

A SMALL PLEISTOCENE MAMMALIAN MEGAFUNA FROM SOUTHERN HONDURAS

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The final land linkage between the North and South American continents during the Pliocene opened the biogeographic doors for the Great American Biotic Interchange. During this period, reciprocal migrations of dozens of North and South American families of plants, vertebrates, and invertebrates exerted profound influences on previously isolated biotas. Although the exchange has been best documented among mammals, faunas from additional fossil deposits throughout Middle America can help to refine knowledge of the dynamics of the interchange. This paper reports a small Pleistocene mammalian megafauna from a site in southern Honduras near its border with Nicaragua. Four families and genera are represented. Fossils of the glyptodont *Glyptotherium floridanum* are among the first reported from outside of the United States. Also represented are the giant megatheriid ground sloth *Eremotherium laurillardii*; the gomphotheriid *Cuvieronius tropicus*; and a relatively small horse of the genus *Equus*. Based on these four species, the fauna most likely represents the early Rancholabrean faunal period.

Key Words: Honduras; Pleistocene; Great American Biotic Interchange; Mammalia; megafauna; *Glyptotherium*

INTRODUCTION

With its completion as a land bridge in the late Pliocene, Central America began its tenure as one of the earth's greatest biogeographic crossroads. The ensuing reciprocal exchange between previously relatively isolated Nearctic and Neotropical biotas—termed the Great American Biotic Interchange—has attracted substantial interest among paleontologists and biogeographers (reviewed by Rich & Rich 1983; Stehli & Webb 1985; Webb 1991). Although sufficient paleontological data exist to have formed the basis of a general understanding of this event, further investigations of late Cenozoic fossils in Central America should permit refinement of this theory.

Fossil sites in general are poorly known from nuclear Central America, the region stretching from the Isthmus of Tehuantepec in southern Mexico to the uplands of northern Nicaragua (Savage 1982). Webb and Perrigo (1984) reviewed our limited paleontological knowledge of Honduras and El Salvador and treated six key local faunas, only two of which included more than a dozen species of vertebrates. More recently, Lucas

(2005) identified only eight Pleistocene mammalian sites from all of Nicaragua, with none represented by more than seven species. Nonetheless, the region is rich in middle to late Pleistocene deposits characterized by two particularly abundant megafaunal elements: *Cuvieronius* (spiral-tusked gomphothere) and *Eremotherium* (giant megatheriid ground sloth). Webb and Perrigo (1984) and Stirton and Gealey (1949) alluded to the existence of several dozen such sites in Honduras and El Salvador, with additional ones in Guatemala and Costa Rica (Lucas et al. 1997). The present contribution describes one such site that we discovered in the mountains of south-central Honduras near the Nicaraguan border. The site is characterized by a small assemblage of megafaunal mammals, including the first confirmation of the glyptodont, *Glyptotherium floridanum*, from Honduras.

LOCALITY

The fossil site reported here lies in the Southern Cordillera subregion of the Serranía physiographic region (Wilson & Meyer 1985) in south-central Honduras, 2.5 km north of the Nicaraguan border (Fig. 1). The site (13°48'15"N, 86°39'24"W) is located 1.75 km southwest of the pueblo of Buena Vista, which lies southeast of Alauca and roughly 11 km southwest of El Paraiso, Departamento El Paraiso, Honduras. The stream that

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Figure 1. Outline map of Honduras with location of La Majadita fossil site indicated.

exposed the fossil bed flows around the south side of a high peak (898 m) known locally as La Majadita, which we hereafter apply to the site itself. The peak, stream, and pueblo are all depicted on the 1965 1:50,000 Dipilto, Nicaragua, topographic map.

MATERIALS AND METHODS

On 9 January 1980, local campesinos led us to an eroding stream bank where they had recovered several ancient bones reputed to be from “un hombre gigante” (later determined to be those of giant ground sloth). Following two hours of surface reconnaissance and shallow digging that revealed an *in situ* vertebrate fossil bed, we departed but later returned on 23 January for five days of careful excavation.

