

NEW PLEISTOCENE VERTEBRATE FAUNA FROM EL SALVADOR

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ABSTRACT - The discovery of an Early-Middle Pleistocene continental vertebrate fauna from El Salvador is here reported. These fossils provide information about a poorly studied geographic area that played an important role during the Great American Faunal Interchange. The fauna is dominated by numerous remains of the proboscidean *Cuvieronius tropicus* and probably represents the largest known concentration of this genus in America. A number of living taxa are first recorded as fossils in El Salvador, including *Crocodylus acutus*, previously unknown as a fossil elsewhere. *Hesperotestudo crassiscutata*, *Glyptotherium arizonae*, *Palaeolama*, *Hemiauchenia* cf. *H. seymourensis* and *Equus conversidens*, are recorded for the first time in Central America. The new locality also holds the oldest record of *Mazama*, and the southernmost records of *Glyptotherium arizonae* and *Equus conversidens*. At least 17 taxa are represented in the new site, constituting the richest Central American continental vertebrate locality hitherto known.

Key words: Mammals, El Salvador, Central America, Pleistocene, Great American Faunal Interchange.

RESUMO – Reporta-se o achado de uma fauna Eo-Mesopleistocênica de vertebrados em El Salvador. Os fósseis aportam informações sobre uma área geográfica pouco estudada que teve um papel relevante durante o Grande Intercâmbio Faunístico Americano. A fauna é dominada por numerosos restos do proboscídeo *Cuvieronius tropicus* e representa, provavelmente, a maior concentração fossilífera deste gênero na América. São registrados como fósseis por vez primeira em El Salvador vários taxa vivos, entre eles *Crocodylus acutus*, do qual inexistem quaisquer registros fósseis prévios em outros países. São assinalados pela primeira vez para a América Central: *Hesperotestudo crassiscutata*, *Glyptotherium arizonae*, *Palaeolama*, *Hemiauchenia* cf. *H. seymourensis* e *Equus conversidens*. A nova localidade possui, também, o mais antigo registro de *Mazama*, e o mais austral de *Glyptotherium arizonae* e *Equus conversidens*. Pelo menos 17 taxa estão representados neste novo sítio, constituindo-se assim, na localidade de vertebrados continentais mais rica já conhecida na América Central.

Palavras-chave: Mamíferos, El Salvador, América Central, Pleistoceno, Grande Intercâmbio Faunístico Americano.

INTRODUCTION

Cenozoic vertebrate faunas in Central America are poorly represented in the fossil record, in spite of fossil outcrops being rather common in the area (Webb & Perrigo, 1984). The search for fossils has been particularly limited. Local factors, including ongoing political strife and warfare in the last three decades, were a significant obstacle to carrying out palaeontological studies in the region. Nevertheless, the importance of Central America in the Neogene, due to its role as both a bridge and a filter during the Great American Faunal Interchange, and the need of extensive studies in the area are widely acknowledged (Stirton & Gealey, 1949; Simpson, 1980;

Webb & Perrigo, 1985; Lucas & Alvarado, 1994; Webb 1991, 1997; Montellano Ballesteros, 1999). The area, acting as a filter, holds the southernmost and northernmost confirmed records for several widespread Plio-Pleistocene mammalian groups of both American continents, such as bovids, notoungulates, mammutids and elephantids (Howell, 1969; Webb & Perrigo, 1984; Webb, 1991; Lucas & Alvarado, 1991; Lucas *et al.*, 1999); and was presumably an evolutionary centre for numerous groups that spread in both directions during the Great American Faunal Interchange. (Simpson & de Paula Couto, 1956; Simpson, 1980; Gillette & Ray, 1981; Webb & Perrigo, 1984; Webb, 1991, 1997).

In 2000, a rich Pleistocene vertebrate locality was

fortuitously discovered at the margins of Río Tomayate, north of San Salvador, El Salvador, by Teófilo Reyes. One year later, Reyes kindly donated the *Cuvieronius* molar found to the Museo de Historia Natural de El Salvador, and indicated the locality where he discovered it. Between April and August of 2001, the museum opened a quarry at the site, collecting a large number of proboscidean and other vertebrate remains, represented by more than a thousand field numbers. In 2002, the property was acquired by Salvadorian government and declared a national monument. The primary goal of this work is to provide a preliminary list of fauna of the new fossil site of Río Tomayate, which is probably the richest vertebrate locality hitherto found in Central America. Dental nomenclature follows in most part Smith & Dodson (2003).

Abbreviations. GAFI, Great American Faunal Interchange; NALMA, North American Land Mammal Age; SALMA, South American Land Mammal Age; MUHNES, Museo de Historia Natural de El Salvador.

STUDY AREA

The fossil site (Figure 1) is located at the margins of Río Tomayate, in Apopa Municipality (13°47' N, 89°10' W), 12 km north from San Salvador, El Salvador. The outcrop is located approximately 3 km north from the Apopa-Quezaltepeque highway bridge over the river. Río Tomayate (known as Río Urbina within the city of San Salvador) is a small tributary of Río Acelhuate and both flow into the Río Lempa Basin. The river drains part of the city of San Salvador and the water is badly contaminated, and hygiene precautions are essential for collecting. No formal geological studies have been done in the work area, which is mostly covered with tropical vegetation that limits the outcrops available (Figure 2), making it difficult to carry out geological work on a regional scale. The river creates local outcrops that consist of a compact claystone locally known as “talpetate”. At the fossil site, the claystone emerges at approximately 2 m from the water level of the river in the dry season. Unique to this exposure are two successive bonebeds that overlay the claystone stratum. The entire fossiliferous package has a lateral extent of about 50 m on both banks of the river, and is approximately 1.6 m thick. The matrix is a light brown unconsolidated ash with abundant pyroclasts and fragmentary fossil vegetal remains. Fossil collecting has been undertaken only at the eastern margin. All fossil vertebrates recovered are disarticulated, with one exception, a partial *Eremotherium* skeleton found in the upper bonebed. The vertebrates bear iron concretions, and recent disturbance by roots is rather common. Nevertheless, the state of preservation of the fossils is good. In each bonebed, the larger and heavier elements occur at the base, gradually decreasing in size towards the top, resulting in a fining upwards sequence. No sedimentary structures were recognized in the fossiliferous strata. The lower bonebed is approximately 0.9 m thick and the majority of the vertebrates were collected here. At the base of the lower bonebed, overlying the claystone, several weathered, subangular to subrounded, dense bones, are found. The latter elements have been reworked and should be older than the entire fossiliferous package, but it has been impossible to identify any of them due to their fragmentary state. The upper bonebed is approximately 0.7 m thick. The upper bonebed is overlain by a pyroclastic stratum of about 4 m in thickness, and is covered by a layer of modern soil that supports dense tropical vegetation. Archaeological artefacts are present in the soil and include pre-Hispanic ceramic and obsidian tools. Exposures of pyroclastic and epiclastic rocks of the Quaternary San Salvador Formation (Schmidt-Thomé, 1975), which are locally known as “tierra blanca”, occur close to the site, but their relation with the fossiliferous packages is unclear.

