Late Pleistocene mammals from Chivacabé, Huehuetenango, Guatemala

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ABSTRACT

Few Pleistocene paleontological faunas are published in detail for most of Central America. Probably the richest locality of vertebrates in Central America is at Tomayate, El Salvador, and dates to the early-middle Pleistocene. Literature about late Pleistocene vertebrate species from Guatemala is especially scarce. The purpose of the present paper is to introduce the late Pleistocene mammalian remains from Chivacabé, in the western highlands of Guatemala. The Chivacabé fauna radiocarbon dates to between 15,700 and 12,920 calendar years ago. The specimens recovered from excavations between 1977 and1992 are probably only a small portion of the entire fauna likely to exist under 4 to 5 m of redeposited tephra and valley alluvium. Recovered specimens include at least one individual of Glyptotherium sp., three individuals of Cuvieronius cf. C. hyodon, one individual of Equus sp., and two individuals of Odocoileus cf. O. virginianus. One specimen that originally was thought to represent a deer antler is in fact a hyoid bone of Cuvieronius. Previous reports of 'peccary' and Eremotherium from Chivacabé are not supported by archived fossils. No faunal specimens exhibit supposed human modification marks purported by previous investigators; all aberrations observed on the bones and teeth can be explained by other taphonomic processes. The Chivacabé fauna represents one of the very few late Pleistocene faunas from Guatemala described thus far. A preliminary list of late Pleistocene localities known in Guatemala suggests that detailed studies of these faunas are warranted.

Key words: Mammals, Pleistocene, Central America, Guatemala.

RESUMEN

Se ha publicado poca información paleontológica detallada de la fauna del Pleistoceno para gran parte de Centroamérica. Probablemente la localidad más rica de vertebrados en Centroamérica es Tomayate, en El Salvador, que data del Pleistoceno temprano a medio. La literatura de especies de vertebrados del Pleistoceno tardío de Guatemala es especialmente escasa. El propósito de este trabajo es presentar los restos de mamíferos del Pleistoceno tardío de Chivacabé, en las tierras altas occidentales de Guatemala. La edad de radiocarbono de la fauna de Chivacabé data de entre 15,700 y 12,920 años calendario. Los especímenes recobrados de excavaciones entre 1977 y 1992 son probablemente una pequeña porción de toda la fauna que existe bajo 4 a 5 m de tefra redepositada y aluvión. Los especímenes

recobrados incluyen un individuo de Glyptotherium sp., tres de Cuvieronius cf. C. hyodon, uno de Equus sp. y dos de Odocoileus cf. O. virginianus. Un individuo que originalmente se pensaba que representaba una cornamenta de venado es de hecho un hueso flotante de Cuvieronius. Reportes previos de "pecaríes" y de Eremotherium de Chivacabé no son sustentados por fósiles archivados. Ningún espécimen de fauna exhibe las supuestas marcas humanas de modificación dadas a entender por investigadores previos; todas las aberraciones observadas en los huesos y en los dientes pueden ser explicadas por otros procesos tafonómicos. La fauna de Chivacabé representa una de las muy pocas faunas del Pleistoceno tardío de Guatemala descritas hasta ahora. Una lista preliminar de localidades del Pleistoceno tardío de Guatemala sugiere que son necesarios estudios detallados de estas faunas.

Palabras clave: mamíferos, Pleistoceno, Centroamérica, Guatemala.

INTRODUCTION

Pleistocene vertebrates of Central America are extremely important as they often represent extinct species that only recently occupied the Panamanian land bridge connection between North America and South America. This land bridge was the avenue and filter for north and south dispersals during the Great American Biotic Interchange (Webb, 1991; Morgan, 2008; Woodburne, 2010). Elevations along this corridor range from sea level up to over 4,000 m in the Sierra de Cuchumantanes in Guatemala. As climate changed through glacial and interglacial regimes where ice sheets waxed and waned at high latitudes, plants and animals of the Central American land bridge were affected.

Many late Pleistocene vertebrate faunas in Central America have been discovered, yet most are biased toward the larger mammalian species, with small mammal, bird, amphibians, and reptiles rarely recovered. Biochronological studies provide a framework in which to document the sequential changes that occurred in both North America and South America (see Woodburne, 2004, 2010) and permit some organization for fossil localities that lack external isotopic age control. As expected, Central American faunas are a mixture of species from both north and south, and it is often difficult to assign these with confidence to a particular biochronological unit.

In North America the arrival of *Bison* south of 55°N signifies the end to the Irvingtonian and the beginning of the Rancholabrean North American Land Mammal Ages (Bell *et al.*, 2004); the Lujanian is the corresponding latest Pleistocene land mammal age in South America. Both the Rancholabrean and Lujanian are utilized to represent late Pleistocene faunas of Central America. Many diagnostic taxa of the North American late Pleistocene, such as *Bison*, *Mammuthus*, and *Euceratherium*, occur no further south than Central America; while some species of rodents, opossums, armadillos, tree sloths, and toxondonts, for example, do not occur significantly north of Central America (Marshall *et al.*, 1982; Webb, 1991; Ferrusquía-Villafranca *et al.*, 2010). To date little is understood about the Central American Pleistocene, yet it is clear that the region holds great importance to the overall understanding of changing faunal communities in the Western Hemisphere.

Overviews and discussions of important sites and specimens exist of the late Pleistocene faunas of Central America and southernmost Mexico: Costa Rica (Gómez, 1986; Lucas *et al.*, 1997; Laurito-Mora, 2003), El Salvador (Webb and Perrigo, 1984; Cisneros, 2005, 2008), Honduras (Jackson and Fernandez, 2005; Lucas, 2008b), Mexico (Arroyo-Cabrales *et al.*, 1997; Arroyo-Cabrales and Polaco, 2003; Ceballos *et al.*, 2010; Ferrusquía-Villafranca *et al.*, 2010), Nicaragua (Lucas *et al.*, 2008), and Panama (Gazin, 1956). Records of late Pleistocene species from Guatemala are scarce in the literature (Mook, 1959; Woodburne, 1968; Ericastilla-Godoy and García, 1994). Probably the richest locality of vertebrates in Central America is at Tomayate, El Salvador, and dates to the early-middle Pleistocene (Cisneros, 2005). With the exception of southernmost Mexico (see references in Ferrusquía-Villafranca *et al.*, 2010), few details about Pleistocene vertebrates are published for most of the rest of Central America. The purpose of the present paper is to document the mammalian remains from the late Pleistocene locality at Chivacabé (originally labeled the Mastodonte de Villatoro), located in the western highlands of Guatemala (Figure 1).

