

LATE PLEISTOCENE MAMMALS FROM EL HATILLO, PANAMA

MAMÍFEROS DEL PLEISTOCENO TERMINAL DE LA LOCALIDAD DE EL HATILLO, PANAMÁ

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ABSTRACT: Late Pleistocene mammals from the El Hatillo locality on the Azuero Peninsula in Panama, originally reported by C. L. Gazin in 1957, are documented here for the first time. The following taxa are present: *Hoplophorinae?*, *Glyptotherium floridanum*, *Eremotherium laurillardii*, *Paramylodon harlani*, *Equus conversidens*, *Platygonus* sp., *Odocoileus* sp., *Mixotoxodon larensis* and *Cuvieronius hyodon*. This is a characteristic assemblage of late Pleistocene mammals from Central America that is dominated by fossils of *Eremotherium* in association with fossils of *Mixotoxodon* and *Equus*. I refer to such associations as EME assemblages and posit that most of these assemblages from Central America are of Late Pleistocene age. EME assemblages represent a mixed fauna of grazers and browsers that was common across Central America during one or more of the Late Pleistocene interstadials.

Keywords: Fossil mammals, *Eremotherium*, *Mixotoxodon*, *Equus*, Panamá, Pleistocene.

RESUMEN: Documentamos aquí por primera vez los mamíferos del Pleistoceno tardío de la localidad de El Hatillo en la península de Azuero en Panamá, originalmente reportado por C. L. Gazin en 1957. Los siguientes taxa están presente: *Hoplophorinae?*, *Glyptotherium floridanum*, *Eremotherium laurillardii*, *Paramylodon harlani*, *Equus conversidens*, *Platygonus* sp., *Odocoileus* sp., *Mixotoxodon larensis* y *Cuvieronius hyodon*. Este es un conjunto característico de mamíferos del Pleistoceno Tardío de Centroamérica destacado por fósiles de *Eremotherium* en asociación con fósiles de *Mixotoxodon* y *Equus*. Me refiero a este tipo de asociación como montaje EME y postulo que la mayoría de estos montajes de Centroamérica son de edad del Pleistoceno Tardío. Los montajes EME representan una fauna mixta de pastadores y ramoneadores que eran muy común en toda Centroamérica durante uno o más de los fines interestadiales del Pleistoceno.

Palabras clave: Mamíferos fósiles, *Eremotherium*, *Mixotoxodon*, *Equus*, Panamá, Pleistoceno.

INTRODUCTION

Leidy (1870) published the first report of a fossil mammal from Panama, part of the humerus of a ground sloth that he identified as *Myiodon robustus* (Fig. 1). This fossil, now in the collection of the Smithsonian Institution in Washington, D. C., was sent there by J. M. Dow and has no locality data other than having originated in Panama. It is the abraded proximal portion of a left humerus, but its relatively gracile morphology (note especially the small deltopectoral crest) indicates it is a megalonychid, not a mylodontid ground sloth (cf. Stock, 1925).

Smithsonian Institution paleontologist C. L. Gazin (1957) published the second record of fossil mammals from Panama, a diverse assemblage from Pleistocene deposits on the Azuero Peninsula (Fig. 2). However, other than that report, which did document some of the ground sloth fossils (Figs. 3-4), no further documentation of the fossils has been published. Recently, Pearson (2005) documented some other Pleistocene mammals from the Azuero Peninsula and published radiocarbon ages associated with these fossils. Miocene fossil vertebrates, including selachians, turtles, crocodylians and diverse mammals (e. g., Whitmore & Stewart, 1965; Gillette, 1984; MacFadden, 2006; Uhen et al., 2010; Cadena et al., 2012; Hastings et al., 2013; Pimiento et al., 2013; Rincon et al., 2013) have also been published from Panama.

Here, I describe and illustrate the Pleistocene fossil mammals from El Hatillo reported by Gazin (1957). They represent what I term the *Ereotherium-Mixotoxodon-Equus* (EME) assemblage, the most common kind of late Pleistocene mammal assemblage found at numerous localities in Central America. In this article, USNM =

National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. All measurements are in mm; l = length, w = width.

PROVENANCE

Gazin (1957) provided a detailed description of two fossil localities on the Azuero Peninsula of southern Panama: (1) La Coca, near the town of Ocutí; and (2) El Hatillo near the town of Pesé (Fig. 2). He also recounted the history of their discovery and excavation.

Both localities were in surficial beds of clay associated with pond and creek deposits. Pearson (2005) found similar deposits with fossil bone at the nearby localities of La Trinidadita and Llano Hato, from which he obtained radiocarbon ages of ~45-47,000 ¹⁴C yr.B.P from charcoal associated with the bones. This apparently dates the bone deposits to the Marine Isotope Stage 3 (MIS 3) interstadial, although I question the reliability of such relatively old radiocarbon dates. Nevertheless, given their occurrence in superficial clay deposits, preservation (relatively un-mineralized) and taxonomic composition, the vertebrate fossil assemblages from the Azuero Peninsula are certainly of Late Pleistocene age.

SYSTEMATIC PALEONTOLOGY

Hoplophorinae?