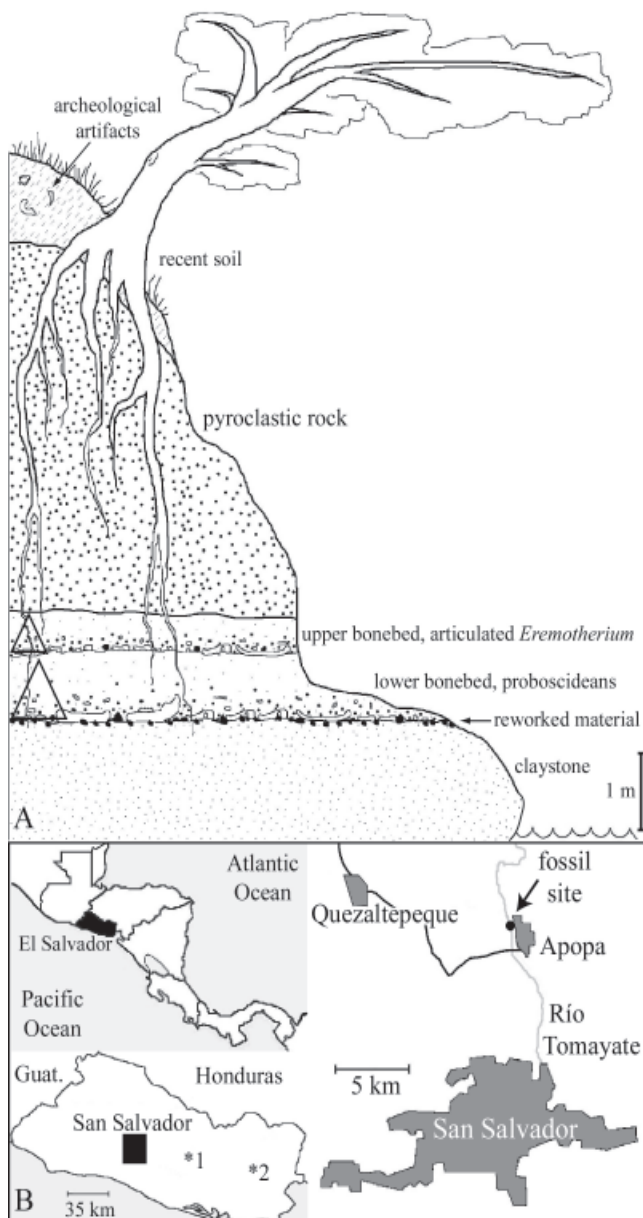


Figure 1. Simplified geologic section of the outcrop at Río Tomayate (A) with Fining upwards sequence (A) and reworked bones (in black). B, Location of the Tomayate outcrop and two other important Pleistocene localities from El Salvador: 1, Río Sisimico, Early-Middle Pleistocene; 2, El Hormiguero, Late Pleistocene.



Figure 2. Photograph of the outcrop on the east shore of Río Tomayate.

SYSTEMATIC PALAEOLOGY

The vertebrate collection from Río Tomayate comprises several hundred specimens, a large number of which remain in plaster jackets or unprepared. This collection is being catalogued, and the numbers here provided are field numbers (preceded by 2SSAP30 or 1SSAP6, field notation from MUHNES). For the sake of brevity, a sample of the most relevant specimens and brief descriptions emphasizing diagnostic characters are given here. These materials will be the subject of detailed descriptions to be provided elsewhere. All specimens are held at MUHNES, in San Salvador.

TESTUDINES Linnaeus, 1758
 CRYPTODIRA Cope, 1868
 TESTUDINIDAE Batsch, 1788
Hesperotestudo Williams, 1950
Hesperotestudo crassiscutata Leidy, 1889
 (Figure 3C, D)

Referred material. 2SSAP30-205 shell fragment, 2SSAP30-207 shell fragment, 2SSAP30-662 costal, 2SSAP30-675a, b shell fragments, 2SSAP30-790 costal and 2SSAP30-509 right xiphiplastron.

Description. Shell fragments remarkably large but noticeably thin and light build in relation to their size. Costals have relatively smooth ornamentation in the form of low longitudinal crests. 2SSAP30-509 is a right xiphiplastron with an obtuse posterior edge, indicating a shallow xiphiplastral notch. The anteroposterior length of the partial costal 2SSAP30-662 is 180-190 mm, indicating a total carapace length of approximately 1.5 m for this individual. The exceptionally large size, smooth ornamentation and shallow xiphiplastral notch are characteristic of *Hesperotestudo crassiscutata* (Auffenberg, 1963).

Remarks. The shell fragments were not found in association and may represent different individuals. The genus name *Hesperotestudo* is used here instead of *Geochelone* following Meylan (2000). The only previous *Hesperotestudo* records

in Central America come from the Lempira site (Late Miocene) in Honduras; and Río Sisimico (or Barranca del Sisimico, Early to Middle Pleistocene,) and El Hormiguero (Late Pleistocene) in El Salvador (Webb & Perrigo, 1984); none of these specimens has been identified at the species level.

EMYDIDAE Rafinesque, 1815
 (Figure 3F)

Referred material. 2SSAP30-123 partial nuchal, 2SSAP30-757 nuchal, 2SSAP30-758 right epiplastron.

Description. These nuchals lack the pronounced ornamentation present in members of the genus *Trachemys*, and could belong to either *Pseudemys* or *Rhinoclemmys*. The epiplastron possesses a gular scute overlap comprising less than half the bone surface, similar to *Pseudemys*. Unlike the latter, the anterior margin is not rounded, being more similar to that of *Trachemys*.

Remarks. The specimens represent the first report of fossil emydids from El Salvador. Disarticulated, chelonian shell fragments are among the most common remains recorded at Río Tomayate. Most of the specimens are probably emydid turtles, but poor preservation prevents positive identification at present.

KINOSTERNIDAE Baur, 1893
Kinosternon von Spix, 1824
Kinosternon sp.
 (Figure 3E)

Referred material. 2SSAP30-229 left hyoplastron.

Description. This single plastral element is referred to *Kinosternon* due to its relatively elongated shape (but wider than *Sternotherus*) and the absence of a dorsally projected buttress. An unusual feature of this hyoplastron is the pronounced humeral scute overlap.

Remarks. This specimen constitutes the first report of the mud turtle *Kinosternon* as a fossil in Central America.