CHIVACABÉ LOCALITY

Chivacabé is located on the farm of Octavio Villatoro (Aldea de Chivacabé) approximately 6 km west of the town of Huehuetenango (N15° 18' 46.3", W 91° 32' 50.1") at 1896 m (6,220 ft) elevation (Figure 1). The site is situated on and in a deep alluvial terrace of a small stream in Cañon de Chivacabé that drains into the Río Selegua of the Huehuetenango Basin. Six kilometers north of the locality is the high Sierra de Cuchumantanes.

Chivacabé is a previously-recorded faunal locality that contains latest Pleistocene megafaunal remains, which was investigated in January 2009. A fluted lanceolate projectile point was recovered from the surface at this locality (Hayden, 1980), and previous archaeological research (Hayden and Cox, 1978; Ericastilla-Godoy, 1992) sought, with mixed results, to determine whether cultural materials were deposited in association with the faunal remains. Considering the importance of a Paleoindian encampment

Figure 1. Map of region showing the faunal locality of Chivacabé, Guatemala.

with associated late Pleistocene fauna in Central America, additional multidisciplinary research was undertaken in 2009 (Lohse and Paiz, 2010). The prime objective of the 2009 research was to determine whether the faunal remains and cultural artifacts present at the on-site museum were associated, or if the two components were deposited independently. Investigations included detailed archaeological excavation of exposed deposits, a geoarchaeological assessment of the depositional context and history, and an appraisal of the taxa present. Radiocarbon dates were determined on sediment samples collected from documented paleosols. Details about the cultural artifacts, geological history, and geochronology are presented in Lohse and Paiz (2010). Conclusions from the 2009 investigations indicate that the faunal deposit (presented here) is not associated with cultural artifacts. Nevertheless, the paleontological assemblage at Chivacabé represents one of the few fully documented late Pleistocene deposits in a poorly known region, and helps to fill in the overall picture for Central American faunal communities during the period immediately preceding the Holocene.

Previous Excavations

The faunal deposit was discovered in 1976 when the landowner Octavio Alvarado Villatoro and his brother dug a water well. From 1977-1978 Herb Alexander and Brian Hayden (from Simon Fraser University, British Columbia,

Canada) excavated a block of sediments adjacent to the well and noted the presence of what they at the time identified as mastodon, horse, glyptodont, peccary, and deer. In 1979 John Cox (Simon Fraser University), who had been a participant in earlier field seasons, conducted limited testing in other areas across the alluvial terrace on which the site is located. Many of the faunal elements previously found (most of which were left *in situ*) and the cultural artifacts appear to have been preliminarily identified and cataloged during the 1979 season. They display catalog markings that include '1979', as do specimens that are known to have been exposed in prior seasons. The *in situ* faunal elements, located approximately 4.5 m below present surface, have been the focus of local and national interest and are part of a covered display adjacent to a small museum that also exhibits removed skeletal remains. According to Hayden (1980) and Hayden and Cox (1978) it was during these early excavations that a glyptodont scapula was recovered, which showed an apparent puncture hole thought to be caused by human action (refuted below). Hayden and Cox (1978) thought that the sediments were deposited in a lacustrine environment; however, geomorphic studies in 2009 indicate that the skeletal elements were part of an alluvial deposit (Frederick and Yelacic, 2010; Yelacic, 2010). In 1992, Guatemalan archaeologist Sergio A. Ericastilla-Godoy produced a small extension of the excavation at Hayden's site; a few additional faunal remains in the same faunal layer were recovered and are also on display *in situ* (Ericastilla-Godoy, 1992, 1996). He also reported additional evidence that was interpreted to represent human modification of skeletal remains, such as cut marks on a deer antler, modified proboscidean molars, and various bone fractures that did not appear to be natural (Ericastilla-Godoy, 1996).

Chronology

The actual age of the bone bed was not understood in detail until conclusion of the 2009 geomorphological work by Frederick and Yelacic (2010). Originally it was thought that the faunal unit included human artifacts in association with extinct species at 4.5 m depth. However, recent analyses indicate that these remains were deposited during a period of general environmental instability following a volcanic event and during which large amounts of poorly consolidated tephra were washed down hillsides and accumulated on terraces and in topographic depressions. On the basis of radiocarbon and stratigraphic data recorded by Frederick and Yelacic (2010), the faunal deposit reported here dates at two standard deviations between 15,700-15,100 calendar years before present (Beta-257570; 13,020±60 radiocarbon years BP) and 13,210-12,920 calendar years before present (Beta-257568; 11,160±60 radiocarbon years BP). These dates are derived from bulk soil humates taken from buried paleosols that bracket what Frederick and Yelacic (2010) label Depositional Unit 1, a layer of reworked tephra that

contains the faunal remains. This unit is well over two me-ters in thickness in the excavation block, and extends con-siderably deeper across much of the Cañon de Chivacabé. The youngest of these dates corresponds with the North American Clovis interval (Waters and Stafford, 2007), and these ages correspond to the Rancholabrean Land Mammal Age of North America (Bell *et al.*, 2004).