USNM 540672 (Fig. 5B) is a hexagonal scute with a maximum diameter of 24.1 mm and a maximum thickness of 7.8 mm. It has a slightly raised central area (weak central figure) and a few small, dispersed pits (foramina) on its external surface. The internal surface is exfoliated.

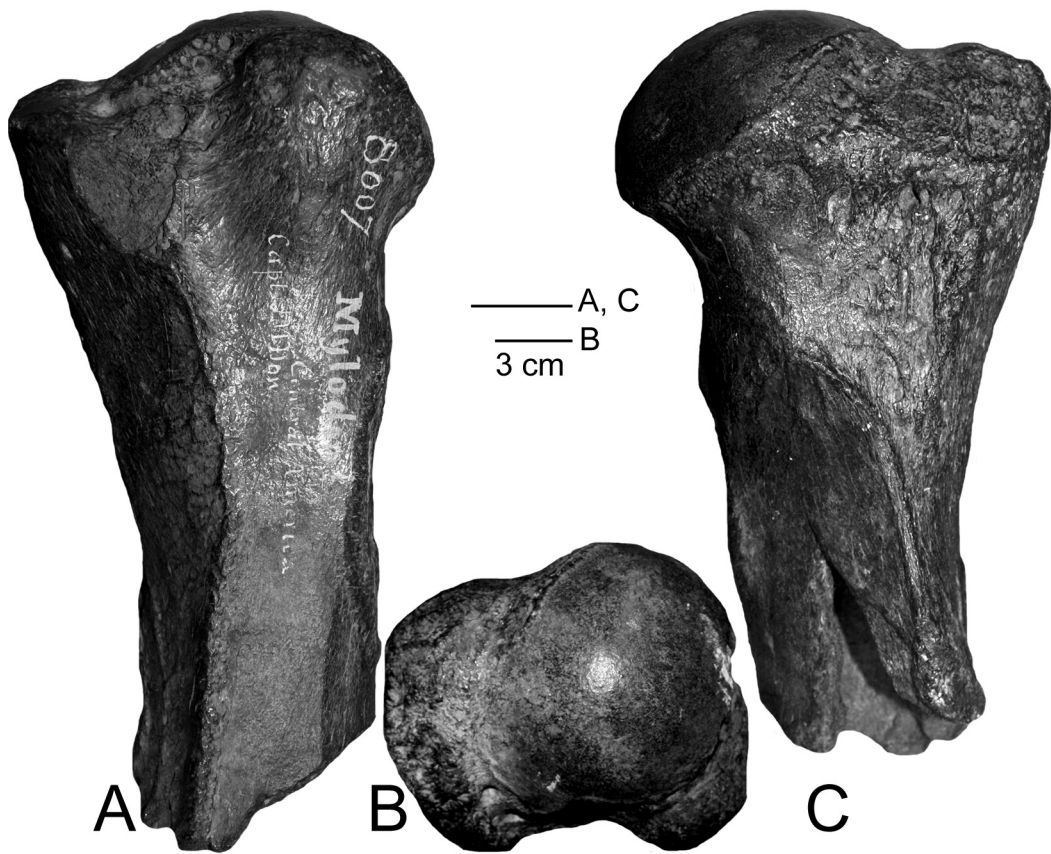


Fig. 1: USNM 8007, proximal end of a left humerus of a megalonychid ground sloth from Panama, in anterior (A), proximal (B) and posterior (C) views. Originally described by Leidy (1870), this humerus has a maximum proximal width of 150 mm.

Gazin (1957, p. 347) suggested that this scute might belong to a “hoplophorid?, possibly *Lomaphorus* sp.”. Comparison to complete material of hoplophorines (e.g., Zurita et al., 2009) supports possible assignment to the subfamily, but the scute is not sufficient morphology upon which to base a more precise identification.

Glyptotherium floridanum

A glyptodont scute (USNM 540667: Fig. 5A) has a large central figure surrounded by seven smaller figures. It has a maximum diameter of 46.5 mm and a maximum thickness of 13.8 mm. This scute closely resembles scutes assigned to

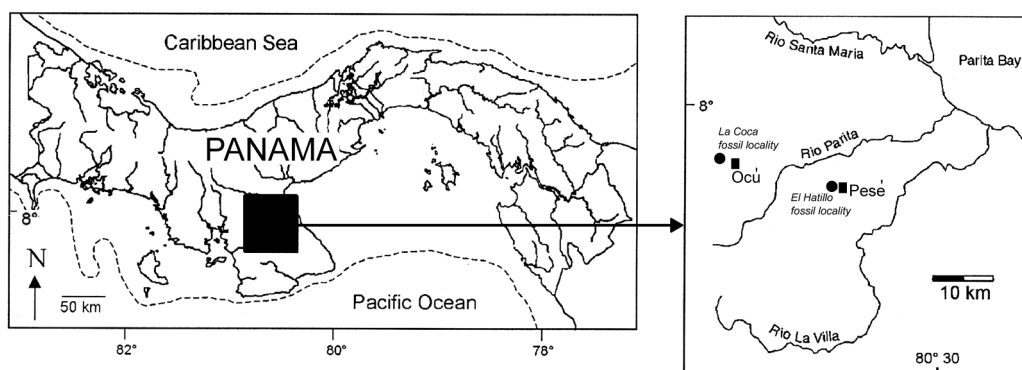


Fig. 2: Map of Panama with inset showing location of Pleistocene mammal localities described by Gazin (1957) on the Azuero Peninsula (after Pearson, 2005).