Preparatory work required removal of dense vegetation and ca. 1.5 m of overburden from one bank of the stream for a length of about 4 m and to a horizontal depth of 1 m. Fossils were mapped and carefully removed, some by jacketing. Presence of flowing water

facilitated washing most fossils on site. Because of logistical difficulty as well as the low success of screen-washing efforts at other Central American sites (Webb & Perrigo, 1984), we did not attempt to screen sediments for remains of small vertebrates; however, we observed none even though we spent many hours carefully picking through the fossiliferous layer. Regrettably, the unstable political and military situation that prevailed along the Honduran/Nicaraguan border at this time, coupled with the onset of acute histoplasmosis in both investigators, necessitated that we conduct the entire excavation in relative haste and depart prematurely.

EF returned to Honduras in the summer to curate the fossils obtained at La Majadita and other sites and to help construct a new paleontology exhibit at the Instituto Hondureño de Antropología y Historia, Tegucigalpa, which houses the specimens described here. DRJ returned in December to photograph and measure the fossils, many of which were incorporated into the new exhibit.

RESULTS

PHYSIOGRAPHY AND STRATIGRAPHY

The site lay in a region of low but relatively steep mountains covered generally by pine forest and dissected by small streambeds. The fossiliferous stratum, only 2-3 m wide and overlain by ca. 1.5 m of soil, was exposed by erosive action of a small (1.25 m wide), semi-permanent stream (tributary of Quebrada Arenosa) flowing east-southeast. Fossils were situated near the interface of a fine gravelly layer resting on a sticky, wet mud, just above the water line and extending upward for no more than 30 cm. Most fossils rested horizontally, with some overlying others, but otherwise appeared to be randomly oriented. The partial jaws of a gomphothere and a ground sloth were situated in inverted, slightly canted positions. Most of the fossils were fragmented and fell apart easily when handled; even the relatively robust glyptodont scutes showed some chipping, indicating tumbling prior to burial. However, the contiguous positions of the lower leg bones of a ground sloth and of three adjoining pairs of glyptodont scutes suggested that post-mortem transport may not have been extensive. Some post-depositional movement was indicated by a 3-cm offset between two halves of a large rib. Fossil color was typically dark maroon, with the exception of the cream-colored enamel of gomphothere teeth, and glyptodont scutes that ranged from nearly black to light cream.

The fossils rested principally at the bottom of a 20-cm thick stratum of fine, reddish-brown gravel, presumably of volcanic origin, that extended downward as much as an additional 35 cm into pockets in the underlying clay. A few fossils appeared to have migrated into adjacent strata. The gravel layer was overlain progressively by 27 cm of dull gray fine gravel and coarse sand with some clay, 35 cm of light brown to yellowish coarse sand and fine gravel, and 10-50 cm of gray-brown humus and fine sediment. Some cross-bedding was present. Except for the underlying clay and surficial humus, all strata appeared to be of pyroclastic origin (Williams & McBirney 1969) and laid down as a fluvial channel (or possibly alluvial fan) deposit.

FAUNAL COMPOSITION

The La Majadita fossils represent four genera of Pleistocene mammalian megafauna. These include a glyptodont (*Glyptotherium*), giant ground sloth (*Eremotherium*), gomphotheriid (*Cuvieronius*), and equid (*Equus*).

SYSTEMATIC PALEONTOLOGY

XENARTHRA

GLYPTODONTIDAE

GLYPTOTHERIUM FLORIDANUM

Material.—Fifty-nine osteoderms (scutes), H7-001-051 (Fig. 2) plus five uncatalogued, mostly intact to large fragments. Included are at least three sets of two or three contiguous scutes (H7-044; H7-028 and 034; H7-048), with one pair (H7-048) apparently fused. Most are from the interior of the carapace, although some thick ones derive from near the margin; at least three (H7-003, 004, uncatalogued) are from the biserate ring of the caudal armor.

Discussion.—All temperate North American glyptodonts of late Pleistocene age are referred to the species *Glyptotherium floridanum*, but there are two additional if somewhat questionable late Pleistocene species from central Mexico, *Glyptotherium mexicanum* and *Glyptotherium cylindricum* (Gillette & Ray 1981). Unfortunately, potentially diagnostic cranial elements are lacking from La Majadita. Nonetheless, Gillette (in litt. 1980), who was provided four carapacial and one caudal scute for identification, referred them to *G. floridanum* based on sculpturing and pattern (e.g., peripheral figures nearly as large as central figures on interior scutes, central figures of many weakly concave). Further, he noted that the five scutes (uncatalogued) appeared to be from a female (less robust than scutes of presumed males; one uncatalogued posterior border scute with pointed, conical boss) and were more likely to be from the early rather than late Rancholabrean, given a hypothesized trend of increasing sexual dimorphism during that period. At least some scutes in the series (including border scute H7-043, 57 mm transverse diameter) probably represent one or more males based on their greater size and thickness (to 30.5 mm for non-border scutes, 46 mm for border scutes).