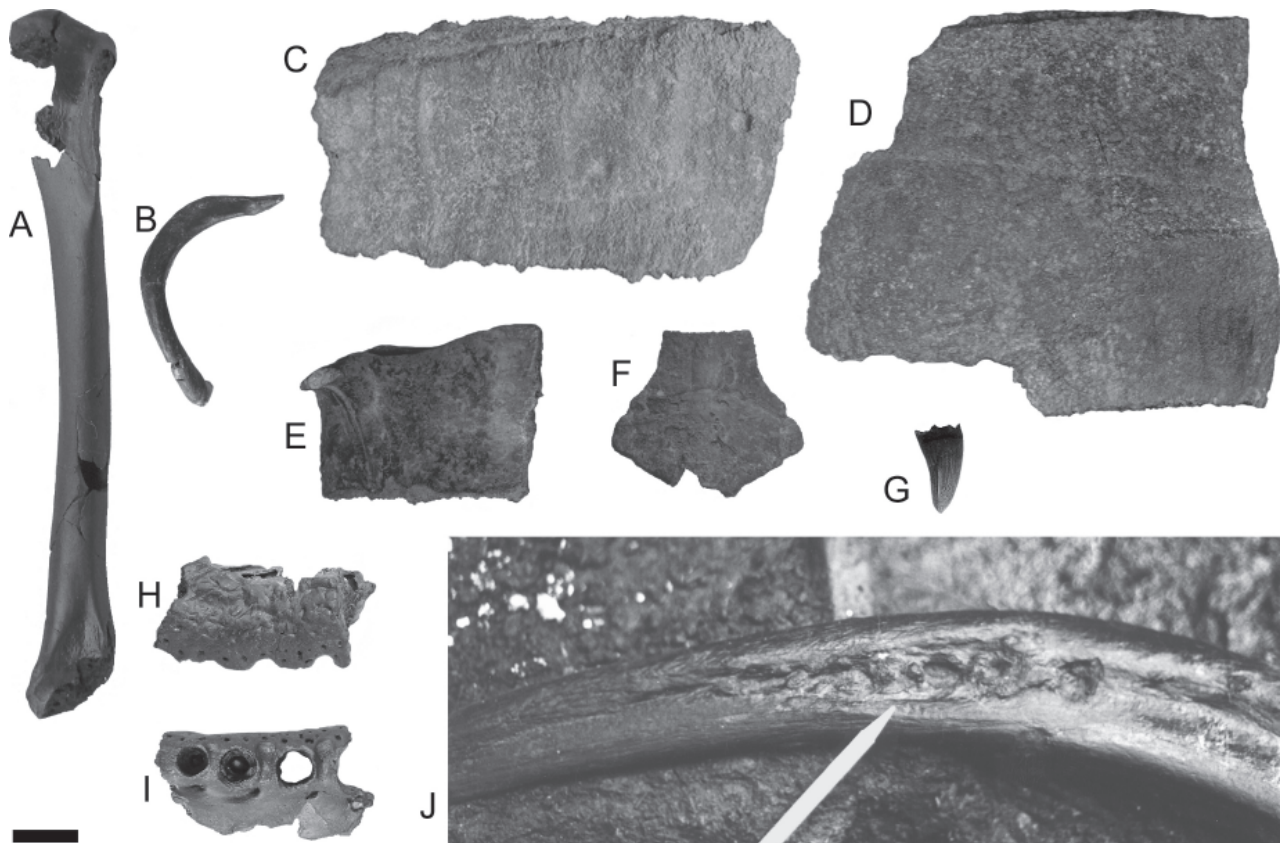


Figure 3. Testudines, crocodylians and birds from Río Tomayate. **A**, 2SSAP30-853 *cf. Anser* sp., left humerus in anterior (palmar) view; **B**, 2SSAP30-545 *cf. Anser* sp., left clavicle in lateral view; **C**, 2SSAP30-790 *Hesperotestudo crassiscutata*, costal in dorsal view; **D**, 2SSAP30-662 *Hesperotestudo crassiscutata*, costal, dorsal view; **E**, 2SSAP30-229, *Kinosternon* sp., left hyoplastron in dorsal view; **F**, Emydidae, genus indeterminate, nuchal in dorsal view; **G**, 2SSAP30-490 *Crocodylus acutus*, isolated tooth; **H**, **I**, 2SSAP30-676 *Crocodylus acutus*, left maxillary fragment in lateral and ventral view; **J**, 2SSAP30-807 in situ photograph of a probable proboscidean rib, bearing a crocodylian bite. Scale bar = 1.5 cm for A and B; 2 cm for E-I; and 3 cm for C and D. In J, the pointing object is a common pencil.

EUSUCHIA Huxley, 1875
 CROCODYLIA Laurenti, 1768
 CROCODYLIDAE Cuvier, 1807
Crocodylus Laurenti, 1768
Crocodylus acutus Cuvier, 1807
 (Figure 3G-J)

Referred material. 2SSAP30-340, 2SSAP30-348, 2SSAP30-481, 2SSAP30-490, 2SSAP30-499 incisive teeth; and 2SSAP30-676 left maxillary fragment.

Description. 2SSAP30-676 is an anterior portion of a left maxilla from a mature specimen. There are three complete alveoli and the mesial portion of a fourth alveolus, separated by wide grooves (maximum length between first and third alveolus is 43 mm). Although damaged, the fourth alveolus appears to be expanded and most likely, it accommodated the enlarged fifth maxillary tooth. Reposition teeth are preserved in the first and second alveoli. A number of isolated, non-associated teeth have also been recovered. They are long-crowned, slender and curved, from the anterior region of a cranium or mandible. Some osteoderms have also been recovered at the site. In addition, evidence of predatory or necrophagous activity

by a crocodylian is shown by tooth marks on a probable proboscidean rib 2SSAP30-807. In this specimen, traces of at least seven large conical teeth are preserved. As in *C. acutus*, the interdental spaces of the maxilla 2SSAP30-676 are wider than in *C. moreletti* and *C. rhombifer*, but not as wide as in *C. intermedius*. The isolated teeth are more robust than in the latter, being compatible with those of *C. acutus*. Therefore, these remains are assigned to *C. acutus*. **Remarks.** There is only one unconfirmed report of fossil *C. acutus*, of Quaternary age, located outside the geographically known range of this species in Florida, USA (Neill, 1971; Meylan, 1995). These materials consisted of isolated teeth; hence, positive identification is not possible. Consequently, specimens from Río Tomayate constitute the first non-dubious fossil record of *C. acutus*, taking the lineage of this species back to the Pleistocene. These remains also constitute the first report of a fossil crocodylian from El Salvador. Only two other fossil crocodylian records are known from Central America: remains of *C. moreletti* were described by Mook (1959) from a poorly known Pleistocene locality at Santa Amelia, Petén, Guatemala; and an unidentified crocodylian reported for the Cucaracha Local Fauna of Early Miocene age of Panama by Whitmore & Stewart (1965).

AVES Linnaeus, 1758
ANSERIFORMES Wagler, 1830
ANATIDAE Leach, 1820
Anser Linnaeus, 1758
cf. *Anser* sp.
(Figure 3A, B)

Referred material. 2SSAP30-853 left humerus, 2SSAP30-545 left clavicle.

Description. The humerus is well-preserved. In the proximal head, the area from the capital groove to the bicipital crest is missing; in the distal head, only the entepicondylar prominence is present. Length is 164 mm; width, at the level of the nutrient foramen, is 12 mm. 2SSAP30-545 is an almost complete left clavicle found in association with the humerus, and is referred to the same individual. Considering the proportions and overall morphology of this humerus, it is provisionally assigned to the genus *Anser*.

Remarks. The specimens represent the first record of a fossil bird in El Salvador and the first fossil record of the genus *Anser* in Central America. Only one previous record of fossil birds is known in the region, the anatid *Cairina moschata*, recovered from El Hatillo, Panama, of Late Pleistocene age (Gazin, 1956).

MAMMALIA Linnaeus 1758
XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
GLYPTODONTIDAE Burmeister, 1879
Glyptotherium Osborn, 1903
Glyptotherium arizonae Gidley, 1926
(Figure 4A, B, G-J)

Referred material. 2SSAP30-510 second upper molariform, 2SSAP30-889 third upper molariform, and a large number of osteoderms.

Description. 2SSAP30-889 is a right third molariform (; max. measurements: meso-distal length = 19.9 mm, labio-lingual length = 9.3 mm), its mesial and distal occlusal borders are damaged, and also the lingual border of the second lobe. This tooth closely resembles the third molariform of *G. arizonae* in specimen UMMP 38761 from Gilliland, Texas, as depicted by Gillette & Ray (1981, fig. 18a), though the Río Tomayate specimen possesses a less developed second lobe. 2SSAP30-510 is a left second molariform (maximum measurements: meso-distal length = 21.4 mm, labio-lingual length = 8.4 mm). This tooth is submolariform, its mesial and distal borders are slightly rounded, and the three lobes are less developed than in the reconstruction provided by Gillette & Ray (1981, fig. 18a) based on the broken third molariform of specimen UMMP 34826 from Gilliland.