Glyptotherium floridanum from North America (Gillette & Ray, 1981, figs. 88-91), Mexico (Lucas, 2008b, figs. 10C-F) and Honduras (Jackson & Fernandez, 2005; Lucas, 2008c, fig. 3E).

USNM 540668 (Fig. 6E-F) is the right dentary fragment of a glyptodont with very damaged teeth. The jaw closely resembles those of *Glyptotherium floridanum*, especially in having a flattened inferior margin of the horizontal ramus (cf. Gillette & Ray 1981, figs. 16-17). A single glyptodont vertebra (USNM 540669) and other uncatalogued scute fragments from El Hatillo also likely belong to *G. floridanum*.

Eremotherium laurillardi

The most common fossils from El Hatillo are of the giant ground sloth *Eremotherium laurillardi* (Gazin, 1957; Anonymous 1958). Two skeletons from the locality are mounted and on exhibition (Fig. 4), and much more material is in the USNM collection. Gazin (1957) illustrated some of these specimens catalogued as USNM 20872 (Fig. 3). Additional specimens are catalogued as USNM 20867 (maxillary fragments) and 546680 (left dentary).

The most recent revision of *Eremotherium* recognizes only one polymorphic Late Pleistocene species, *E. laurillardi*, and identified the specimens illustrated by Gazin (1957) as *E. laurillardi* (Cartelle & De Iuliis, 1995). Indeed, size and some key morphological features (e.g., relatively

ventral orbit and zygomatic arch, relatively shallow mandibular bulge and mandibular symphysis under m1) identify almost all of the El Hatillo sloth fossils as *E. laurillardi*.

Paramylodon harlani

USNM 540666 is a left dentary fragment with parts of three molariform teeth that immediately follow a nearly square (canine) alveolus (Fig. 5C-E). The first two molariform teeth are relatively short, but the last is long, consisting of multiple columns. The dentary is relatively short and deep (depth below the posteriormost molariform tooth is 85 mm) and lacks a mandibular bulge. Approximate dental measurements are: anteriormost molariform tooth l = 26.0, w = 18.0; second molariform tooth l = 18, w = 26; posteriormost molariform tooth l = 45, w = 22.

Gazin (1957) identified this fossil as cf. *Glossotherium tropicum*. However, in light of the work of McAfee (2009), I assign it to *Paramylodon harlani*. This is because USNM 540666 has a relatively straight, backward slope to its coronoid process and a relatively narrow symphyseal edge, suggesting a narrow premental spout, features that distinguish *Paramylodon* from *Glossotherium* in McAfee's analysis. Metrics and morphology readily support assignment of the El Hatillo dentary fragment to *P. harlani* (cf. Stock, 1925; McDonald, 1995).