Gillette (in litt. 1980) observed that the present material represents the first confirmed record of *G. floridanum* south of Vera Cruz, Mexico, from where it had been provisionally recorded; most records are from the U.S. southeastern Coastal Plain. Thus, when collected, the specimens represented the first record for Honduras and only the second outside of the United States. During a subsequent survey of a second Honduran site in June 1980, the junior author excavated a single *Glyptotherium* carapacial border scute (H8-174), in association with *Cuvieronius* and *Eremotherium*, from near Mt. Picacho, Departamento de Francisco

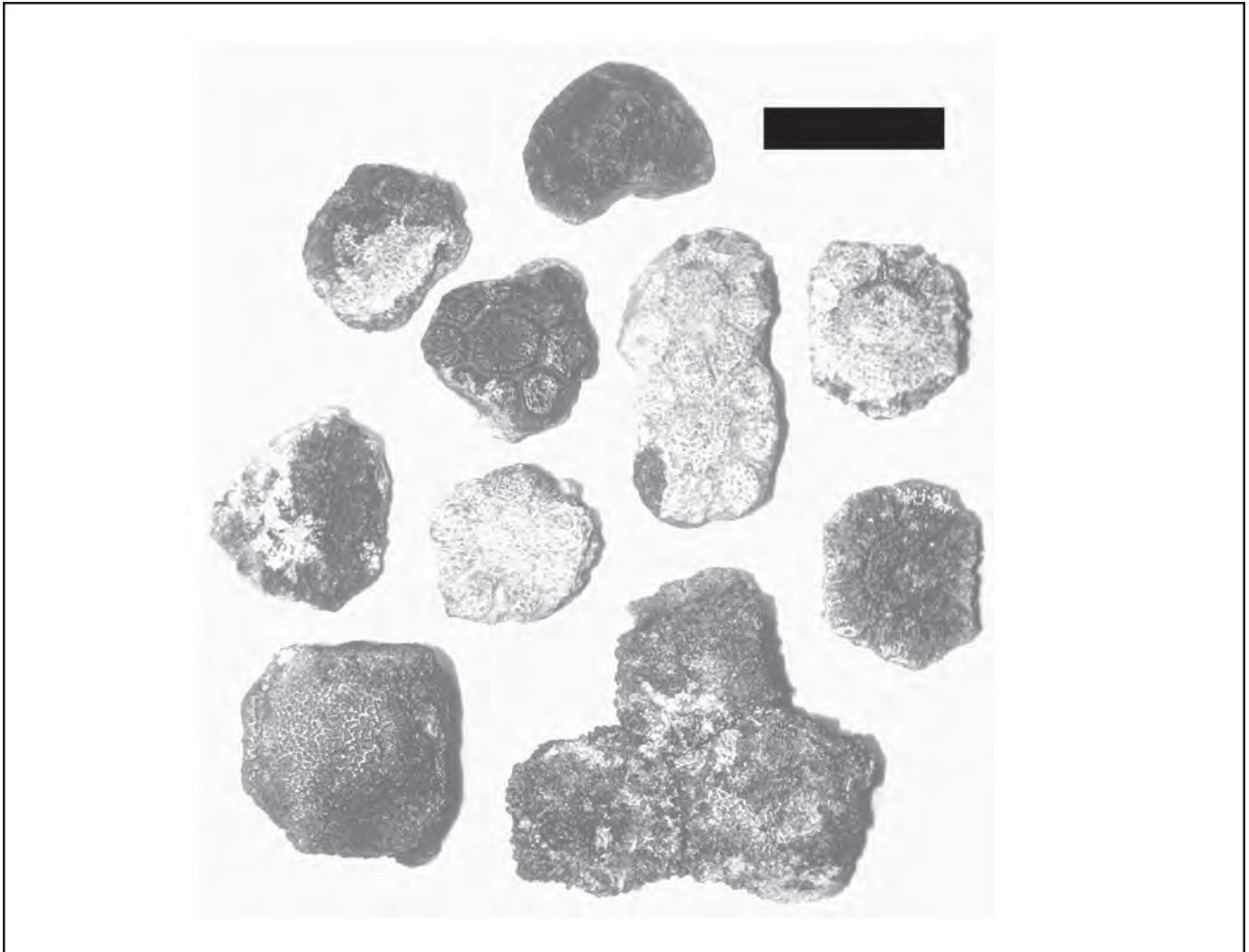


Figure 2. Osteoderms of *Glyptotherium floridanum* from the Pleistocene La Majadita site, Honduras. Scale bar depicts 5 cm.