Approximately two hundred carapace fragments have been recovered at Río Tomayate. In most specimens, central figures are subcircular and somewhat larger than the peripherals, resembling *Glyptotherium arizonae* and *G. cylindricum*. In this respect, these scutes differ from those of *G. texanum* and *G. mexicanum*, in which the central figure is much larger than the peripherals, and from *G. floridanum*, in which the central

figure and the peripherals are subequal in size (Gillette & Ray, 1981). In scutes from the interior and lateral regions of the carapace, central figures are slightly elevated above the plane of peripheral figures with a smooth medial depression; and in scutes from the posterior region, the central figure is flattened. The morphology of interior and lateral scutes distinguish the Río Tomayate material from *G. cylindricum*, where central figures are flattened or concave, therefore, making it possible to assign the new material to *G. arizonae*, in which interior and lateral scutes possess slightly convex central figures.

Remarks. The specimens represent the first record of *Glyptotherium arizonae* in Central America, and its southernmost occurrence. *Glyptotherium* remains were collected at both bonebeds in Río Tomayate, but are particularly abundant in the upper bonebed. It is possible that the osteoderms recovered at the upper bonebed and found in association with the molariform 2SSAP30-889, belong to a single individual, the remains of which could still be in situ. In addition, less diagnostic glyptodontid postcranial and fragmentary cranial material has been recovered at the lower bonebed. The genus *Glyptotherium* has also been reported for the Late Pleistocene localities of El Hormiguero, El Salvador; Yeroconte, Honduras; and El Hatillo, Panama (Gazin, 1956; Webb & Perrigo, 1984) but none of the material has been identified at the species level.

PHYLLOPHAGA Owen, 1842
MEGATHERIIDAE Gray, 1821
Eremotherium Spillman, 1948
Eremotherium sp.
(Figure 4E, F, K)

Referred material. 1SSAP6-25 cranium and jaw. Partially articulated specimen: 2SSAP30-718, 720-722, 724 vertebral epiphyses; 2SSAP30-725-729, 735, 736, 750 vertebrae; 2SSAP30-730, 733, 751-755 ribs.

Description. A complete cranium and mandible of *Eremotherium* was recovered. Unfortunately, the cranium was badly damaged during transportation from MUHNES to Museo Nacional de Antropología. As a result, only the mandible is available for study. The overall morphology of this mandible is characteristic of *Eremotherium*, in particular the shallow tooth-bearing ramus, and the articular process that lies below the plane of the alveolar border (*sensu de Iuliis & Cartelle, 1999*). A partially articulated adult individual was recovered in the upper bonebed; it is composed of an atlas and eight articulated cervical and thoracic vertebrae, with five associated ribs. This specimen remains in plaster jackets and it is the most complete individual of any taxon recovered at Río Tomayate.

Remarks. *Eremotherium* is a predominant taxon at Río Tomayate. In addition to the material listed here, several other fragmentary cranial and disarticulated postcranial remains have been collected, a large number of which are in plaster jackets or unprepared. In the lower bonebed, seven astragali were collected, indicating the presence of at least four individuals, a number that can be higher because some astragali are not completely

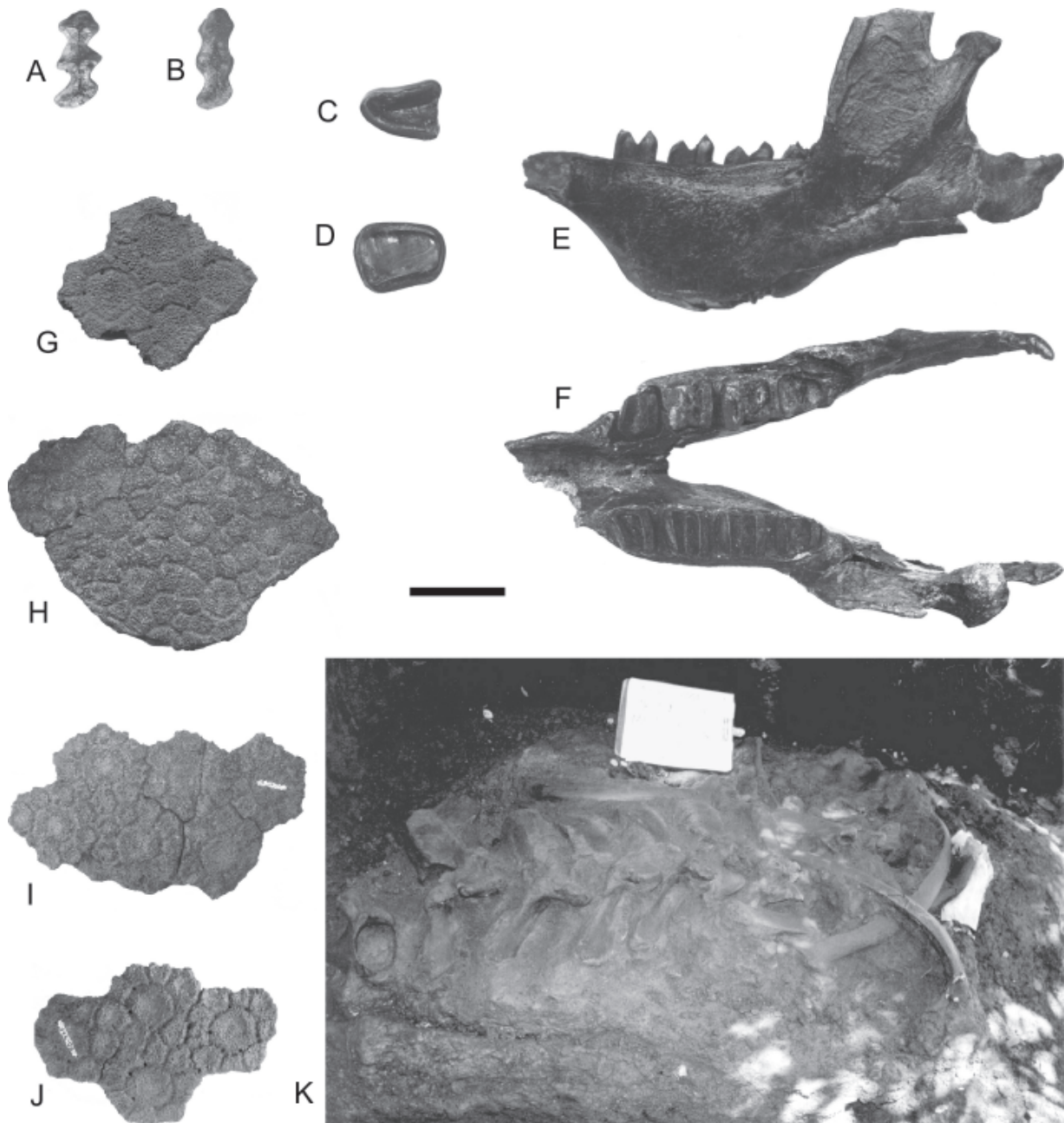


Figure 4. Xenarthrans from Río Tomayate. **A**, 2SSAP30-889 *Glyptotherium arizonae*, right third upper molariform in occlusal view; **B**, 2SSAP30-510 *Glyptotherium arizonae*, left second upper molariform in occlusal view; **C**, 2SSAP30-518 *Megalonyx* sp., right second molariform in occlusal view; **D**, 1SSAP6-65 *Megalonyx* sp. mandibular molariform in occlusal view; **E** and **F**, 1SSAP6-25 *Eremotherium* sp., mandible in left lateral and occlusal view; **G**, 2SSAP30-464 *Glyptotherium arizonae*, posterior carapace fragment; **H**, 2SSAP30-569 *Glyptotherium arizonae* interior carapace fragment; **I**, 2SSAP30-549 *Glyptotherium arizonae* lateral carapace fragment; **J**, MUHNES 70-964 *Glyptotherium arizonae* lateral carapace fragment; **K**, *in situ* photograph of a partially articulated *Eremotherium* sp. found at the upper bonebed, 2SSAP30-718, 720-722, 724-730, 733, 735, 736, 750-755. Scale bar = 25 mm for A-D, 5 m for G-J, and 87.5 mm for E and F.