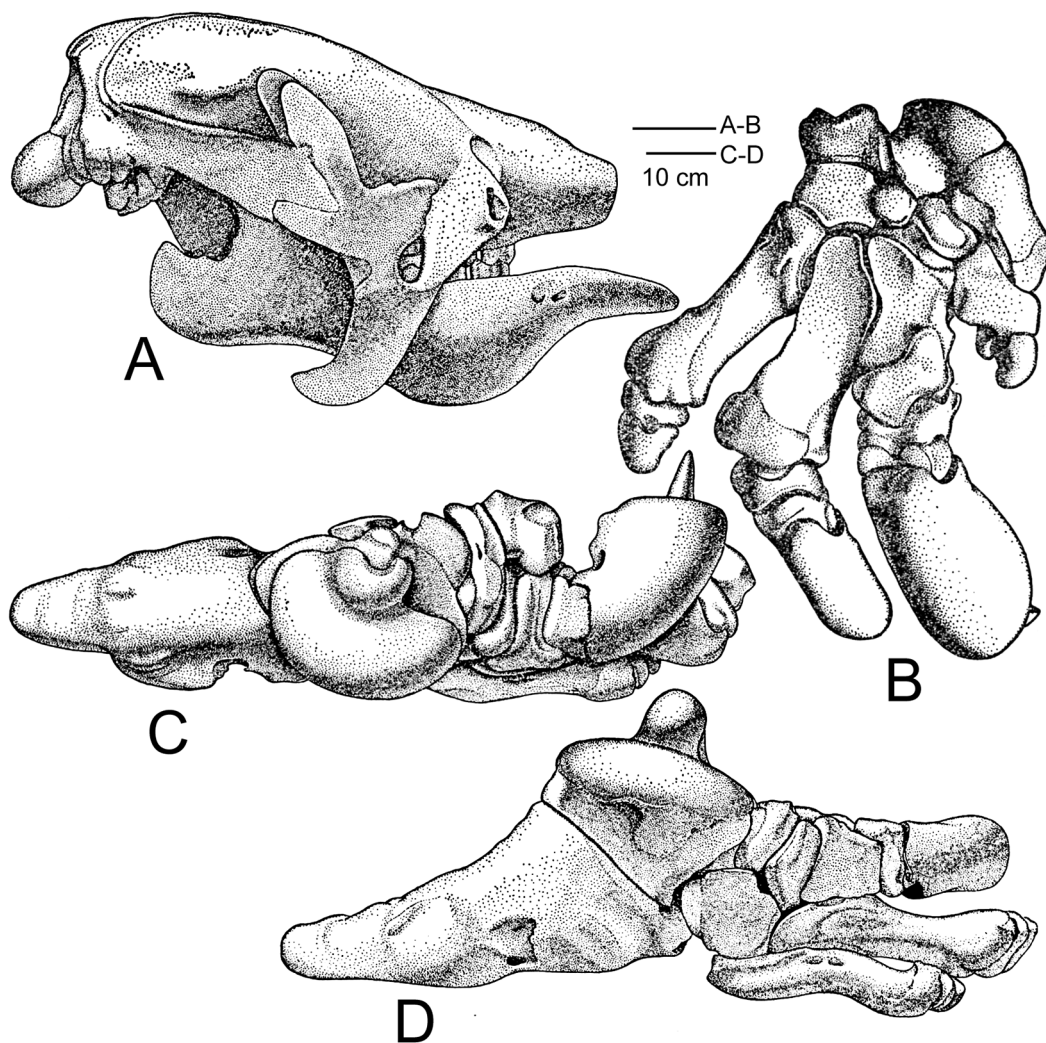


Fig. 3: *Eremotherium laurillardii*, USNM 20872, selected elements (from Gazin, 1957). A, Skull and lower jaw in right lateral view. B, Composite right manus. C-D, Composite right pes in medial (C) and lateral (D) views.

Equus conversidens

The second most abundant fossils at El Hatillo are of horses (Fig. 7). Material includes USNM 540676, an essentially unworn left M3 (Fig. 7C-E), 540677, a right M? (Fig. 7A), 540678, an incomplete upper molar (Fig. 7B) and 540679, a relatively short, broad proximal phalanx. These molars are morphologically complicated---worn crowns have relatively complex fossettes and a small pli cabillin. Measurements

are: USNM 540676, $l = 27.4$, $w = 21.5$; 540677, $l = 27.9$, $w = 23.2$; 540678, $l = 26.5$; 540679, phalanx $l = 75.4$, proximal $w = 51.5$, distal $w = 43.5$. The proximal phalanx is short and stout, very close to the range of metrics reported for *E. conversidens* from New Mexico by Harris and Porter (1980, table 1). Metrically and morphologically the El Hatillo horse teeth fall within the range of variation of *E. conversidens*, to which they are assigned (e.g., Hibbard, 1955, fig. 3; Reynoso-Rosales & Montellano-Ballesteros, 1994).