CHIVACABÉ LOCAL FAUNA

The Chivacabé local fauna is represented only by large mammals. All specimens are curated by IDAEH (Departamento de Monumentos Prehispánicos y Coloniales del Instituto de Antropología e Historia de Guatemala) and are archived at the locality. All numbers refer to field speci-men numbers assigned by H. Alexander and B. Hayden, and possibly J. Cox. The list of vertebrates recovered varies from annual report to annual report, and no publication could be identified specifically about the fossils and how they were identified. Ericastilla-Godoy (1992, 1996) provides the most recent compilation of species from Chivacabé and includes *Odocoileus* sp. (deer), 'gliptodonte' (glyptodont), *Equus* (horse), 'mastodonte' (mastodon, referring to a gomphoth-ere), *Tayassu tajuco* (peccary), and *Eremotherium* (giant ground sloth). During the 2009 field season, all specimens that remain exposed in the block, as well as a number that had been removed and stored either in the on-site museum or in the Villatoro home were reexamined. Those fossils *in situ* were left in place and documented as completely as possible. All of the available faunal specimens discovered during the various excavations discussed above were examined.

Many of the skeletal remains were left *in situ*, and we observed in 2009 that many of these fossils were highly degraded and falling apart. Polyethylene glycol 1500 was used at some point to preserve the bones during one of the previous field seasons. This preservative was decaying and peeling off some of the bones. Apparently the late Dr. Oscar Polaco (part of the 1991 field crew from Mexico who came to assist S. Ericastilla-Godoy) did extensive repair on the bones using a dental plaster. Earlier photos taken by the excavation crews from Simon Fraser University (still available on the internet; http://www.sfu.museum/hola/en/slides/) show that the bones were originally in a good state of preservation. However, many of the same elements exhibit degradation by 2009. As these are an important component to the on-site display, current plans are for the entire *in situ* assemblage to remain in place. During the course of our field season, we attempted to improve the conserved condition of the assemblage by hand-cleaning the fossils and then applying PaleoBond (Penetrant, 40, 100), Paleo-Poxy, or Butvar 76. Because many of the skeletal elements had to be left *in situ*, the certainty of identification was greatly reduced.

Most specimens have a 3-part field number assigned by the various researchers. This sequence is made up of a two-digit number that seems to correspond with a field season during which they were exposed or recorded, a unit designation (1 through 12 for the Simon Fraser University excavations or '92' for the Ericastilla-Godoy field season), and what appears to be a serial specimen number within each unit designation. We observed many specimens that had no apparent field number assigned to them, or such numbers have since degraded, and many specimens had '79' as well as either '77' or '78' suggesting that they had been exposed in an earlier field season and then re-cataloged later. When these specimens were critical for our study we would assign them our own field number, first labeling it by the skeletal element (*e.g.*, molar No Number 5).

Glyptodont

North American glyptodonts are distinct and placed in their own genus *Glyptotherium*, which is closely related to the South American *Glyptodon* (Gillette and Ray, 1981). *Glyptotherium* sp. has been recorded from Pleistocene localities in El Salvador, Honduras, and Panama (Gazin, 1956; Webb and Perrigo, 1984). *Glyptodon* sp. is reported from Guatemala and Costa Rica (Gómez, 1986). Some of the Costa Rican osteoderms, according to Lucas *et al.* (1997:421), are heavily abraded yet they "clearly do not belong to *Glyptotherium*"; however, no defining char-acters were provided for identification by either set of authors. Jackson and Fernandez (2005) and Lucas (2008b) recovered osteoderms from Honduras that are reported as *Glyptotherium floridanum*. Until a detailed analysis is conducted on glyptodont osteoderms with associated cranial remains that permit accurate identifications, it is not certain that *Glyptodon* is known from Central America. We assume that the osteoderms recovered from Chivacabé represent *Glyptotherium* because the genus is found immediately north in Mexico and south in Honduras (Arroyo-Cabrales and Polaco, 2003; Ferrusquía-Villafranca *et al.*, 2010).

The dermal armor of glyptodonts is their most rec-ognizable characteristic. Consequently, the morphology of the osteoderms that make up the carapace has long been recognized as taxonomically significant (Gillette and Ray, 1981). Each osteoderm is polygonal in shape (six- or four-sided) and sutured to its neighbors (see Holmes and Simpson, 1931). The typical osteoderm has a central fig-ure and several peripheral figures symmetrically arranged surrounding the center which creates a rosette pattern (see Hill, 2006). Diagnostic characters used here are slightly modified from Gillette and Ray (1981) and as in Mead *et al.* (2007). In *Glyptotherium texanum*, the central rosette is larger than the peripherals, and is convex and slightly raised above the level of the flattened peripherals. In. *G arizonae* and *G. cyclindricum* the central figures are relatively smaller than the peripherals, less than 50% of the entire osteoderm diameter, and are generally flat to weakly convex. The cen-tral figure in *G. floridanum* is approximately equal to and

larger in size than the peripherals, and is typically raised and weakly concave. The central figure of the osteoderm of *G. mexicanum* is generally large, never smaller than 50% of the diameter. Although seemingly distinct for all recognized species of *Glyptotherium*, we acknowledge that there is variation in the rosette size and pattern within and among species. Complicating the issue is the fact that *G. cyclindricum* and *G. mexicanum* are less than adequately understood, being known mainly from the type localities (McDonald, 2002). *Glyptotherium arizonae* and *G. texanum* are known only from early Pleistocene and earlier faunas, and are not known from late Pleistocene localities (Gillette and Ray, 1981). Clearly much remains to be understood about Central American glyptodonts.

Glyptodont skeletal remains from Chivacabé represent at least one individual of *Glyptotherium* sp. The following specimens are identified: osteoderm (78-5-A, 78-5-3, 78-5-10, 78-5-11, 78-6-12, 78-6-13, 78-6-26, 78-7-4, 78-10-1, 78-10-3, 78-11-2, 78-11-5, 78-11-9, 78-11-10, 78-11-17, 79-11-39, 79-11-41, 79-11-43, 79-11-66), long bone fragment (79-11-196), ilium fragment (No Number; on display in museum as 'mastodonte'). The greatest width of the individual osteoderms varies from 41.0 to 53.9 mm (*n*=10) (Figure 2). Width of the rosettes varies from 17.4 to 29.5 mm. Ratios of these two measurements are expressed as the rosette percentage of the entire width; these vary from 35.6% to 59.3%. None of the central figures are raised or convex; this omits *G. texanum* (known in North America only from pre-late Pleistocene localities) from consideration. The central figures on osteoderms from Chivacabé all have flat to concave structures. These characters would seem to indicate that some of the osteoderms might be identified as *G. floridanum*, whereas other specimens would appear to be from *G. cyclindricum* or *G. mexicanum*. Because we feel there is only a single individual glyptodont preserved at Chivacabé, we believe that the species cannot be adequately determined with the recovered specimens. The postcranial remains are fragmentary and too poorly preserved to permit adequate identification. Hayden (1980) and Ericastilla-Godoy (1992) state that specimen 78-8-1c/d is a scapula of a glyptodont; however, we identify this specimen as an ilium belonging to *Equus* (see below).