Morazán. Webb and Perrigo (1984) recorded specimens of *Glyptotherium* sp. from the late Pleistocene Yeroconte local fauna in northwestern Honduras and the Hormiguero local fauna in eastern El Salvador.

MEGATHERIIDAE

EREMOTHERIUM LAURILLARDI

Material.—H7-052, right mandibular ramus with four molariform teeth, lacking articulating surface (Fig. 3); H7-053, isolated molariform; H7-121, proximal end of humerus; H7-122, left ulna of juvenile; H7-123-125, femoral fragments; H7-126, fragmented molariform; H7-127, fragmented fibula of juvenile; H7-128, fragmented second phalanx.

Lower jaw fragment H7-052 is 231 mm long, with

a tooth row measuring 175.2 mm maximum. Tooth measurements (length x width, in mm), from anterior to posterior, are 35.2 x 37.2, 38.3 x 38.3, 40.2 x 34.6, and 36.5 x 29.5 mm.

Discussion.—Reevaluation of late Pleistocene megatheriid ground sloth material from throughout North, Central, and South America has shown only a single, large-sized species of *Eremotherium*, *E. laurillardi*, that varied widely in morphology and size (Cartelle & De Iuliis, 1995). This giant herbivore was previously documented in northwestern Honduras from a site in or near Departamento de Copán (McGrew 1942; Webb & Perrigo 1984; Cartelle & De Iuliis 1995; presumably the site referred to as the Yeroconte Quarry by Webb and Perrigo 1984, who mapped it in adjacent Departamento

