FIRST RECORD OF *ARCTOTHERIUM* (URSIDAE, TREMARCTINAE) IN NORTHWESTERN ARGENTINA AND ITS PALEOBIOGEOGRAPHIC SIGNIFICANCE.

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The fossil record of bears of the Subfamily Tremarctinae (Mammalia: Ursidae) in South America is restricted to the Pleistocene and earliest Holocene (San Roman et al., 2000; Prevosti et al., 2003; Soibelzon et al., 2005). Many authors have proposed several nominal forms since the first fossil remains were discovered (e.g., Gervais and Ameghino, 1880; Kraglievich, 1926; Kraglievich and Ameghino, 1940; Kurtén, 1967; Berman, 1994). Recently, all the South American fossil bears were recognized as belonging to only one genus, *Arctotherium* Burmeister (Soibelzon, 2002; Soibelzon, 2004; Soibelzon, et al., 2005). This genus includes five species: (1) *A. angustidens* Gervais and Ameghino (Ensenadan, Early-Middle Pleistocene); (2) *A. vetustum* Ameghino (Bonaerian, Middle Pleistocene); (3) *A. wingei* Ameghino; (4) *A. bonariense* (Gervais); (5) and *A. tarijense* Ameghino (the last three from the Bonaerian and Lujanian, Middle Pleistocene to Early Holocene) (Soibelzon, 2004; Soibelzon et al., 2005). Although *Arctotherium* is widely distributed geographically from northern Venezuela to southern Patagonia (Prevosti et al., 2003; Soibelzon et al., 2005), most records of *Arctotherium* come from the Argentinean Pampean region, particularly Buenos Aires Province. In fact, there are large areas in South America with no record of fossil bears at all.

Here we describe the first remains of *Arctotherium* from Late Pleistocene deposits of Catamarca Province, northwestern Argentina. This material narrows the geographical gap between two previously known fossiliferous localities separated by more than 1200 km.

Institutional Abbreviations—BMNH, Natural History Museum, United Kingdom; **GP**, Museu Paulista, Universidade de Sâo Paulo, Brazil; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; **MMMP**, Museo Municipal de Mar del Plata ‘Lorenzo Scaglia’, Argentina; **PVL**, Colección Paleontología de Vertebrados Lillo, Tucumán, Argentina; **UZM**, Zoological Museum, University of Copenhagen, Denmark.

Anatomical Abbreviations—m, lower molar; **p**, lower premolar.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Family URSIDAE Gray, 1825

Subfamily TREMARCTINAE Merriam and Stock, 1925

Genus *ARCTOTHERIUM* Burmeister, 1879

ARCTOTHERIUM sp.

(Fig. 1)

Referred Specimen—PVL 6158 (Fig. 1). Nearly complete left dentary of a very old individual with canine, p1, and m1-3. The material shows some weathering.

Locality and stratigraphic context—Five kilometers south of El Rodeo, Ambato Department, Catamarca Province, Argentina (28º 18’ 02’’ S, 65º 53’ 33’’ W, 1640 masl) (Fig. 2). The dentary was found in a road cut within a layer constituted by massive silts in loessic sediments assigned to Late Pleistocene (Fig. 3).

Description—The dentary is remarkably small and slender with a very low horizontal ramus. The mandibular symphysis is short and deep, extending posteriorly to the p2 alveolus. A straight anterior margin can be inferred for the coronoid process although only the base of the process is preserved. The condyloid process is almost complete with a well-developed neck and mandibular notch. The masseteric crest is poorly developed with its lower end slightly curved backward, reaching the level of the masseteric line. A deep masseteric fossa occupies almost the entire thickness of the mandibular body. The premasseteric fossa is short and shallow, reaching the level of the anterior edge of m3. Mental foramina are conspicuous;

the anterior foramen is located below the p4 alveolus and the posterior foramen is below the posterior root of m1. The lingual surface of the dentary is poorly preserved, with no evident features.