preserved, being difficult to orientate them. Taking into consideration the probable Early Pleistocene age of Río Tomayate fauna (see discussion), it is likely that these megatheriid remains belong to the recently described Late Blancan-Irvingtonian species *E. eomigrans* (de Iuliis & Cartelle, 1999), since *E. laurillardi* seems to be restricted to the Late Pleistocene (Cartelle & de Iuliis, 1995; de Iuliis & Cartelle, 1999). Without conclusive morphological evidence, however, it is better not to assign this material to any particular species. Further study of the diagnostic

features of the postcranial material in the collection (abundant postcranial material remains unprepared) may clarify the identity of the Río Tomayate megatheriid.

Eremotherium specimens have also been recovered in El Salvador at Río Sisimico and El Hormiguero localities (Webb & Perrigo, 1984). Stirton & Gealey (1949) collected several giant sloth specimens at El Hormiguero quarry, and assigned them to the genus *Megatherium* but these were later assigned to *Eremotherium* by Webb & Perrigo (1984).

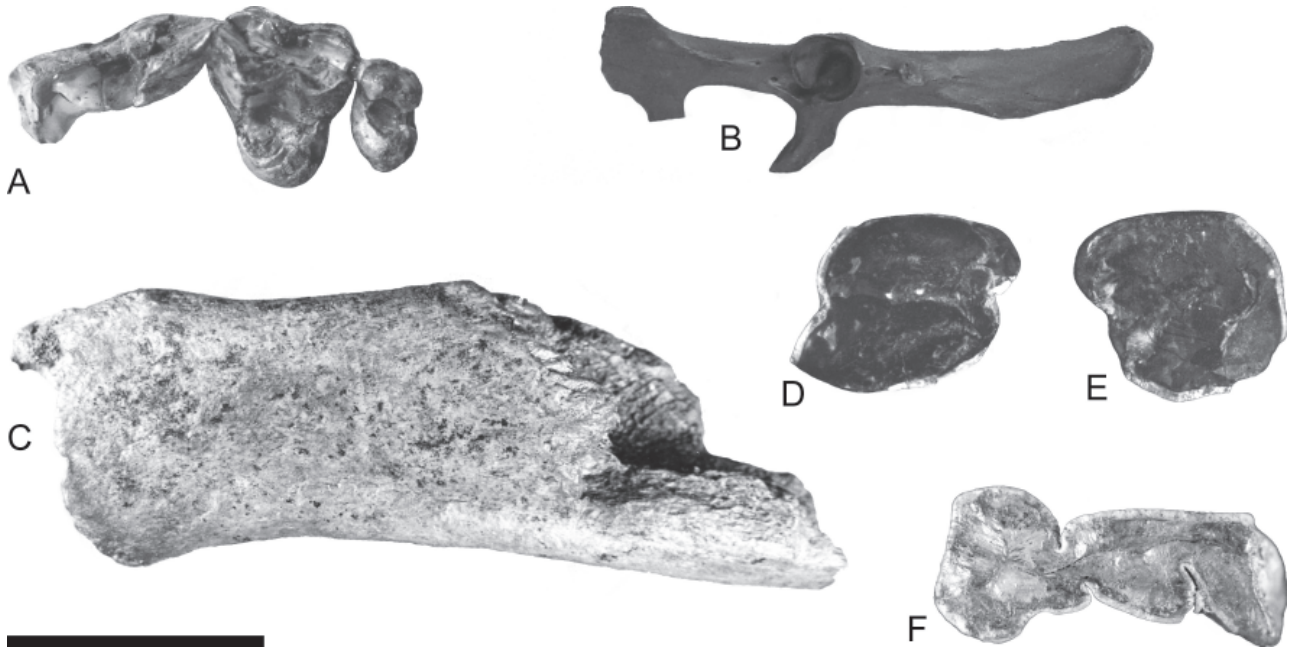


Figure 5. Canids, toxodontids and lagomorphs from Río Tomayate. **A**, 2SSAP30-734 aff. *Canis*, right maxilla in occlusal view; **B**, 1SSAP6-174 *Sylvilagus* sp., right pelvis in lateral view; **C**, 2SSAP30-80 indeterminate bone with evidence of gnawing; **D**, 2SSAP30-610 *Mixotoxodon larensis*, LP3 in occlusal view; **E**, the same, in root view; **F**, 2SSAP30-157 *Mixotoxodon larensis*, Rm1 in occlusal view. Scale bar = 30 mm for A-B, D-F; and 60 mm for C.

MEGALONYCHIDAE Gervais, 1885

Megalonyx Harlan, 1825

Megalonyx sp.

(Figure 4C, D)

Referred material. 1SSAP6-65 molariform, 2SSAP30-518 right second molariform.

Description. The teeth were not found in association. 2SSAP30-518 is a RM2, it is subtriangular in occlusal view and slightly recurved in labial view, its mesial border is convex and the distal border, concave (max. measurements: labio-lingual length, 21.5 mm; meso-distal length, 16 mm). 1SSAP6-65 is trapezoid in occlusal view and slightly recurved (max. measurements: labio-lingual length, 24.2 mm; meso-distal length, 8.3 mm).

Remarks. Two megalonychids are known from El Salvador, *Megalonyx obtusidens* and *Meizonyx salvadorensis* (Webb & Perrigo, 1985), both are endemic forms from Río Sisimico. The overall morphology of the specimens from Río Tomayate, however, precludes referring it to the primitive genus *Meizonyx*, which has no subtriangular or trapezoid teeth; or to *Megalonyx obtusidens*, in which all molariform teeth are ovoid in occlusal view. Although these specimens certainly belong to the genus *Megalonyx*, they are not diagnostic to the species level. Other Central American localities have yielded *Megalonyx* remains, all of Late Pleistocene age: El Bosque, Nicaragua (Page, 1978); Río Humuya, Honduras (Webb & Perrigo, 1984) and Santa Amelia, Guatemala (Woodburne, 1969); none of these specimens were identified to species level.

LAGOMORPHA Brandt, 1855

LEPORIDAE Gray, 1821

Sylvilagus Gray, 1867

Sylvilagus sp.

(Figure 5B)

Referred material. 1SSAP6-174 right pelvis.

Description. A well-preserved adult pelvis missing most of the pubis. It is distinguished from *Brachylagus* due to its larger size and from *Lepus* by a more slender ilium, a prominent posterior acetabular ridge and a thinner ischium with anteriorly expanded tuber ischii. Therefore, it is assigned to the cottontail rabbit, *Sylvilagus*.