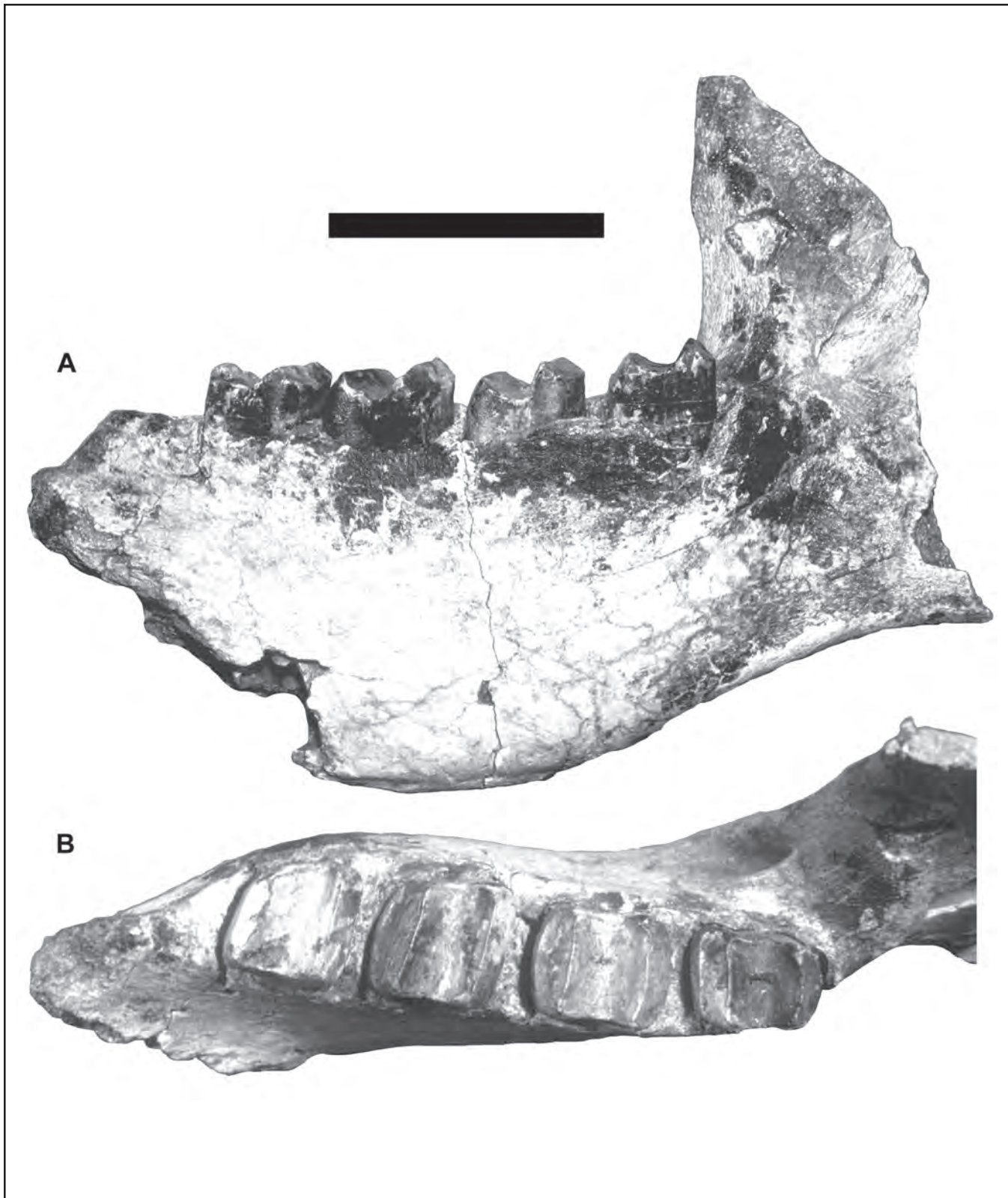


Figure 3. Medial (A) and occlusal (B) aspects of right mandible (H7-052) of *Eremotherium laurillardi* from the Pleistocene La Majadita site, Honduras. Scale bar depicts 10 cm for A.