Dentition—The canine is prominent, with a strong wear facet on the inner surface. The first lower premolar is damaged, with no observable features. Alveoli of p2 and p4 are very small and the alveolus of p3 is absent, probably because the alveoli closed during life after the tooth was lost. The occlusal surfaces of the molars are heavily worn, with just a few recognizable structures. The trigonid of the m1 is wide with a relatively large paraconid and the antero-lingual surface of the trigonid possesses a well-developed groove. Lingual and labial grooves between trigonid and talonid are not well defined. The labial edge of the talonid is slightly extended labially. The m2 is transversely expanded and shorter than the m1. The m2 trigonid is larger than the talonid with a conspicuous labial groove between these areas. The lingual edge of the m2 is convex without any groove. The outline of m3 is subelliptical in occlusal view. This tooth is much shorter than m2 and no cusp or crown division can be distinguished.

Comparisons—The most striking difference between PVL 6158 and all the recognized species of *Arctotherium* (sensu Soibelzon, 2004; Soibelzon et al., 2005), except *A. wingei*, are its slenderness and small size (Table 1; Figure 4).

The specimen from El Rodeo can be distinguished from *A. angustidens* (Figure 5A) by a shorter and remarkably less developed masseteric crest, less excavated premasseteric fossa, narrower trigonid of m1, and a proportionally larger m3 with respect to m2. PVL 6158 shares with *A. angustidens* a m3 that is clearly longer than wide.

Arctotherium vetustum (Figure 5B) differs from PVL 6158 in the masseteric crest morphology. In *A. vetustum*, as in other species of *Arctotherium*, this structure is prominent and relatively straight on its lower end, whereas in PVL 6158 the crest is much weaker and

shorter. The specimen MACN 1201 is a more robust mandible, with the condyle situated well above the alveolar level. Moreover, the canine is more procumbent than PVL 6158 and the premasseteric fossa is absent. However, in MMMP 1233M these differences are attenuated because the mandible is less robust, the condyle is lower and there is a moderately excavated premasseteric fossa. The general shape and relative size of the molars as well as the proportions between them are similar both in this species and PVL 6158.

Arctotherium bonariense (Figure 5C) shows the same general differences described above, with a more prominent canine and a premolar row length shorter than PVL 6158. The masseteric crest is well developed and the premasseteric fossa is absent. The trigonid of the m1 of *A. bonariense* is broader and longer with respect to the talonid than in PVL 6158.

Similar differences can also be found between *A. tarijense* (Figure 5D) and PVL 6158. The specimen MACN 2667 has a very short premolar area and p1-3 are arranged in a triangle, but the type (MACN 1458) has a slightly longer premolar row that is arranged in a line. In both specimens the trigonid of m1 is also relatively broader and longer with respect to the talonid than in PVL 6158.

The type specimen of *A. wingei* (MACN 1453; Figure 5E), from Tarija (southern Bolivia), is the most similar to PVL 6158 considering the small size, the slenderness, a long area for the premolar row, and a shallow premasseteric fossa. However, there are some differences such as a more antero-posteriorly elongated m1 and a more prominent trigonid on m2. The masseteric crest can not be compared because MACN 1453 lacks the posterior half of the dentary. Brazilian specimens (UZM 5249 and GP/2T-4) referred to *A. wingei* by Soibelzon (2004) have a more prominent masseteric crest and a very shallow premasseteric fossa. These specimens are larger and more robust than MACN 1453 and PVL 6158.

It should be noted that the weathering could be masking the true development of the masseteric crest in the PVL 6158. However, a detailed analysis of the surface clearly indicates

that the weathering did not modify the development of this structure. Furthermore, other attributes of the masseteric crest that are not affected by this factor, such as the length and trajectory, distinguish it from other specimens.

In summary, the main differences between the specimen from El Rodeo and four of the recognized species of *Arctotherium* can be explained by size. The measurements reported in the literature (e.g. Trajano and Ferrarezzi, 1994; Soibelzon, 2002, 2004) indicate that *A. wingei* is the smaller species of this genus. The type of this species is the most similar specimen in size to PVL 6158.