Discussion. This *Sylvilagus* specimen represents the first record of a fossil lagomorph in El Salvador. At present, it is not possible to provide species-level identification based on a pelvis. The genus *Sylvilagus* has also been recorded at the Late Pleistocene site of Río Humuya, Honduras (Webb & Perrigo, 1984).

CARNIVORA Bowdich, 1821

CANIDAE Gray, 1821

Canis Linnaeus, 1758

aff. *Canis* sp.

(Figure 5A, C)

Referred material. 2SSAP30-734 partial left maxilla.

Description. This maxilla belongs to a large canid. It bears a P4, M1, and M2. P4 is damaged, lacking the surface of the mesial portion of the crown and all cusps. M1 is better

preserved, but lacks the paracone and metacone cusps. M2 is the only entirely preserved element in the dental series. Maximum measurements: P4-M2 length, 52 mm; P4 meso-distal length, 28.6 mm; M1 meso-distal length, 18.8 mm, labio-lingual length, 21.5 mm; M2 meso-distal length, 8.3 mm, labio-lingual length, 13.5 mm. Unidentified long bones exhibiting evidence of gnawing, presumably by a canid, were also recovered at Río Tomayate.

Remarks. The overall morphology of the teeth suggests affinities with a large species within the genus *Canis*. The teeth are considerable bigger than in *C. latrans*, *C. rufus* and most *C. lupus* specimens; and suggest to the larger *C. arbrusteri* and *C. dirus*. The hypocone of the M1 in the Río Tomayate specimen, however, is reduced, in contrast to that in *C. arbrusteri*. Furthermore, the M2 of this specimen is very slender and mesodistally compressed. This condition differs from the species within the genus *Canis*, and resembles that of South American forms such as *Theriodictis*. It is not possible at this time to identify the Río Tomayate canid with any certainty based on this fragmentary material. The possibility that this specimen represents a new taxon cannot be discarded.

NOTOUNGULATA Roth, 1903

TOXODONTIDAE Owen, 1845

Mixotoxodon van Frank, 1957

Mixotoxodon larensis van Frank, 1957

(Figure 5D-F)

Referred material. 2SSAP30-157 lower molar, 2SSAP30-610 upper premolar, 2SSAP30-674b fragment of a lower molar.

Description. The specimen 2SSAP30-157 is a well-preserved Rm1, lacking most of the root and a small portion of the hypoconid. Its maximum labio-lingual length, measured at the trigonid, is 18.5 mm and its maximum estimated mesio-distal length is 42 mm. This tooth has an overall morphology compatible with *Mixotoxodon*, including the presence of a deep meta-entoconid fold, also seen in the holotype (van Frank, 1957, fig. 8a) from the Pleistocene of Venezuela, and in the *Mixotoxodon* cranium from the Lower Pleistocene of Costa Rica (Lucas *et al.*, 1999, fig. 5a). The Río Tomayate specimen, however, differs in having a straighter labial margin of the talonid and a paraconid less developed meso-lingually than in the holotype (unfortunately the trigonid is not preserved in the Costa Rican specimen). The specimen 2SSAP30-610 is an LP3 almost indistinguishable from the P3 figured by van Frank (1957, fig. 9C), except for the presence in the former of a thin enamel band on the trigonid surface of the lingual fold. The absence of enamel in the lingual margin of the upper premolars is a diagnostic character of *Mixotoxodon larensis* (van Frank, 1957). The overall morphology of this P3 is, however, more similar to the P3 of *Mixotoxodon* than to the same element in *Toxodon* or any other well-known Pleistocene toxodontid. These materials are assigned to *Mixotoxodon larensis* despite minor, perhaps individual or geographical differences, observed in 2SSAP30-157 and 2SSAP30-610. 2SSAP30-674b is provisionally assigned to *Mixotoxodon*

larensis due to its presence in the same outcrop, though these specimens were not found in association.

Remarks. In El Salvador, *Mixotoxodon* has been recorded in the Early to Middle Pleistocene Río Sisimico site (Webb & Perrigo, 1984) and in the Late Pleistocene El Hormiguero site (van Frank, 1957). In Honduras, *Mixotoxodon* has been recorded in the Late Pleistocene sites of Yeroconte and Orillas del Humuya (Webb & Perrigo, 1984), and in Costa Rica, at the Early Pleistocene Bajo Barrantes site (Laurito Mora, 1993; Lucas *et al.*, 1999). From northern Nicaragua, Leidy (1886) described a Lm2 and a Ri3, collected at the Late Pleistocene Río El Chorro locality, which he assigned to the genus *Toxodon*. These teeth were discussed by van Frank (1957), who questioned Leidy's identification, particularly if the teeth were associated (information not provided by Leidy), which could allow *Mixotoxodon* affinity. The Nicaraguan molar (see van Frank, 1957, fig. 6a) is similar to 2SSAP30-157 if it is considered to be a Lm1 rather than a Lm2, which would support its assignment to *Mixotoxodon*. Another probable Nicaraguan toxodontid comes from the Late Pleistocene site of El Bosque (Espinoza Estrada, 1976; Page, 1978). The notoungulate mentioned by Woodburne (1969) from the Santa Amelia locality, Guatemala, must be a toxodontid. In La Coca, Panama, a toxodontid was referred to *Toxodon* by Gazin (1956), yet, because this discovery was prior to the proposal of the genus *Mixotoxodon* by van Frank (1957), it is likely that it is *Mixotoxodon*.

PROBOSCIDEA Illiger, 1811

PROBOSCIDEA Illiger, 1811

GOMPHOTHERIIDAE Hay, 1922

Cuvieronius Osborn, 1923

Cuvieronius tropicus (Cope, 1884)

(Figure 6)

Referred material. 2SSAP30-44 and 45 complete mandible; 2SSAP30-505 complete mandible; 1SSAP6-120 and 145 left mandible; 1SSAP6-1, 1SSAP6-24, 1SSAP6-126, 2SSAP30-468, 2SSAP30-674 right mandibles; 2SSAP30-202, 1SSAP6-2, 1SSAP6-9 tusks.

Description. The mandibles are generally brevirostrine, with a short symphysis. Molars display a moderately simple gomphotheriid pattern of enamel folding. When present, m2 are bunolophodont and m3 have four-and-a-half to five angular lophs. Opposite pretrite and postrite cusps alternate within the posterior lophs. Facets of wear display simple trefoils. The isolated tusks exhibit a distinctive spiral enamel band. Additional mandibular material, several isolated molars, deciduous premolars and abundant disarticulated postcranial remains are found at Río Tomayate; many still lie in plaster jackets. All these materials are likely to belong to *Cuvieronius*. All proboscidean material from Río Tomayate has been recovered from the lower bonebed.

Remarks. It seems evident, from the size disparity in the sample, that there is a large sexual dimorphism in *Cuvieronius* from Río Tomayate. Mandible 2SSAP30-44 and 45, here considered a female, belongs to a small individual of advanced



Figure 6. The proboscidean *Cuvieronius tropicus* from Río Tomayate. **A**, 2SSAP30-468 partial right mandible; **B**, 1SSAP6-2 tusk; **C**, 2SSAP30-593 mandible; **D**, 1SSAP6-1 right mandible; **E**, 2SSAP30-674 partial right mandible; **F**, 1SSAP6-9 tusk; **G**, 1SSAP6-126 partial right mandible; **H**, 2SSAP30-44 and 45 mandible; **I**, 1SSAP6-120 and 145 left mandible. All mandibles are in occlusal view. Scale bar = 100 mm.