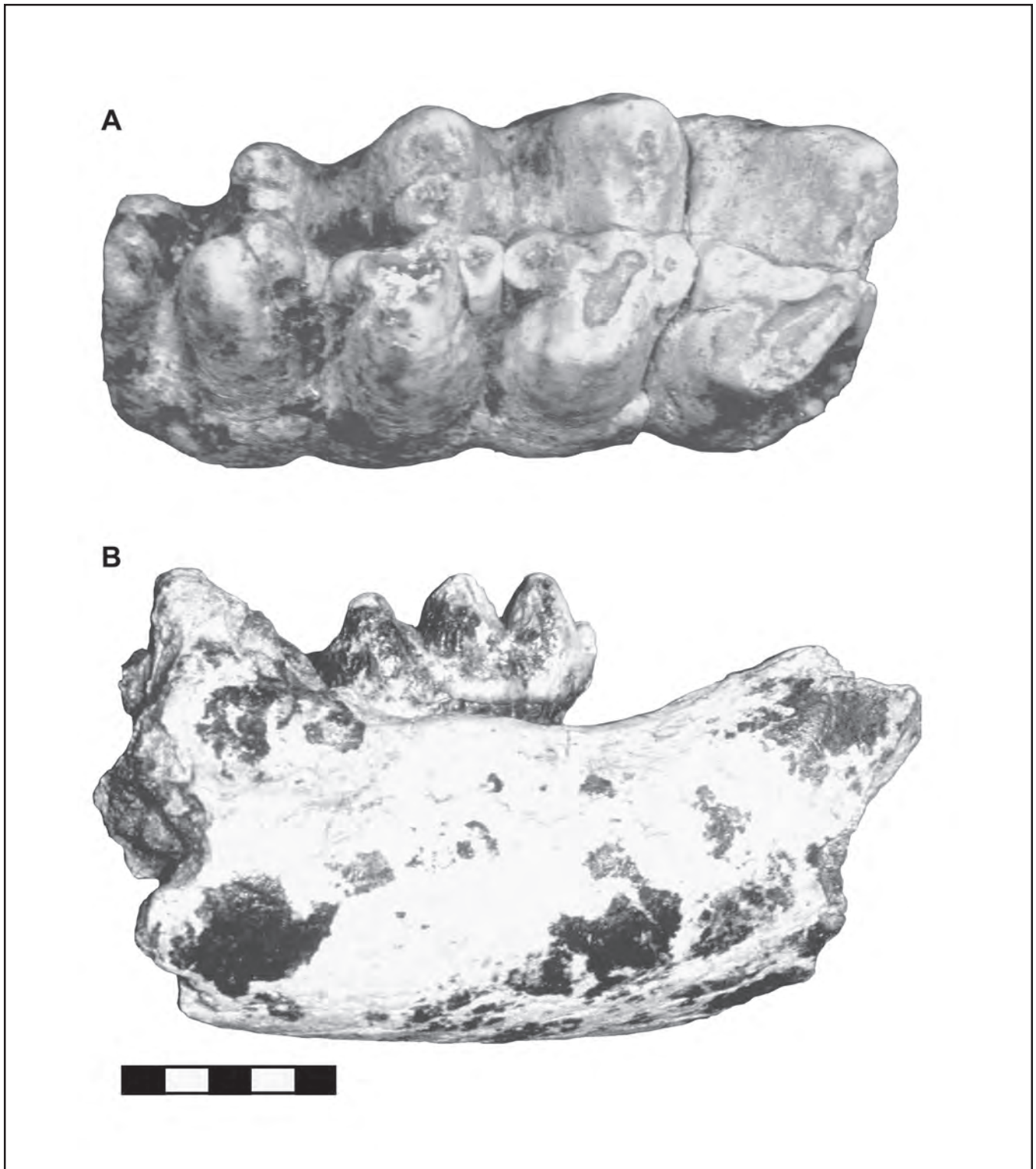


Figure 4. Teeth and jaws of *Cuvieronius tropicus* from the Pleistocene La Majadita site, Honduras. A. Occlusal aspect of adult m3 (H7-058). B. Lateral aspect of juvenile left mandible (H7-056) with molar (H7-060). Scale bar depicts 1 cm intervals for B only; dimensions of H7-058 provided in text.

de Santa Barbara), in central Honduras from Orillas del Humuya (Webb & Perrigo 1984), and in El Salvador from San Miguel (Cartelle & De Iuliis 1995) and the Hormiguero Quarry (Webb & Perrigo 1984). Shortly after our excavation at La Majadita, the partial skeleton of a second *Eremotherium* was unearthed near Trinidad de Copán, Departamento de Copán. Remains of the species probably occur at dozens of other late Pleistocene sites throughout Central America (Rodríguez 1942; Larde y Larin 1950; Webb & Perrigo 1984; Lucas et al. 1997).

PROBOSCIDEA
GOMPHOTHERIIDAE
CUVIERONIUS TROPICUS

Material.—H7-058, lower third molar (Fig. 4A); H7-056, fragmented juvenile left mandible with molar H7-060 (Fig. 4B); H7-057, fragmented left mandible; H7-059 (left), 061, 062, and 129, isolated molars; H7-065, 069, fragmented tips of tusks; H7-070, fragmented left maxillary; H7-075, second phalanx; H7-081, 082, fragmented pelvis; plus other fragments.

Maximum crown length of presumptive young adult molar H7-059 is 173.6 mm; lophs are high and distinct with some wear on peaks, and measure 86.0, 90.8, 82.8, and 66.5 mm in maximum width (fifth loph very small) from anterior to posterior. Measurements of adult molar H7-058, set in jaw, are 189 mm maximum length, with loph widths of 84.3, 97.0, 85.8, 78.0, and 57.5 mm; wear is slight and lophs are high. Maximum measurements of molars H7-61 and H7-129 are, respectively, 166.0 x 88.8 mm and 119.5 x 85.6 mm. Juvenile molar (dp4) H7-060, in jaw, measures 65.0 mm long x 40.5 mm wide, with three sharply raised lophs 33.0, 41.2, and 38.0 mm in width. Tusk tip H7-065 is 214 mm and laterally compressed.

Discussion.—The genera *Cuvieronius* and *Haplomastodon*, both known from Central American Pleistocene deposits, are distinguished principally by morphology of the tusks (Lucas et al. 1997), which are inadequately represented in the La Majadita fauna to make definitive assignment. However, *Haplomastodon* is quite rare in Central America, whereas *Cuvieronius* occurs commonly from Costa Rica to Mexico (Lucas et al. 1997). Based on this, and the good conformation of La Majadita molars with those of *Cuvieronius* as depicted by Lucas et al. (1997), we assign the gomphothere remains to *C. tropicus*, believed to be the sole member of the genus represented in the Central American Pleistocene (in litt., G. Morgan).