Gomphothere

Proboscideans known to have inhabited Central America from southern Mexico through to South America during the Pleistocene include elephants (*Mammuthus*, Elephantidae), gomphotheres (*Cuvieronius*, *Haplomastodon* [including *Stegomastodon*] Gomphotheriidae), and mastodonts (*Mammut*, Mammutidae; see among others, Lucas *et al.* 1997; Arroyo-Cabrales *et al.*, 2002; Montellano-Ballesteros, 2002; Cisneros, 2005, 2008; Lucas 2008c; Lucas *et al.*, 2008; Lucas and Alvarado, 2010). Ferretti (2008) and Prado *et al.* (2005) reviewed the gomphotheres
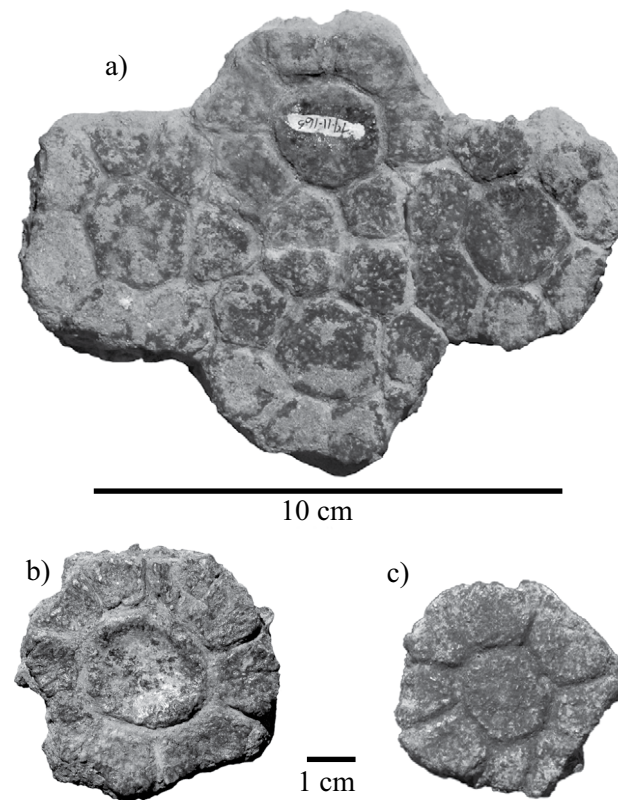

Figure 2. Osteoderms of *Glyptotherium* sp. from Chivacabé. a) four articulated osteoderms (79-11-166); b) isolated osteoderm (78-10-3); c) isolated osteoderm (78-5-3).

of South America. Tooth and tusk morphology of skeletal elements in the Chivacabé local fauna indicates that a few individuals of a gomphothere were recovered and left largely *in situ*. The systematics and phylogeny of gomphotheres is still not fully resolved (*e.g.*, Shoshani, 1996; Ferretti, 2008; Lucas, 2008c; Lucas and Alvarado, 2010).

The following remains were recovered: tusk fragments (78-5-15 [only tip exposed]; 78-6-8, 78-8-15, 78-10-15); mandible fragment (78-4-11); dp/3? (77-5-4); M3 (77-6-13, 77-6-15, 78-4-12, 78-5-13, 79-11-2, No Number 5); M1-2s (77-5-5, 77-6-18, 77-3-19?, 78-4-13 [in mandible fragment], 78-10-16, 78-10-17, 78-11-23, 78-11-24, 78-11-26, 79-11-4, 79-11-152, No Number 1-4); stylohyoidium (78-2-6); atlas (78-5-18); axis (78-6-3); cervical vertebra (78-2-8, 78-6-7); thoracic vertebra (78-3-4, 78-3-13); vertebral fragment (78-2-8); patella (78-7-9); rib (78-5-26, 78-6-5, 78-6-6, 78-6-19, 78-6-20, 78-6-21, 79-11-218, 79-11-219); left humerus (78-2-9); right humerus (78-2-4 [sub-adult], 79-11-200, 79-11-238); ulna (78-2-1, 79-11-170); femur (78-3-1); left femur (78-5-16); right tibia (78-2-5).

The morphology of the juvenile mandible (78-4-11) fragment illustrates that the lower jaw does not have a sharply downturned symphysis and therefore does not belong to *Rhyncotherium* (see Lucas and Morgan, 2008). Preservation is not complete but the existing fragment does

not show evidence of lower tusk alveoli that would be present in *Rhyncotherium*, but not in *Cuvieronius* (Shoshani, 1996; Lucas, 2008a). This observation implies that 78-4-11 belongs to either *Cuvieronius* or *Haplomastodon* (see Lucas and Alvarado, 2010).