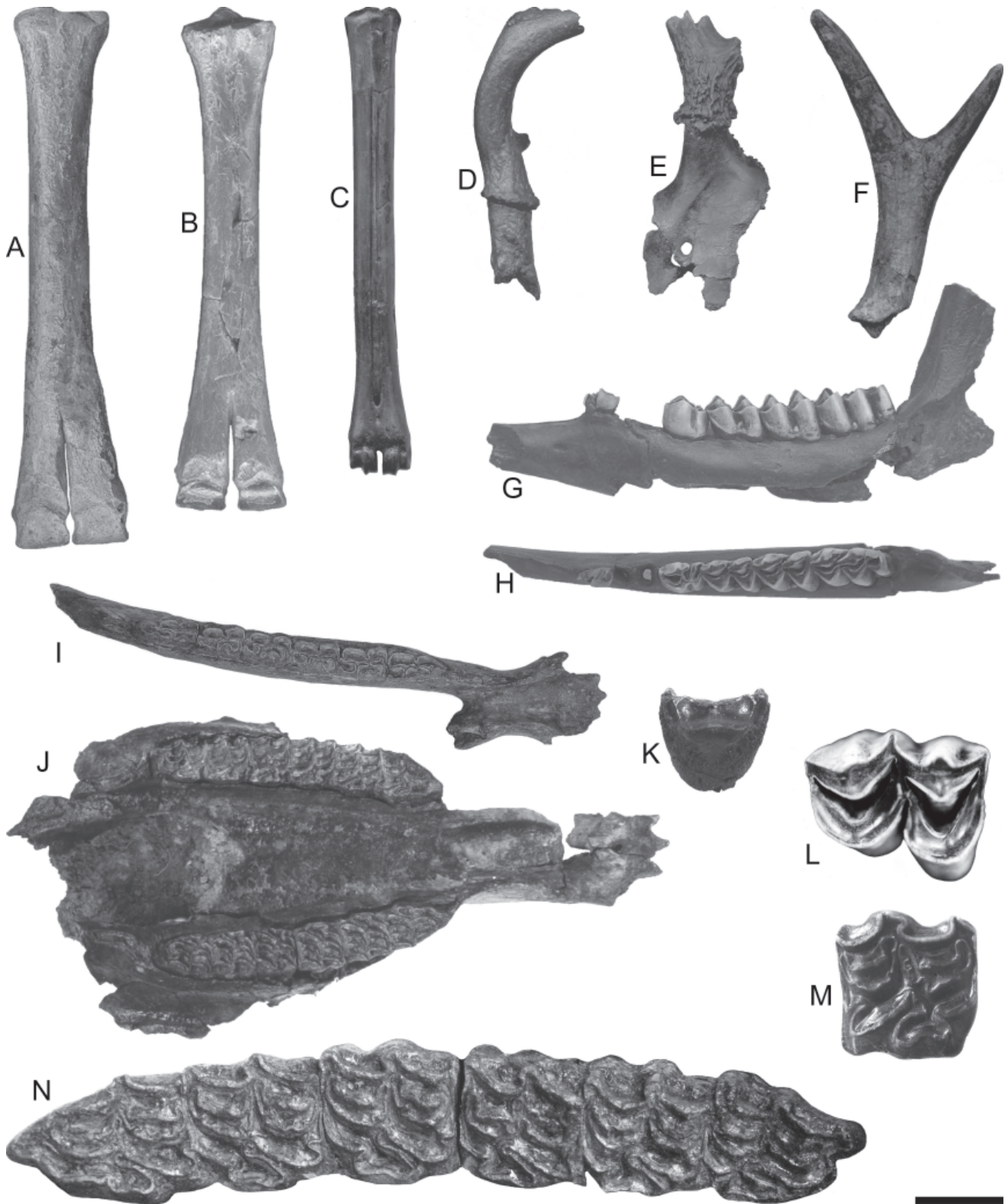


Figure 7. Artiodactyls and equids from Río Tomayate. **A, B**, 1SSAP6-144 *Palaeolama* sp., **A**, metacarpus in posterior view and **B**, metatarsus in anterior view; **C**, 2SSAP30-482 *Mazama* sp. metatarsus in anterior view; **D**, 2SSAP30-843 *Odocoileus* cf. *O. virginianus*, left antler; **E**, 2SSAP30-792 *Odocoileus* cf. *O. virginianus*, left antler and frontal bone in dorsal view, **F**, 2SSAP30-529 *Odocoileus* cf. *O. virginianus*, antler; **G**, 1SSAP6-23 *Mazama* sp., left mandibular ramus in lateral view; **H**, 1SSAP6-23 *Mazama* sp., left mandibular ramus in occlusal view; **I**, 2SSAP30-109 *Equus conversidens*, left mandible in occlusal view; **J**, 2SSAP30-135 *Equus conversidens*, cranium in palatal view; **K**, 2SSAP30-887 *Equus conversidens*, ungual phalanx in dorsal view; **L**, 2SSAP30-875 *Hemiauchenia* cf. *H. seymourensis*, RM3 in occlusal view; **M**, 2SSAP30-296 *Equus conversidens*, Lp4 in occlusal view; **N**, 2SSAP30-135 *Equus conversidens*, detail of left premaxillary and maxillary dentition. Scale bar is 50 mm for A-B, I-K; 35 mm for C-F, 20 mm for G, H; 17 mm for M, N; 13 mm for L.

age, as indicated by the solely presence of an m3 heavily worn. This mandible is much smaller than the immature 1SSAP6-126, a massive right ramus in which m1 has recently fallen, m2 is still present, and m3 has just erupted. Judging by the preserved dimensions of the incomplete 1SSAP6-126, the specimen suggests a male individual some 30% larger than 2SSAP30-44 and 45. A comparable degree of sexual dimorphism is known to occur in the modern *Elephas maximus* and *Loxodonta africana*, as well as in the fossil *Mammuthus primigenius* and *Mammot americanum* (Haynes, 1991). *Cuvieronius* is generally considered to be a “small-sized” proboscidean, nevertheless, the largest remains from Río Tomayate are comparable in size to those of the American mastodon *Mammot americanum*.

The status of *Cuvieronius* species in both North and South America is the subject of much nomenclatural debate. Recent authors recognize only one species in the genus, *C. tarijensis* (Ficcarelli *et al.*, 1995) or *C. hyodon* (Alberdi *et al.*, 2004; Prado *et al.*, 2003, 2005). These authors, however, restricted their discussion to South American material, and ignored North American species. Moreover, the name *C. tarijensis* was erroneously erected as a “new species” by Ficcarelli, and is in fact a *nomen nudum* (Cabrera, 1929; Hoffstetter, 1952). The species *C. hyodon* is also problematical. It is based on a single m2 that could be either referred to *Cuvieronius* or *Stegomastodon* (Montellano Ballesteros, 2002). Recently described Mexican material was referred to *C. tropicus* by Montellano Ballesteros (2002), based on the similarities in morphology and measurements with the holotype. In the same work, this author emphasized the ambiguous differences between *C. tropicus* and the species *C. oligobunis*, also from Mexico, although she did not formally synonymize them. The opinion that *C. hyodon* is a dubious species is endorsed here, and the name *C. tropicus* is preferred due to its name priority over *C. oligobunis* (ICZN, 1999).