Discussion

Taxonomic and paleobiogeographic significance—The specimen from El Rodeo is similar to the type of *A. wingei* and more slender than the Brazilian specimens assigned to this species (sensu Soibelzon, 2004; Soibelzon et al. 2005). However, it must be noted that most ursid species display a wide range of individual variation unrelated to geographic distribution (Kurtén, 1966, 1967; Trajano and Ferrarezzi, 1994). There is notable sexual dimorphism in size and shape of skulls; males are markedly larger than females (Trajano and Ferrarezzi, 1994; Emslie, 1995). The Brazilian specimens of *A. wingei* have strong, long, and straight masseteric crests, similar to the other species of *Arctotherium*. In contrast, the dentary from El Rodeo shows a poorly-developed crest. Unfortunately, it is not possible to compare this character with the Tarija specimen (MACN 1453) because it lacks the posterior half of the dentary (Figure 5E).

Soibelzon (2002), in spite of recognizing that the type of *A. wingei* is remarkably small, argued that this specimen and those from Brazil can be referred to the same species. Based on this referral, *A. wingei* has a strong, straight and well-developed masseteric crest. One of the specimens from Brazil (GP/2T-4) referred to *A. wingei* by Soibelzon (2004) was originally described by Trajano and Ferrarezzi (1994) as *A. brasiliense*. They considered this specimen a

female because of the poor development of the sagittal crest. This specimen also has a strong and almost vertically disposed masseteric crest. If it can be assumed that the GP/2T-4 specimen is effectively a female, the poor development of the masseteric crest in PVL 6158 could be related to taxonomic differences instead of sexual dimorphism. Moreover, studies of sexual dimorphism in tremarctines have focused on size variation (Kurtén, 1966, 1967; Soibelzon, 2002; Schubert and Kaufmann, 2003 and references therein) but no author has used masseteric crest development as a sexual dimorphism indicator. Thus, until new remains are found, we choose to maintain an open taxonomic hypothesis; we do not assign PVL 6158 to any known species of *Arctotherium* and refrain from proposing the existence of a new taxon.

Most of the known specimens of *Arctotherium* come from the Pampean region of Argentina, mainly from Buenos Aires Province (Soibelzon et al., 2005). The specimen from El Rodeo constitutes the first mention of a tremarctine bear from the northern region of this country. Furthermore, it represents the first record of a bear, fossil or living, from this region. The nearest previous records come from the Argentinean provinces of San Luis, Entre Ríos and Santa Fe and the Tarija Valley in Bolivia. The specimen from El Rodeo shares more similarities with the specimen from Tarija than with the Brazilian specimens. Both localities are situated at medium altitude Andean valleys, separated from tropical and subtropical Yungas forest by eastern mountain ranges. Today these areas share a similar mesic and temperate climatic pattern, vegetation, and many mammal species (Morlans, 1995; Anderson, 1997; Mares et al., 1997; Navarro and Maldonado, 2002). These morphological similarities, as well as shared geographic and environmental conditions, may indicate the presence of an Andean group of *Arctotherium* distinguishable from the species found at lowland and eastern regions of South America.

Comments on the age of the sediments—Although the sediments at the locality have not been dated, several researches have focused on similar loessic sequences in the area. Sayago et al. (2005) described a loess-paleosol sequence from the Balcozna area, 50 km east of El Rodeo, whose AMS radiocarbon dates range between 32,500 and 4,500 yBP. These authors assigned this sequence to the Tafí del Valle Formation (Collantes et al., 1993; Zinck and Sayago, 1999, 2001) and indicated that it lithostratigraphically resembles profiles observed in other southern Andean valleys such as El Rodeo-Las Juntas area. The Tafí del Valle Formation was described in the Tafí Valley, Tucumán Province, where some of the thickest and best-exposed loess-paleosol outcrops in northwestern Argentina are found (Zinck and Sayago, 1999, 2001; Schellemberger et al., 2003; Schellemberger and Veit, 2006). Based on radiocarbon data, Sayago et al. (2005) indicated for this formation a time span from ca. 47,000 to 8,600 yBP. However, recent optically stimulated luminescence (OSL) dates for the basal part of the sequence ranged from ca. 195,000 to 150,000 yBP (Kemp et al., 2003; 2004). Moreover, magnetostratigraphic data showed that the loess-paleosol sequence is older than previously thought, indicating that the Tafí del Valle Formation deposition began at least 1.15 Ma ago (Schellenberger et al., 2003; Schellemberger and Veit, 2006). Despite these proposed older ages, one of us (PEO) dated collagen from rodent bones exhumed from a similar loessic sequence at Las Juntas, 20 km north of El Rodeo, indicating an age between 13,310–13,100 yBP. Therefore, the similarities between the sediments of Las Juntas and those yielding the studied material suggest, at least preliminarily, that the level containing PVL 6158 can be possibly referred to Late Pleistocene.