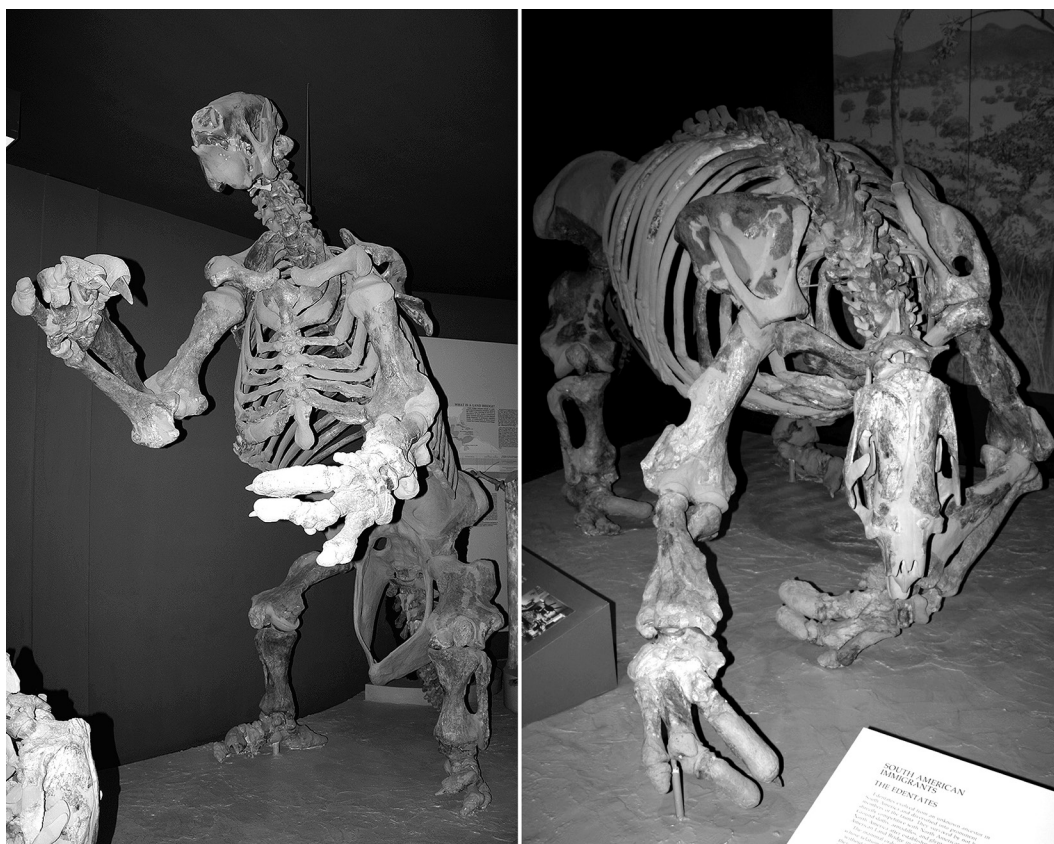


Fig. 4: Skeletons of *Eremotherium laurillardi* from El Hatillo on display at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Platygonus sp.

An isolated canine, USNM 540673 (Fig. 6A-B), belongs to a peccary. It has a crown l of 10.4 mm and a crown w of 7.2 mm. Assignment to *Platygonus*, the common Late Pleistocene peccary, is reasonable.

Odocoileus sp.

UCNM 540670 (Fig. 8A-B) is a small, dichotomously forked antler with a steeply rising beam. Total length = 167 mm, and diameter of the base = 29 mm. This antler is a good match for antlers of *Odocoileus* (cf. Frick, 1937), but not sufficient material upon which to base a species-level identification.

Mixotoxodon *larensis*

USNM 540671 (Fig. 6C-D) is an incomplete cheek tooth that has a crown length of at least 50 mm and is very hypsodont (crown height exceeds 136 mm). This tooth clearly is part of an upper molar of a toxodont. It corresponds well to material from northern South America and Central America referred to *Mixotoxodon larensis* (Van Frank, 1957; Laurito, 1993; Lucas et al., 1997; Lucas, 2008c), so I assign it to that taxon.

Cuvieronius *hyodon*

The only gomphothere fossil from El Hatillo in the USNM collection is USNM 540665, a very worn M3 (Fig. 8C-D). It has