Four tusk fragments (78-5-15, 78-6-8, 78-8-15, 78-10-15) are well preserved. Tusk 78-5-15 had its base broken during hand-excavation of the well that resulted in the initial discovery of the locality. The tip of the tusk has an enamel band that continues the 100 cm length; the broken base has a diameter of 169.3 mm. Tusk fragment 78-10-15 has been repaired (apparently by Dr. Oscar Polaco; Figure 3a). Tusk fragment 78-8-15 has an enamel band (66.7 mm wide at base of tusk) that spirals from the tip down the length of the straight tusk; length of tusk is 680 mm and base diameter is 177.4 mm (Figure 3b). An enamel band (greatest width= 23.7 mm) begins at the tip of the tusk and spirals the length of the fragment for 320 mm, ending at the broken base,
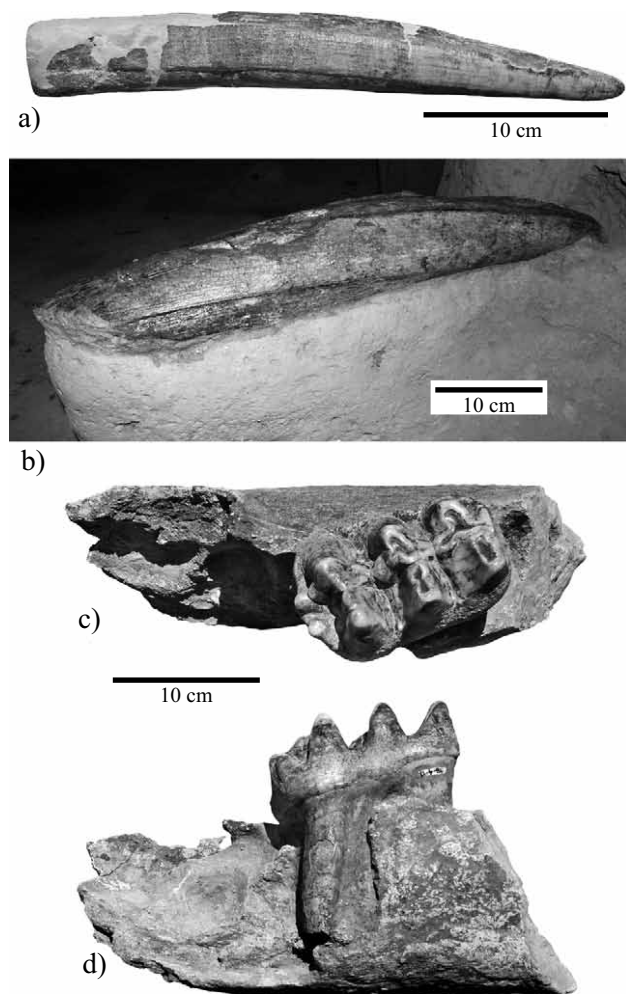

a)

b)

c)

d)

Figure 3. a-b: Proboscidea of Chivacabé. Tusks a) 78-10-15; b) 78-8-15 showing the enamel band representing *Cuvieronius* cf. *C. hyodon*. c-d: M/2, 78-4-13 of *Cuvieronius* cf. *C. hyodon* in its fragmentary mandible; c) occlusal view; d) lateral view.

which has a diameter of 40.7 mm. Specimen 78-6-8 is too damaged and highly repaired to permit description.

Haplomastodon does not have an enamel band. Shoshani (1996) and Lucas (2008c) state that the enamel band is usually absent on *Haplomastodon*, but when present, it is highly reduced. Thus, we have identified the three best-preserved tusks containing prominent enamel bands as belonging to *Cuvieronius*. Based on preserved tusks, at least two individuals of *Cuvieronius* cf. *C. hyodon* are present at Chivacabé. Until there is a detailed study of the Pleistocene gomphotheres, we will follow Lucas (2008a) in using the species name *C. hyodon* (Fischer, 1814) instead of utilizing *C. tropicus* (Cope, 1884).

Most teeth are isolated specimens; only the M/2, 78-4-13, is in a fragment of a mandible (Figures 3c, 3d). An alveolus for the M/3 is apparent and suggests that the tooth was *in situ* but subsequent to or during excavation the molar became isolated. The M/2 is 120.7 mm long, with the width of the protolophid 70.9 mm and the width of the tritolophid 82.7 mm. There is occlusal wear on the first two lophids and slightly apparent on the tritolophid. Specimen 78-4-12 is an unerupted M/3 (no wear on the lophids; Figure 4b) and may well belong adjacent to specimen 78-4-13. The length is 182.5 mm with the width of the tritolophid 83.7 mm; 4.5 lophids are present. The assumption with these two specimens is that they belong to one individual *Cuvieronius* with a lower M/2 almost in full wear and an M/3 that is unerupted; this would correspond to a subadult individual.

We are not sure which of the many isolated molars might represent an M/1 that could be associated with 78-4-13. However, there is a heavily worn, small molariform tooth (77-5-4; Figures 4c, 4d) that appears to be deciduous premolar. According to Shoshani (1996, features 27, 23), *Cuvieronius* does not have premolars P2/2-P4/4 but it does have a dp3. Figures 4c and 4d show what we believe is a dp3 in an extreme state of occlusal wear. The greatest preserved length is 61.8 mm with a width of the metalophid of 38.0 mm.

Five additional M3s were recovered (77-6-13, 77-6-15, 78-5-13, 79-11-2, No Number 5). All M3s have 4.5 lophs (4 plus a 5th as a buttress; 77-6-15: Figure 4a); four are in a state of full occlusal wear on all lophs, and one has only slight wear on the buttress loph. We assume that the four M3s with full wear are from one fully-adult individual. Specimen No Number 5 must represent a second adult individual in the deposit.

Specimen 79-11-152 is a fragmentary molar of *Cuvieronius* that was suggested by Hayden and Cox (1978) to possibly show evidence indicating modification by humans. Although the molar is heavily battered, nothing is evident to us to represent human modifications or pathological abnormality. The tooth roots exhibit normal taphonomic rounding and battering as a result of transport in an active alluvial depositional environment.