Paleoenvironment—The fossil was excavated from a layer of loessic sediments indicative of temperate arid and semiarid environments (see Zinck and Sayago, 2001; Sayago et al., 2005).

Trajano and Ferrarezzi (1994) suggested that the species of *Arctotherium* probably were dwellers of open areas in arid and semiarid paleoenvironments. These conditions differ from the present mesic climate in this area (mean annual rainfall = 700 mm; mean annual temperature = 14.4ºC), with Chacoan vegetation (sensu Cabrera, 1976) that includes *Schinopsis haenckeana* woodlands and *Stipa* and *Festuca* grasslands (Morláns, 1995) as well as some elements from humid Yungas such as *Podocarpus parlatorei* forests. The presence of populations of *Arctotherium* in this area could be related to some of the last glacial events of the Late Pleistocene that produced arid and cold environment in northwestern Argentina.

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TABLE 1. Mandibular and dental measurements (in mm) of PVL 6158 compared to specimens of the five species of *Arctotherium*.

Measurements of BMNH 32916 taken from Soibelzon (2002).

	A. angustidens (BMNH 32916)	*A. angustidens* (MACN 851)	*A. tarijense* (MACN 1458)	*A. vetustum* (MACN 1201)	*A. bonariense* (MACN 9646)	*A. bonariense* (MACN 2668)	*A. wingei* (MACN 1453)	*Arctotherium* sp. (PVL 6158)
Mandibular height at p3	76.3	78.1	58.1	47.7	46.3	43.2	45.4	39.2
Mandibular height at m1	72.9	76.6	61.8	48.7	42.7	38.3	43.1	36.8
Mandibular width below m1	33.9	38.5	28.6	22.3	28.0	34.6	15.2	15.0
Mandibular height at m2	70.0	…	62.8	52.0	46.0	45.8	41.3	37.0
Mandibular width below m2	35.1	…	30.3	23.7	30.6	39.6	16.0	17.3
Mandibular height at m3	85.8	…	…	57.2	50.9	49.1	41.4	42.8
Total mandible length	395.0	…	…	227.3	205.6	206.5	…	180.0
m1 length	38.3	46.0	41.5	28.5	39.4	40.0	25.5	24.1
m1 width	21.0	28.7	22.0	17.0	24.9	24.7	14.8	15.3
m2 length	31.8	…	36.7	23.0	32.6	29.8	25.0	22.4
m2 width	26.0	…	24.1	18.5	26.6	26.7	16.5	16.0
m3 length	23.0	…	…	16.7	20.6	21.0	…	15.3
m3 width	20.0	…	…	15.6	17.4	17.7	…	13.8
m1-m3 length	92.5	…	…	68.1	93.5	90.6	…	64.8
m2-m3 length	59.6	…	…	39.6	72.0	51.3	…	37.5

FIGURES

FIGURE 1. Left dentary of *Arctotherium* sp., PVL 6158. **A**, lateral view; **B**, detail of molars in oclussal view. Scale bar equals 20 mm.

FIGURE 2. Map of northwestern Argentina showing the location of the El Rodeo-Las Juntas Valley and the fossil locality (asterisk).

FIGURE 3. Schematic stratigraphic profile indicating the location of the fossil remains of *Arctotherium* sp., PVL 6158.