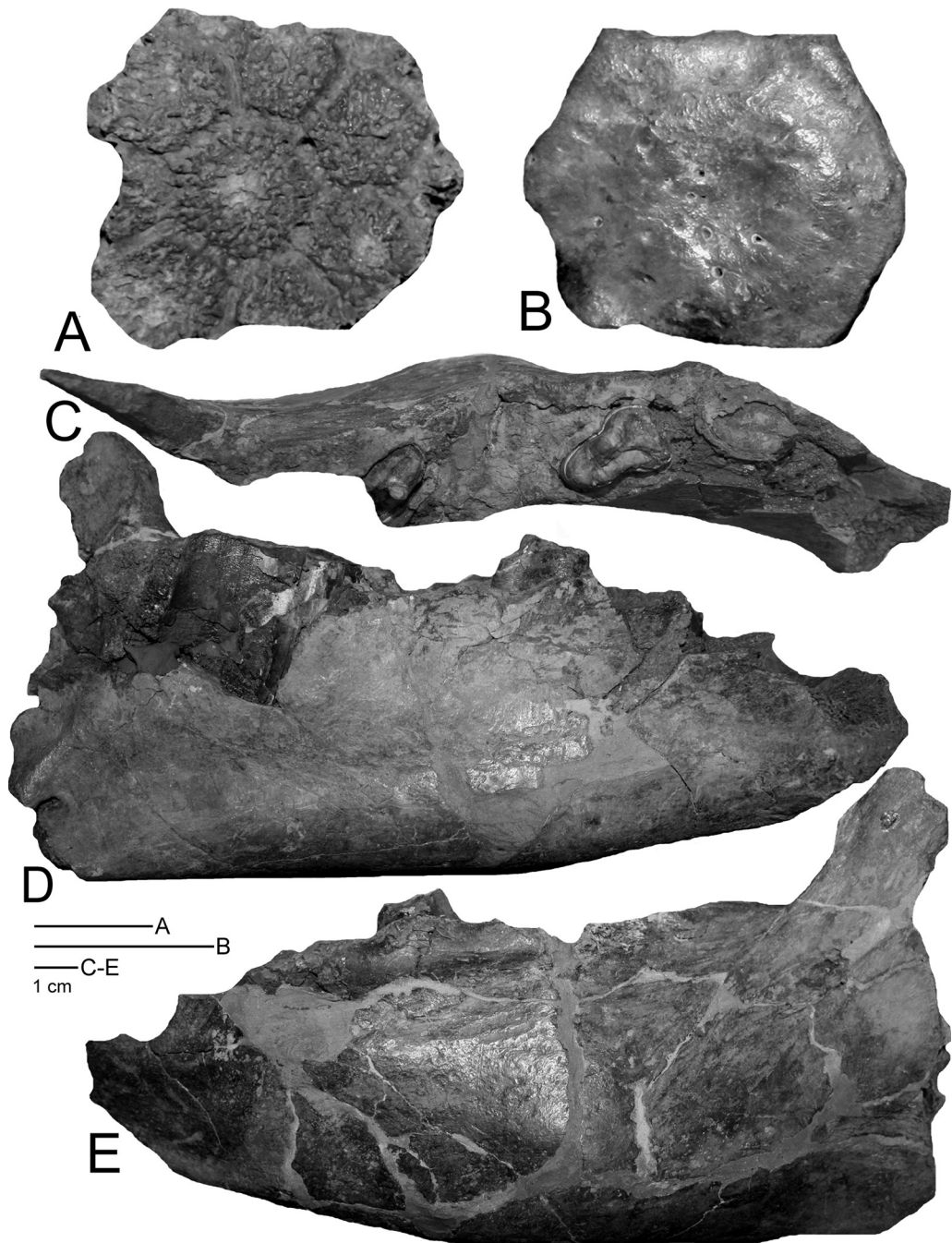


Fig. 5: A, *Glyptotherium floridanum*, USNM 540667, scute. B, Hoplophorinae?, USNM 540672, scute. C-E, *Paramylodon harlani*, USNM 540666, left dentary fragment in occlusal (C), lingual (D) and labial (E) views.

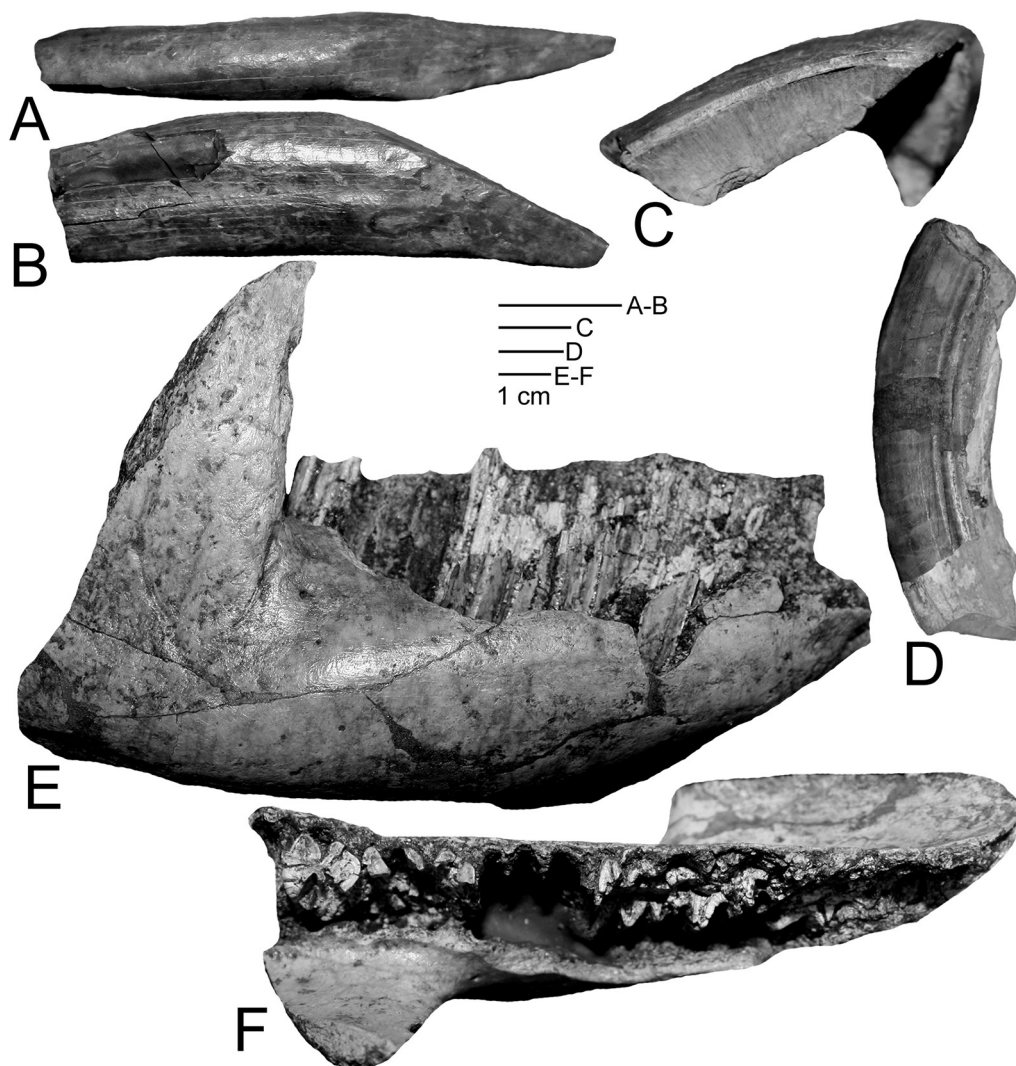


Fig. 6: A-B, *Platygonus* sp., USNM 54067, canine in occlusal (A) and lateral? (B) views. C-D, *Mixotoxodon larensis*, incomplete upper molar in occlusal (C) and posterior (D) views. E-F, *Glyptotherium floridanum*, USNM 540668, right dentary fragment in labial (E) and occlusal (F) views.

five lophs, a maximum length of 185 mm and a maximum width of 92 m. The tooth closely resembles molars of *Cuvieronius hyodon* from Florida, Costa Rica and El Salvador (Lucas et al., 1997; Cisneros, 2005; Lucas, 2008a). However, isolated molars of Neotropical gomphotheres are not generically diagnostic of *Cuvieronius* or *Notiomastodon* (e.g., Lucas & Alvarado, 2010; Lucas, 2013). Nevertheless, the only Pleistocene gomphothere from Central America is *C. hyodon*

(Lucas & Alvarado, 2010), so referral of the El Hatillo molar to this species seems reasonable.