Hayden and Cox (1978) discussed a specimen that they felt represented a deer antler fragment (78-2-6; Figure
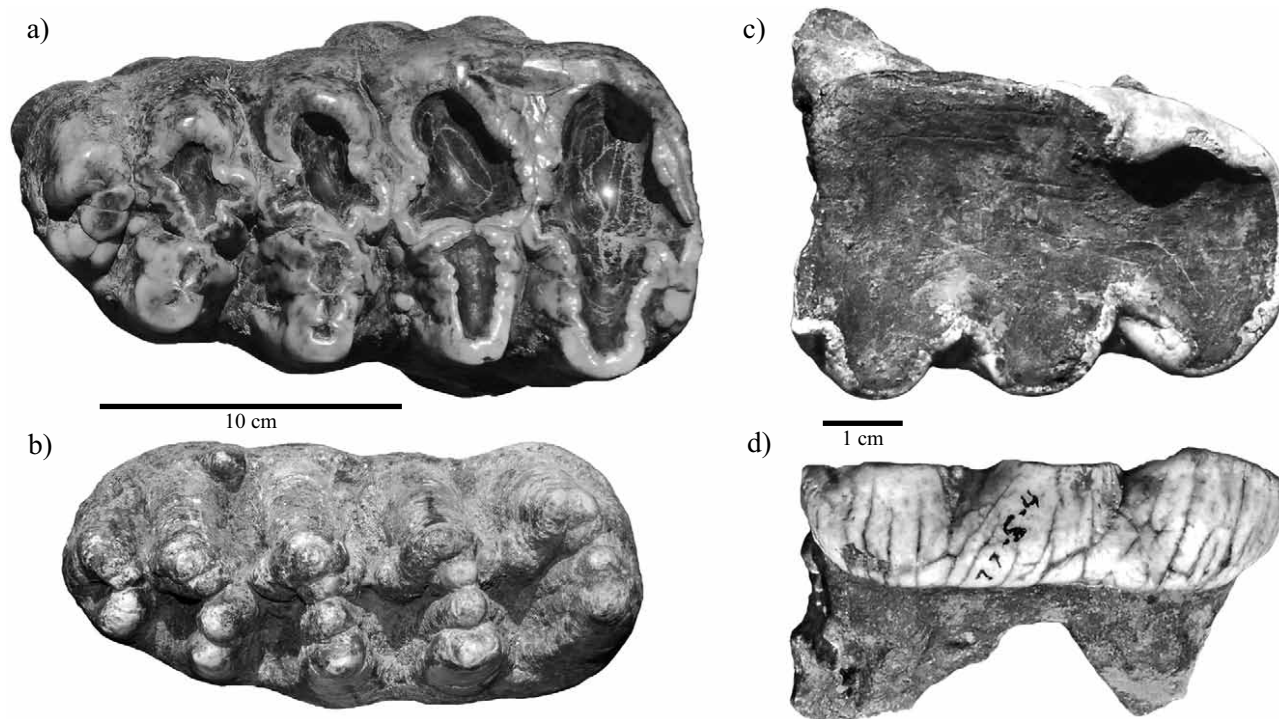
a)

c)

10 cm

b)

d)   1 cm

Figure 4. Molars of *Cuvieronius* cf. *C. hyodon*. a) M3 (77-6-15); b) specimen 78-4-12 is an unerupted M/3 that we suggest is associated with the M/2 in Figure 3 (c, d). A small molariform tooth of *Cuvieronius* cf. *C. hyodon* that we identify as a dp3 (77-5-4) in an extreme state of occlusal wear; c) occlusal view; d) lateral view.

5a). The interior structure is not that found in antlers. The cortex is thin and the cross-section is ovoid, not circular as found with antlers at the burr. We have determined that the bone is instead a fragment of a hyoid. Based on its large size it is probably from a gomphothere and may represent *Cuvieronius*. The hyoid apparatus supports the base of the tongue, pharynx, and larynx, and is constructed of three components: two thyrohyoidea, one basihyoideum, and two stylohyoidea (see Graham, 1986, Shoshani and Marchant, 2001). We believe that specimen 78-2-6 is a portion of the stylohyoideum (Figure 5a). The posterior ramus illustrates the surface that attaches to muscle tissue. The articular surface of the superior ramus articulates with the styloid process of the temporal (squamosal) bone. The ventral shaft of the inferior ramus is absent. Hyoid bones from gomphotheres are rare and have received little attention (Shoshani and Marchant, 2001).

Most postcranial skeletal elements are too poorly preserved to adequately identify. Identification is hampered because most of the bones are in situ and exposed only one or two sides for examination. All postcranial elements are identified as *Cuvieronius* cf. *C. hydon* as they are proscidean elements associated with tusks and molars identified to that taxon.

The atlas (78-5-18; Figure 5b) is complete and remains in situ, which hampers analysis. The greatest dorso-ventral length is approximately 210 mm and the greatest medial width is approximately 360 mm. The axis (78-6-3; Figures

5c, 5d) was complete and in situ but we were allowed to remove the bone for detailed preservation and analysis. The greatest width across the cranial articular processes on either side of the odontoid process is 198.8 mm; greatest dorso-ventral height is 204.5 mm; greatest width across centrum caudal surface is 126.6 mm; and greatest width across the posterior articular processes is 145.5 mm (measurements as in Göhlich, 1998).

Most of the limb elements were either highly degraded at the articular ends or had repairs made with plaster making accurate measurements unattainable. The greatest dorso-ventral length of the patella (78-7-9) is 129.9 mm and the greatest width is 89.7 mm (measurements as in Göhlich, 1998).

