack of a modern ursid analogue. Presence of a premasseteric fossa in the lower jaws of both *Arctodus* and *Agriotherium*, used as evidence of large amount of plant materials in their diets (Sorkin, 2006a), is tantalizing but its muscular functions remain unexplored.

With a total humeral length of 507 mm (Table 1), *Agriotherium schneideri* has comparable front limb length of *Arctodus simus* (*e.g.*, Emslie and Czaplewski, 1985; Richards and Turnbull, 1995; Christiansen, 1999; Sorkin, 2006a; Figueirido *et al.*, 2010), although our Mexican specimen is smaller than the largest individuals of the latter. As suggested by Sorkin (2006a), these two giant bears may share ecological similarities such as diet and locomotion. However, detailed anatomical differences as outlined above are likely inherited from distinct evolutionary lineages that went their separate ways many million years ago.

## CONCLUSIONS

The MPGJ 5676 humerus is the only complete humerus of *Agriotherium* known. It shows great similarity with the characteristics in L 45063 mentioned by Hendey (1980). In particular, the Mexican specimen shares many similarities with the only known distal end from South Africa especially on the medial epicondyle, where the metacarpal and fingers muscles are inserted, and on the size and shape of the lateral epicondylar crest where the brachialis and brachioradialis muscles originate allowing the rotation of the arm. The reduction of these structures is a factor that limited the effectiveness of *Agriotherium* for hunting and retention of large prey. These factors influenced the diet of *Agriotherium* that was not strictly carnivorous (Sorkin, 2006a; Hendey, 1980; Oldfield *et al.*, 2012).

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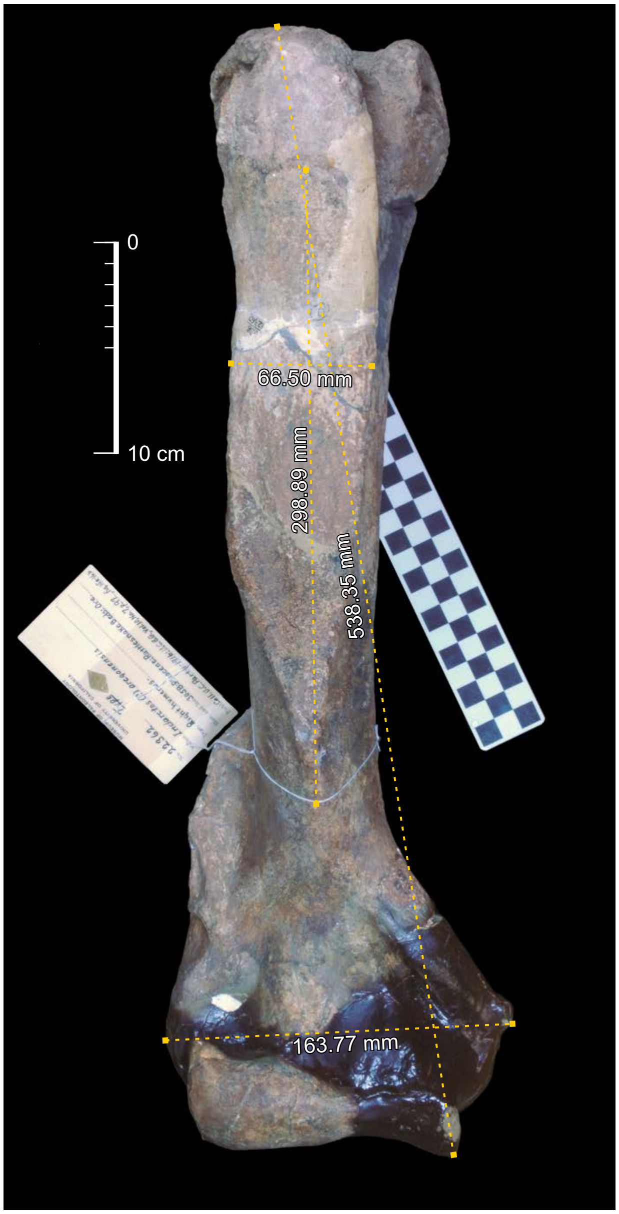

Figure 8. UCMP 22362 *Indarctos oregonensis* anterior view of the humerus: the main difference is the presence of the entepicondylar foramen, absent in *Agriotherium*. The measurements provided were calculated based on the scale of the photograph.

ash associated with the humerus. Master in IEVEA Cesar Contreras Zamora for the Technical Support in computing processes and Eng. Bernardino Rodríguez Morales, for their collaboration in the adaptation of the Museum for the preservation of the fossils in the collection.

## SUPPLEMENTARY MATERIAL

For a better view, Figures S1 and S2 illustrate, in high definition and without dimension lines, the figures of the Mexican *Agriotherium* shown in this paper. Figure S1 joins Figures 2a, 3, 5a and 6, while Figure S2 shows the Figure 4 of the previous text. This material can be downloaded at www.rmcg.unam.mx, in the abstract page of this paper.

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