DISCUSSION

The El Hatillo fossil mammals are a characteristic assemblage of Late Pleistocene mammal fossils from Central America. Thus, like most other Central American Late Pleistocene

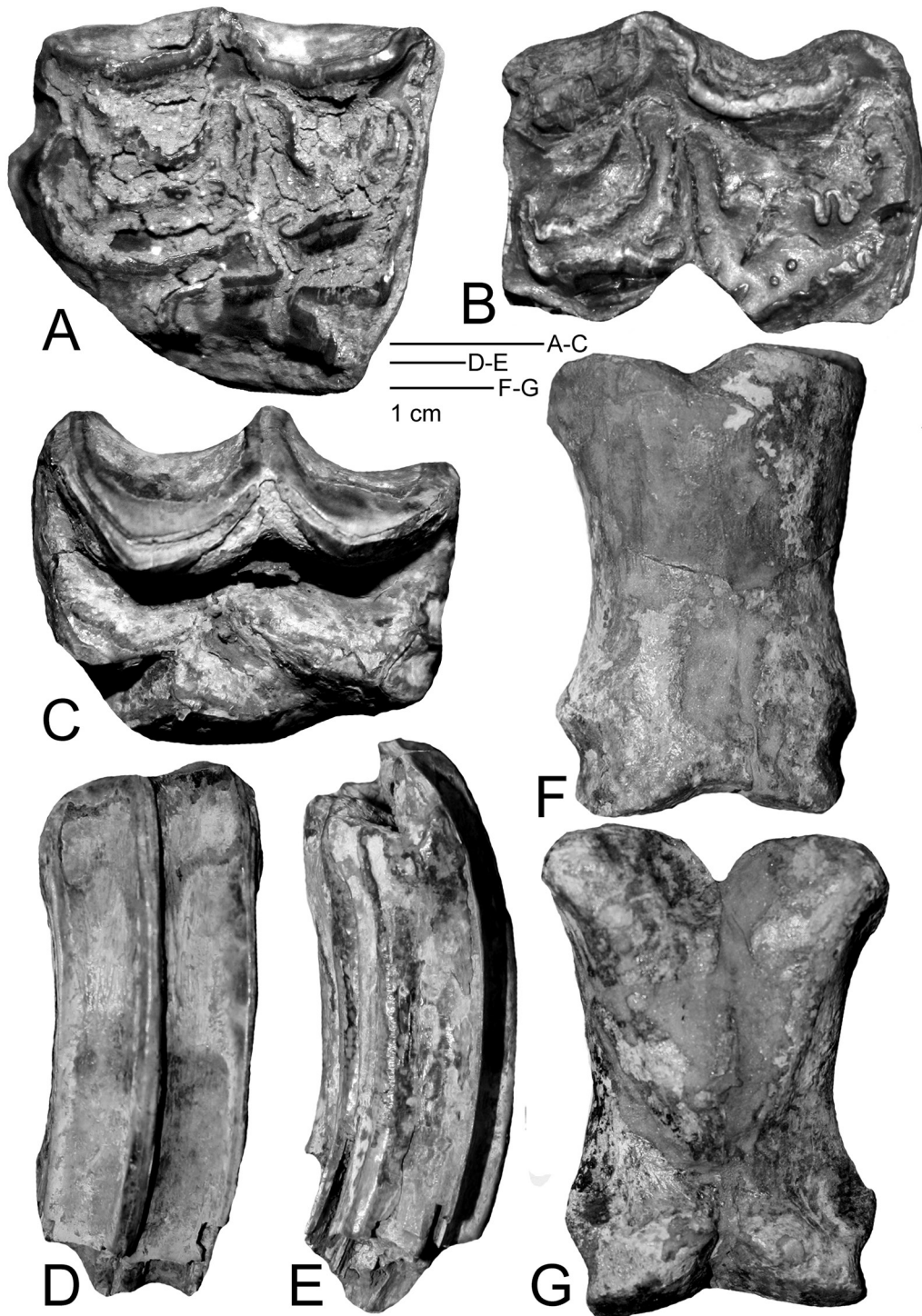


Fig. 7: *Equus conversidens*. A, USNM 540677, occlusal view of right M2? B, USNM 540678, occlusal view of incomplete upper molar. C-E, USNM 540676, unworn left M3 in occlusal (C), labial (D) and posterior (E) views. F-G, USNM 540679, phalanx in dorsal (F) and ventral (G) views.