Equid

At least one individual horse was recovered (*Equus* sp.). The following remains were identified: molars (77-3-1, 77-3-9, 77-9-1; two with no numbers; Figure 6a), scapula (79-11-158), fragment of ilium (78-7-9; 78-8-1c/d; Figure 6c), acetabulum and pubis (78-8-2), and tibia (no number). The molars are large (Table 1) and likely represent a larger species of *Equus*. The scapula is nearly complete with the epiphysis fused representing an adult individual. The length is 27.8 cm from greatest projection of the glenoid fossa to the dorsal edge of the bone; this area is slightly degraded
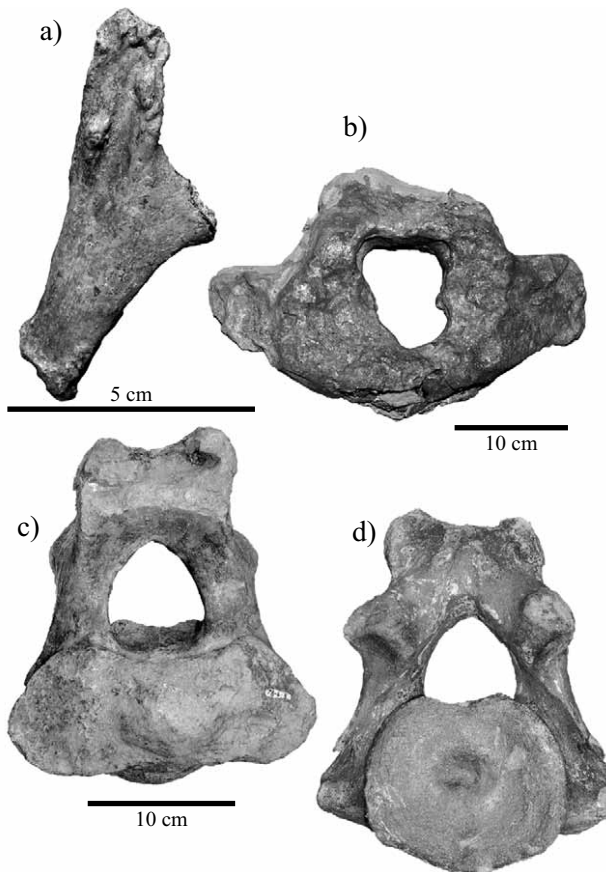
Figure 5. a) Specimen 78-2-6 is a portion of the stylohyoideum of *Cuvieronius* cf. *C. hyodon*; b) cranial view of atlas (78-5-18) of *Cuvieronius* cf. *C. hyodon*. Axis (78-6-3) of *Cuvieronius* cf. *C. hyodon*; c) cranial view; d) caudal view.

assume that a carnivore scavenged the carcass. A canine will sometimes leave not only a deep, circular puncture but the curved base of a lower canine will create a lateral, oblique impression adjacent to the depression caused by the posterior portion of the tooth. A series of additional small indentations occur across the iliac flange (lateral face) and may represent tooth 'chatter marks' that indented the bone but did not penetrate the cortex.

Cervid

Two individual-deer (*Odocoileus* cf. *O. virginianus*) are documented on the basis of the recovery of two right antlers (78-10-7/8, 78-11-15; Figure 6b). *Odocoileus* has recurved antlers whereas those of *Mazama* are straight. Both specimens are naturally-shed antlers and do not represent specimens that were adhering to a skull at death. Antler 78-11-15 is nearly complete; diameter of the base at the burr measures antero-posteriorly 40.6 mm and medio-laterally 36.7 mm. Measurement from the burr to the first tine is 43.8 mm, 1st to 2nd tine is 103.8 mm, 2nd to 3rd tine is 60.1 mm, and 3rd to 4th tine 76.4 mm. The second antler (78-10-7/8) is fragmentary but has approximately the same measurements. Hayden and Cox (1978) mentioned a third antler specimen
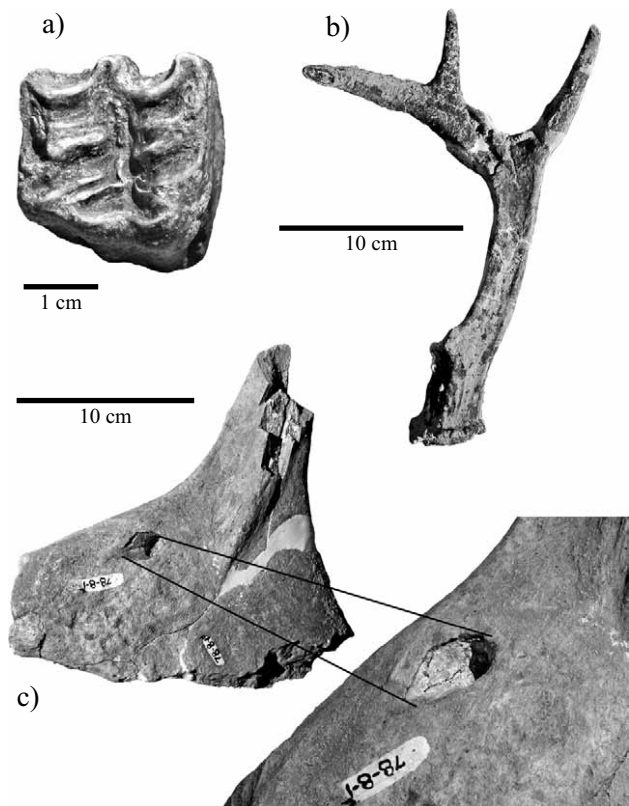
by exposure post-excavation or carnivore gnawing. Based on comparisons with modern *Equus* skeletons, the scapula 79-11-158 is from the same sized animal as the acetabulum and pubis (78-8-2). Measurement across the acetabulum is 63.7 mm. The acetabulum exhibits a slight puncture mark that is consistent with one made by a carnivore on green bone. The tibia is fragmentary, with heavily worn breakage at the mid-diaphysis. The bone was repaired with plaster by Dr. Oscar Polaco.

A fragmentary ilium is identified here as belonging to *Equus* (78-8-1c/d; Figure 6c). Hayden and Cox (1978) and Ericastilla-Godoy (1992) both determined that this bone was a scapula of a glyptodont, 'escapula de gliptodont'. An indentifying mark is found on the bone that Hayden and Cox (1978) and Ericastilla-Godoy (1992) refer to as evidence of an impact depression from a wooden projectile point. Scapulas on live glyptodonts are located beneath (interior to) the dermal armor of the carapace. We believe that the bone is actually an ilium of *Equus*. The ilial shaft is broken and preserves a green-bone breakage pattern. Close examination of the indentation (Figure 6c), agrees with an indentation made by a canine from a large carnivore. We

Figure 6. *Equus* and *Odocoileus* from Chivacabé. a) *Equus* tooth (77-9-1) in occlusal view; b) antler of *Odocoileus* cf. O. *virginianus* (78-11-15); c) ilium of *Equus* (78-8-1) with an indentation interpreted as having been made by a carnivore (see inset and discussion in text).

Table 1. Measurements (mm) of *Equus* sp. molars from Chivacabé, Guatemala.