FIGURE 4. Diagram for selected mandibular measurements of PVL 6158 compared to specimens of the five species of *Arctotherium*. **Abbrevations**: **Hp3**, Mandibular height at p3; **Hm1**, mandibular height at m1; **Wm1**, mandibular width below m1; **Hm2**, mandibular height at m2; **Wm2**, mandibular width below m2; **Hm3**, mandibular height at m3; **TML**, total dentary length.

FIGURE 5. Recognized species of *Arctotherium*. **A**, *Arctotherium angustidens*, MACN 5132; **B**, *Arctotherium vetustum*, MACN 1201; **C**, *Arctotherium bonariense*, MACN 9646; **D**, type of *Arctotherium tarijense*, MACN 1458; **E**, type of *Arctotherium wingei*, MACN 1453. Scale bar equals 20 mm.

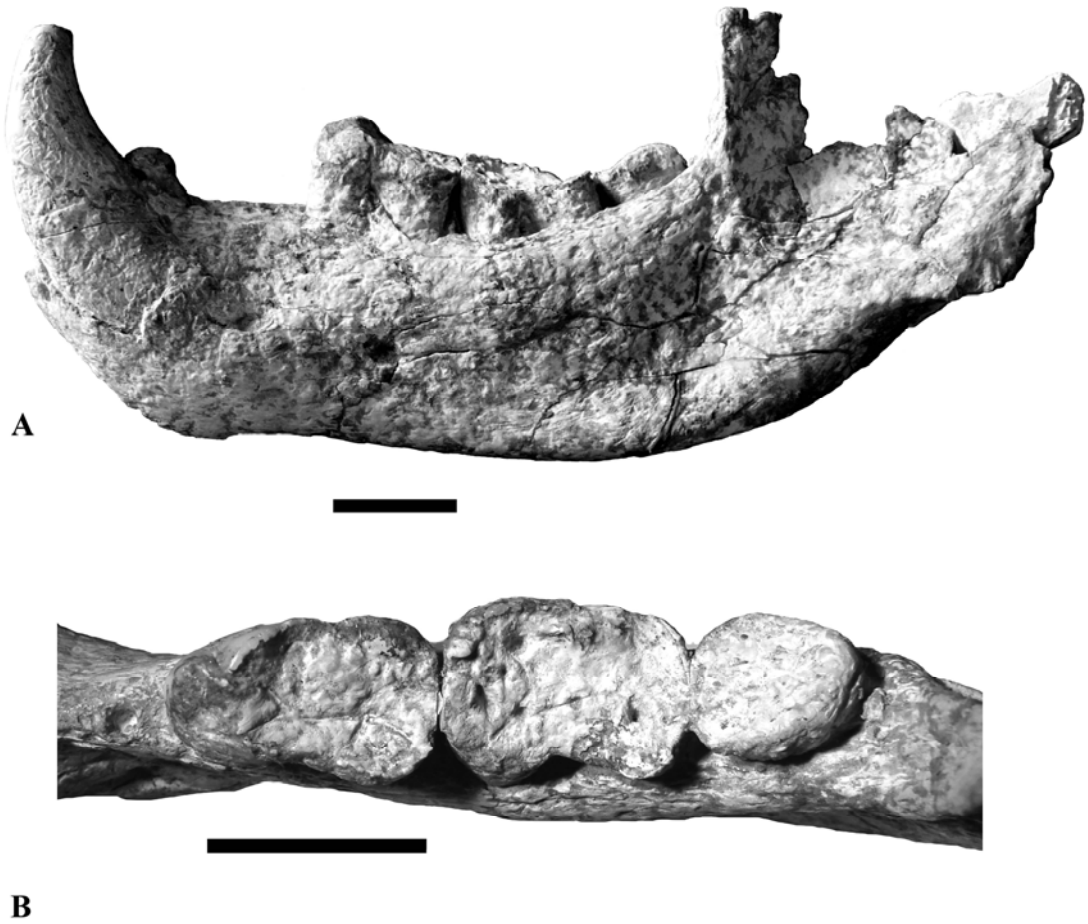