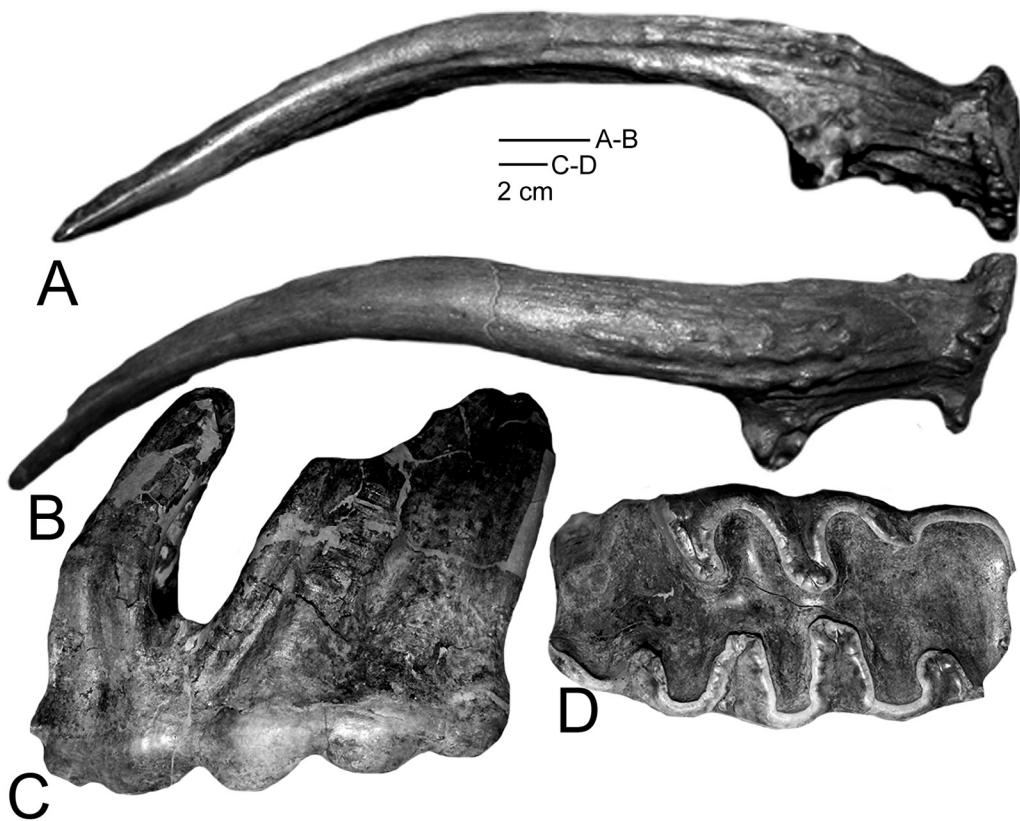


Fig. 8: A-B, *Odocoileus* sp., USNM 540670, antler. C-D, *Cuvieronius hyodon*, M3 in lateral (C) and occlusal (D) views.

mammal assemblages, a microfauna, especially of rodents, was not collected at El Hatillo. Also, like other Central American late Pleistocene mammal assemblages, the El Hatillo mammals are almost all large edentates and ungulates, and are a nearly equal mixture of South American (glyptodonts, sloths, toxodonts) and North American (horses, peccaries, deer, proboscideans) immigrants. *Eremotherium laurillardii* dominates the El Hatillo assemblage, and also dominates many other Late Pleistocene assemblages in Honduras, El Salvador, Guatemala, Nicaragua, Costa Rica and Panama (e.g., Webb & Perrigo, 1984; Lucas et al., 1997, 2007, 2008; Cisneros, 2005; Jackson & Fernandez, 2005; Lucas, 2008c). Indeed, *Eremotherium* is one of the most characteristic Late Pleistocene mammal fossils in Central America.

I term such Central American assemblages EME assemblages, for the association of *Eremotherium*, *Mixotoxodon* and *Equus*. Furthermore, most of these assemblages appear to be of Rancholabrean age in the North American land-mammal biochronology and Lujanian in the South American biochronology. Thus, in some of these assemblages, *Bison* is present, providing prima facie evidence of a Rancholabrean age. The minimum age of EME assemblages in Central America presumably is end-Pleistocene, ~ 10 kya, as this is the minimum age of extinction of the megafauna in Central America (cf. Barnosky & Lindsey, 2010). The oldest age of the EME assemblages is less certain. In North America, *Eremotherium* has its oldest record in the Blancan of Florida, so it must have been among the early

immigrants from south to north after the initiation of the great American biotic interchange. And, a few Central American fossil mammal assemblages with *Eremotherium* and *Mixotoxodon* are older than Rancholabrean (e.g., Cisneros, 2005).

Thus, the association of *Eremotherium* and *Mixotoxodon* is common in Central America, and mostly of Rancholabrean age. I conclude that most of the EME assemblages in Central America are of Late Pleistocene age, between 250 and 10 kya; most are likely younger than 100 kya. They thus represent a mixed fauna of grazers and browsers that was common across Central America during one or more of the late Pleistocene interstadials.

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