Field number	Occlusal length	Occlusal width	Height along anterior edge
No number	24.4	27.4	47.0
No number	29.5	25.8	76.0
77-3-1	27.3	27.4	74.6
77-3-9	27.3	26.5	73.5
77-9-1	25.7	26.1	72.1

(78-2-6); however, this specimen is identified here as a hyoid (see above discussion on gomphotheres; Figure 5a).

DISCUSSION AND CONCLUSIONS

Central America (that region from the Isthmus of Tehuantepec to Colombia) was the north-south avenue for dispersal of vertebrate species during the Great American Biotic Interchange. The trans-isthmian exchange of vertebrates (especially mammals) from North America and South America began in earnest at about 2.6 Ma and ended sometime after the fourth phase began at about 0.125 Ma (Woodburne, 2010). Many important details about the dispersal events and the taxa involved are still inadequately understood. Included among these details is which in-situ Central American faunas remained after the culmination of the interchange during the latest Pleistocene (Rancholabrean-Lujanian). Although tectonic elements of the land bridge were present well before the onset of the series of dispersal pulses, it appears that climate was the primary controlling factor during the events (Woodburne, 2010).

Habitats during the interglacials of the Pleistocene (as at present) would have been predominantly tropical rainforests across the land bridge, as also occurred during the Miocene and Pliocene (Graham and Dilcher, 1998). Glacially-driven climatic regimes would have resulted in the development of significantly drier landscapes during glacial episodes (Piperno, 2006). Central American lowlands from approximately 20,000 to 10,000 years ago had plant communities that reflected climates which were drier and cooler than present; forest canopies may have been more open than at present and rainfall was decreased by possibly 30% to 50% (Piperno, 2006). The area around Chivacabé is reconstructed to have been mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation certainly during the full glacial period (approximately 18,000 to 16,000) (Piperno, 2006; Woodburne, 2010). With the onset of glacial climates, the mosaic of the local plant communities would have changed at all elevations; there is no apparent modern analog for these Pleistocene biomes (Piperno, 2006). During the final phase of the late glacial (~ 10,000 years ago; post-faunal occupation at Chivacabé),

the pollen records indicate that the climate quickly warmed substantially, became considerably wetter and highly seasonal, and atmospheric concentrations of CO_2 increased.

The Chivacabé fauna dating to between 15,700 and 12,920 calendar years ago was preserved immediately prior to the waning phase of the cooler and drier glacial climate regime. Specimens reported here include: at least one individual of a glyptodont (*Glyptotherium* sp.) represented by osteoderms and various postcranial long bones; three individuals (one juvenile and likely two adults) of a gomphothere (*Cuvieronius* cf. *C. hyodon*) represented by tusk fragments, numerous teeth, vertebrae, and limb elements; one individual of a horse (*Equus* sp.) represented by teeth and numerous postcranial elements; and two individuals of a deer (*Odocoileus* cf. *O. virginianus*) represented by two right, naturally-shed antlers. An additional specimen that originally was thought to represent a deer antler is identified here as a hyoid bone pertaining to *Cuvieronius*. We did not observe any vertebrate remains that could be assigned to *Tayassu* or *Eremotherium* as stated by Hayden and Cox (1978) and Ericastilla-Godoy (1996). Thus, we conclude that these species are not part of the Chivacabé local fauna. In discussing the fossils recovered and archived in the museum, Octavio Villatoro commented that he had never seen any skeletal remains that were thought to represent peccary (although its recovery would not be unusual, Woodburne, 1968). Octavio Villatoro also noted that some previous researchers thought that the giant ground sloth should be found at the locality so it was included on the original list, but he had never seen such remains at Chivacabé. No faunal specimens exhibit human modification, hunting, or butchering marks as suggested by previous investigators; all aberrations observed on the bones and teeth can be explained by physical taphonomic processes.

The Chivacabé fauna represents one of extremely few described late Pleistocene faunas from Guatemala. Ericastilla-Godoy (1996) and Ericastilla-Godoy and García (1994) provided lists of apparent late Pleistocene localities of Guatemala; we have annotated this and added the Chivacabé fauna (Table 2). Late Pleistocene faunas from surrounding countries are much better represented in the literature than those from Guatemala, yet none of the Central American faunas are adequately understood and almost all are heavily biased toward the megamammal taxa. Mammalian microfaunas and herpetofaunas (amphibians and reptiles) are almost unheard of from the late Pleistocene of Central America.

Table 2. List of probable late Pleistocene faunas (created by Ericastilla, 1996), updated here with footnotes, and including the Chivacabé fauna reported here. Common names of mammalian species are used here until specimen identifications can be verified and/or are published.

Locality	Taxon
Chinautla	gomphothere
Chiticoy	proboscidean
Chivacabé	*Glyptotherium* sp., *Cuvieronius* cf. *hyodon*, *Equus* sp., *Odocoileus* cf. *virginianus*
Ciudad Real[1]	*Cuvieronius*, *Equus conversidens*, *Eremotherium* sp., *Toxodon* sp., *Odocoileus* sp.
Estanzuela	glyptodont, camel, mammoth, gomphothere, tapir, horse, megathere
Hidroelectrica Chixoy	glyptodont
Jutiapa	mammoth
Malacatancito	gomphothere
Mixco	gomphothere
Río la Pasión[2]	*Dicotyles tajacu*, cf. *Felis*, cf. *Cuvieronius*, toxodont, horse, *Tapirus*, camel, *Mazama*, ?bovid, *Dasypus*, *Pampatheriuim*, glyptodont, *Megalonyx*, *Megatherium*, *Mylodon*, *Hydrochoerus*
El Rosario-Ipala	gomphothere, megathere, deer
Salama	megathere
Santa Cruz Barillas	proboscidean
Tivoli	glyptodont, gomphothere, horse, mammoth?
"Treasure Island"[3]	*Crocodilus moreletii*
Tulumaje	megathere
Tulumajillo	proboscidean

1: Thurmond (1973) presented this fauna in an abstract; 2: remains recovered by Barnum Brown from a playa deposit and reported by Woodburne (1968); 3: a nearly complete left maxillary was recovered by Barnum Brown and described by Mook (1959) as of probable middle Pleistocene age.

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