Figure 1

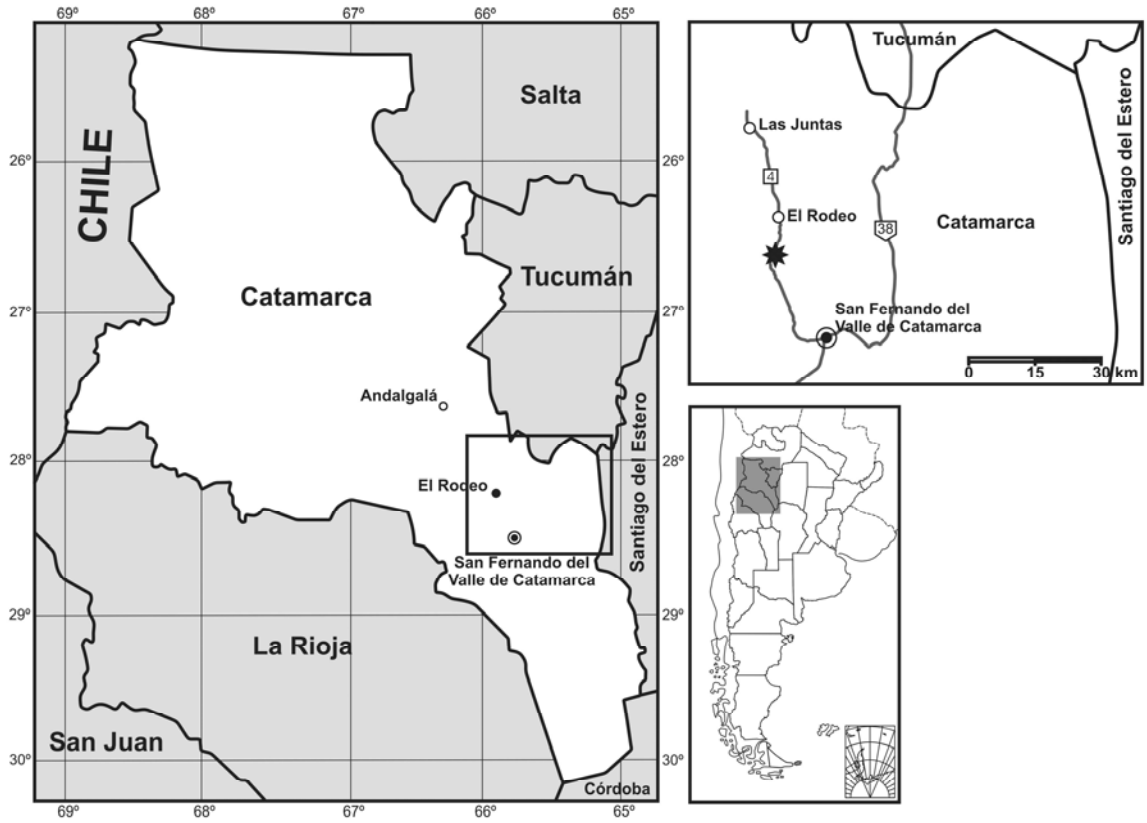
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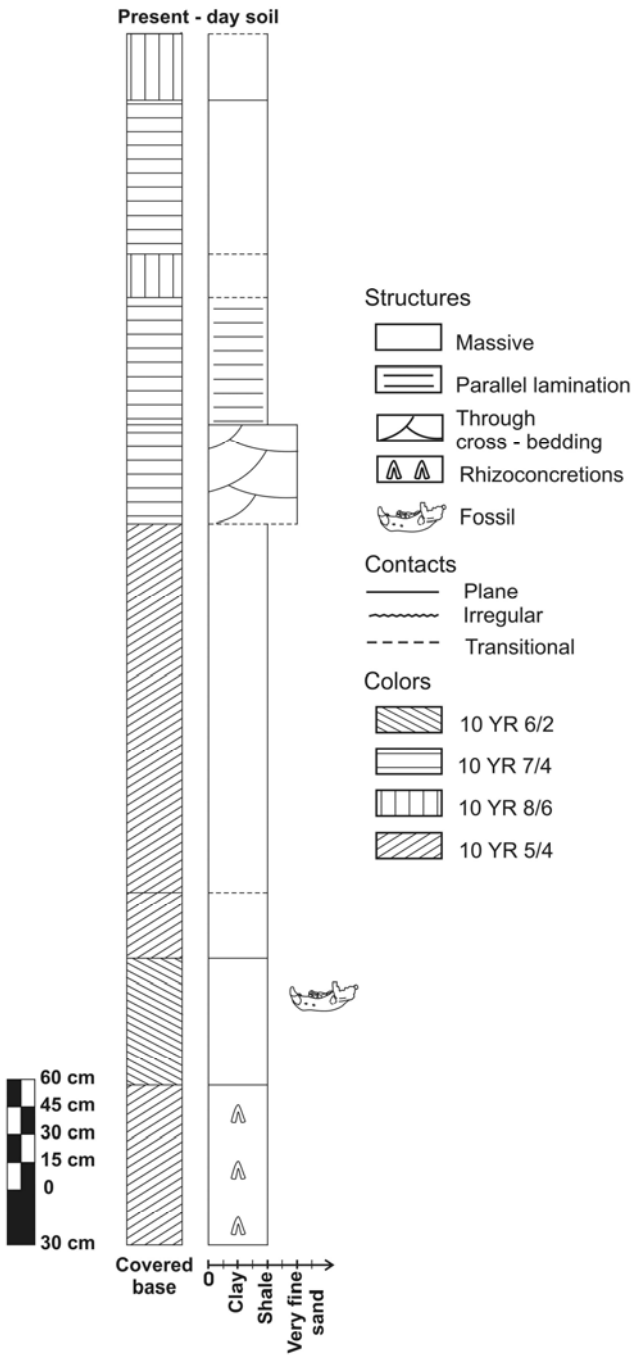
Figure 2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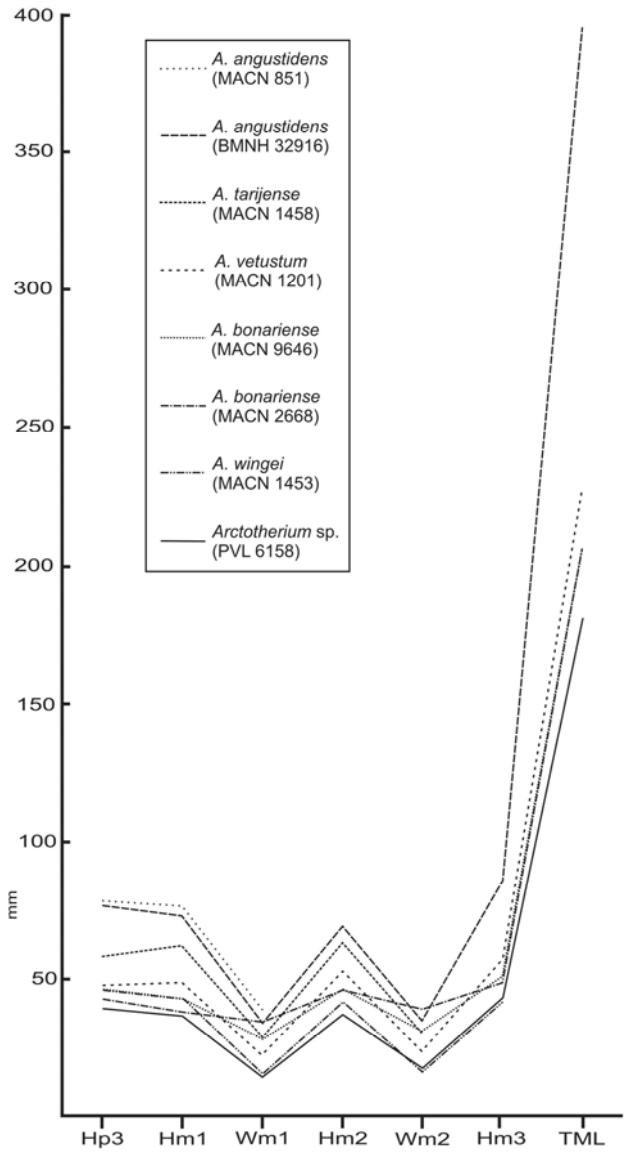
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Arctotherium sp. (PVL 6158)
Hp3
Hm1
Wm1
Hm2
Wm2
Hm3
TML