PERISSODACTYLA
EQUIDAE
EQUUS cf. *CONVERSIDENS*

Material.—H7-066, adult right upper cheek tooth (Fig. 5); H7-067, distal end of radioulna; H7-094, vertebral centrum with transverse process; H7-099 and 100, proximal and distal ends of femur.

Measurements of cheek tooth H7-066 are: maximum height with broken root, 54 mm; crown height, 34.6 - 43.6 mm; maximum anteroposterior length of occlusal surface, 24.3 mm; and maximum transverse breadth of occlusal surface, 25.2 mm. The crown is worn but with enamel ridges still raised, and the tooth is well fossilized.

Discussion.—The La Majadita horse presumably falls within one of the three major species groups of late Pleistocene North American horses recognized by Winans (1989): the *Equus alaskae*-group, *E. laurentius*-group (recently redesignated as the *E. niobrarensis*-group by Morgan & Lucas 2005), and *E. francisci*-group (small horses, large horses, and stilt-legged horses, respectively). We consider available material to be insufficient to confirm specific diagnosis. However, measurements of the only available tooth suggest a small



Figure 5. Occlusal surface of adult right upper cheek tooth (H7-066) of *Equus* cf. *E. conversidens* from the Pleistocene La Majadita site, Honduras. Tooth dimensions provided in text.

horse within the *E. alaska*-group. Many workers now apply the name *E. conversidens* to these small horses, which were widespread in Rancholabrean faunas throughout North America (Morgan & Lucas 2005).

DISCUSSION

Like most mammalian fossil sites from Central America (Webb & Perrigo 1984; Lucas et al. 1997), La Majadita yielded mostly isolated elements of large mammals. Nonetheless, based on similarities of the fauna to known late Pleistocene faunas from the region—especially the Hormiguero local fauna, El Salvador, and the Yeroconte local fauna, northwestern Honduras (both reevaluated by Webb & Perrigo 1984)—we assign the La Majadita fauna to the late Pleistocene (Rancholabrean). Strongest support for this assignment comes from the presence of *Glyptotherium floridanum*, which, based on scute thickness, may even suggest a possible age of early Rancholabrean.

All of the La Majadita taxa represent families known to have participated in the Great American Biotic Interchange (Stehli & Webb 1985; Webb 1991). Several families of edentates, including the Glyptodontidae and Megatheriidae, were among 10 genera and seven families of South American mammals that arrived in North America during the Pliocene following establishment of the isthmian land bridge between the two continents. The Equidae and Gomphotheriidae were but two of six ungulate families that successfully migrated in the opposite direction during the same time period or the ensuing early Pleistocene (Webb 1991), although *Cuvieronius* may have been a Neotropical offshoot of the gomphotheriid proboscideans (Webb 1974). All four of the La Majadita genera were primary immigrants, i.e., those with members that came directly from the other continent, in contrast to those whose founding species apparently evolved from primary immigrants after their arrival on the other continent (Marshall et al. 1982). Interestingly, all four of the families represented at La Majadita subsequently became casualties of the late Cenozoic waves of extinction that decimated the New World mammalian fauna; only the Equidae continued to survive in the Old World.

Webb and Perrigo (1984) suggested that most late Pleistocene Central American fossil assemblages were deposited under more paludal conditions, and that increased aridity of the Pacific slopes of Honduras and El Salvador is a post-Pleistocene event. The present high upland position of the La Majadita site is thus likely the result of post-depositional orogenic uplift of the fossil-

bearing bed. Gillette and Ray's (1981) notion that glyptodonts, including *G. floridanum*, lived along water courses in moist, lowland tropical to subtropical habitats supports the suggestion of a less arid environment during deposition of the La Majadita local fauna. Additional evidence is provided by *Cuvieronius*, believed to have been a mesic-adapted browser that was extirpated from the southwestern U.S. by increasing aridity during the Pleistocene, and by *Eremotherium laurillardi*, whose absence from Pleistocene sites in the arid southwest also presumably reflects adaptation to mesic, semitropical conditions (Morgan & Lucas 2005). Within the lush, lowland ecosystem that we picture to have occurred at La Majadita in the early Pleistocene, megafaunal mammals undoubtedly exerted a profound ecological influence on local habitats and their biotas (e.g., Janzen & Martin 1982).

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