Figure 4

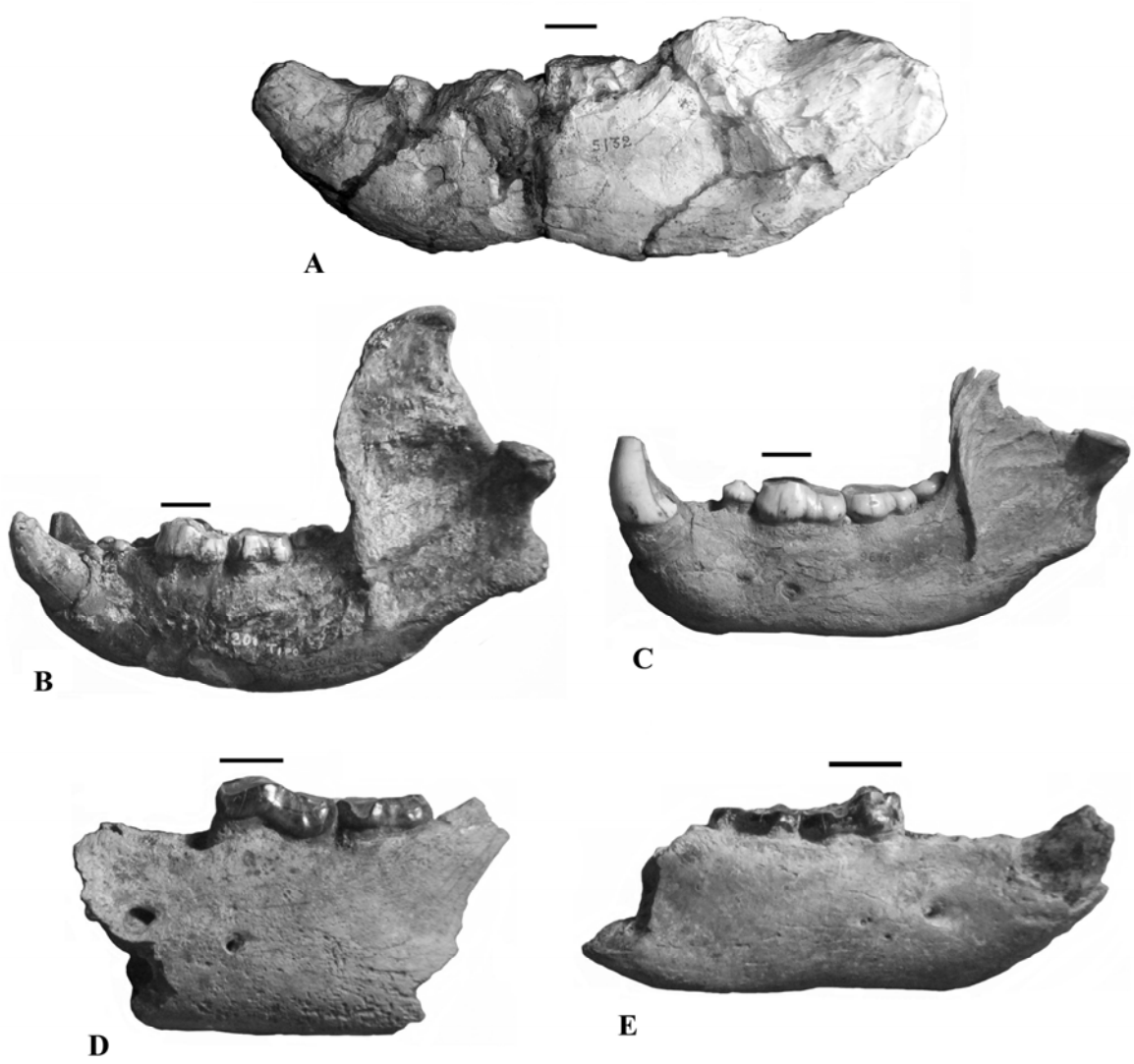

Figure 5