Cuvieronius has been previously reported at El Salvador at Río Sisimico (Stirton & Gealey, 1949; Schmidt-Thomé, 1975; Webb & Perrigo, 1984), El Hormiguero (Webb & Perrigo, 1984) and an unidentified locality in La Unión (Stirton & Gealey, 1949). The genus is also known from several localities in the Pleistocene of Guatemala, Nicaragua, Costa Rica and Panama (Leidy, 1886; Gazin, 1956; Woodburne, 1969; Laurito Mora, 1988; Acuña Mesén & García Díaz, 1998; Lucas *et al.*, 1999).

PERISSODACTYLA Owen, 1848
EQUIDAE Gray, 1821
Equus Linnaeus, 1758
Equus conversidens Owen, 1869
(Figure 7I-K, M, N)

Referred material. 2SSAP30-135 cranium, 2SSAP30-109 left mandible and 2SSAP30-296 left fourth premolar.

Description. 2SSAP30-135 is a small cranium, the roof and the braincase are heavily weathered, the material is otherwise damaged by the recent intrusion of roots. All molars and premolars are present. No incisors are present, but the alveoli

are preserved, as well as the alveolus that accommodated the left canine. 2SSAP30-109 is a partial left mandible, found less than 0.5 m from the cranium and it is assigned to the same individual. The mandible is also damaged by intrusion of roots mostly located within the meckelian fossa. The ascending ramus is absent, as is the ventral surface of the horizontal ramus. The symphysis area is well preserved, and the entire anterior portion of the right ramus between the Rm2 and the symphysis is present. All left cheek teeth are preserved, including the canine. Left and right incisors are missing, but their alveoli are preserved, as well as the right canine alveolus. The specimens belong to an adult individual with pronounced wear on upper and lower teeth. 2SSAP30-296 is a well-preserved Lp4 of a young individual.

Several dental characters in the Río Tomayate specimens are listed the most common characters found by Reynoso Rosales & Montellano Ballesteros (1994) within the range of variation of *E. conversidens* specimens from Cedazo, Aguascalientes, Mexico. These include: (i) deep meso-metastyle valleys in premolars, but flattened in molars; (ii) prominent parastyles with flattened ends in premolars, and rounded ends in molars; (iii) pli paraconules present; pli caballin present in premolars, absent in molars; (iv) one quarter of the protocone placed anterior to the isthmus; (v) protocone with concave labial border and rounded ends; (vi) linguaflexid in wide “V” shape; (vii) acute metastylid end; (viii) isthmus in lower premolars complete, in lower molars intermediate; and (ix) absence of protostylid (for a discussion of these characters see the aforementioned authors). On this basis, the materials here presented are referred to *E. conversidens*, the common small horse from the Pleistocene of North America. Isolated postcranial remains are also present at Río Tomayate and these are provisionally referred to *E. conversidens*.

Remarks. The specimens represent the first confirmed report of *E. conversidens* in Central America, and its southernmost record. There are several reports of Pleistocene *Equus* remains for Honduras, El Salvador, Nicaragua, Costa Rica and Panama (Leidy, 1886; McGrew, 1942; Gazin, 1956; Espinosa Estrada, 1976; Webb & Perrigo, 1984; Lucas *et al.*, 1999). However, none was identified at species level, probably because of the fragmentary nature of most records, in addition to the problematical state of *Equus* nomenclature in North America.

ARTIODACTYLA Owen, 1848
RUMINANTIA Scopoli, 1777
CERVIDAE Gray, 1821
Odocoileus Rafinesque, 1832
Odocoileus cf. *O. virginianus* Zimmerman, 1780
(Figure 7D-F)

Referred material. 2SSAP30-529, 2SSAP30-792 and 2SSAP30-843 antlers.

Description. The specimens were not found in association and represent different individuals. 2SSAP30-792 is the base of a left antler and portion of the frontal bone, in which the dorsal margin of the orbit and the supraoccipital foramen can

be seen. 2SSAP30-529 is a two-pointed antler and 2SSAP30-843 is the base of a left antler. *Odocoileus* is the only deer known in Central America to possess branched antlers, on this basis, the specimens are assigned to this genus.

Remarks. The specimens represent the first fossil record of the white-tailed deer *Odocoileus* in El Salvador. No antlers recovered at Río Tomayate have been preserved completely enough to verify the branching pattern that distinguishes the two *Odocoileus* species. *O. virginianus*, however, is the only species present in Central America in modern times, with a wide distribution, from Canada to Bolivia, in contrast with the more limited geographic range of the mule deer *O. hemionus*, restricted to western North America. Hence, *Odocoileus* specimens from Río Tomayate are provisionally referred to *Odocoileus* cf. *O. virginianus*. Fossil *Odocoileus* remains, not identified to species level, have been recovered at Yeroconte, Honduras (Webb & Perrigo, 1984); El Hatillo, Panama (Gazin, 1956); and El Bosque, Nicaragua (Espinosa Estrada, 1976; Page, 1978).

Mazama Rafinesque, 1817

Mazama sp.

(Figure 7C, G, H)

Description. 1SSAP6-23 is a well-preserved left mandibular ramus of an adult individual, bearing p2, p4-m3 (see Table 1 for measurements). The area of the symphysis is missing as is most of the ventral surface of the dentary. Most of the coronoid process is present, but the mandibular condyle and the angular process are missing. In labial view, the mental foramen can be seen close to the p2. The specimen 2SSAP30-482 is a well-preserved adult right metatarsus (maximum measurements: length, 199 mm; width of proximal head, 25 mm; width of distal head, 26 mm).

Discussion. This represents the first non-dubious fossil record of the red brocket deer in Central America. Identification of the specimens from Río Tomayate as *Mazama* relies mainly on their measurements. These belong to adult individuals, as indicated by the presence of permanent dentition and fused epiphyses; they are smaller than the same elements in female *Odocoileus*, but comparable to those in female or male *Mazama* individuals. The remains, however, do not allow a specific identification. Interestingly, there are no historical records of the genus *Mazama* in El Salvador, except for

exceptional sightings in altitude forests close to the border with Honduras and Guatemala (Ricardo Ibarra, pers. comm.). *Mazama* material from the Late Pleistocene site at Santa Amelia, in Guatemala, cited by Woodburne (1969) were based on Barnum Brown's field notes and should be considered unconfirmed.

TYLOPODA Illiger, 1811

CAMELIDAE Gray, 1821

Palaeolama Gervais, 1867

Palaeolama sp.

(Figure 7A, B)

Referred material. 1SSAP6-144 a metatarsus and a metacarpus.

Description. These metapodial elements found in association, possess comparable dimensions and presumably belong to the same individual. The metacarpus maximum length is 309 mm, its proximal maximum width is 50 mm and its distal maximum width is 64 mm. The metatarsus maximum length is 287 mm, its proximal maximum width is 53 mm and its distal maximum width is 63 mm. Among Pleistocene llamas, relatively short and robust proportions are indicative of *Palaeolama* (Menézag & Jaureguizar, 1995; Webb & Stehli, 1995).

Remarks. These materials represent the first report of the genus *Palaeolama* in Central America. Llama material from Río Tomayate also includes some isolated teeth, and presumably several postcranial elements, not listed here. Taking into account the geographical position of El Salvador, the occurrence at Río Tomayate either of the North American *P. mirifica* or the South American *P. weddelli* seems equally parsimonious. According to Webb & Stehli (1995) the specimens of *P. weddelli* from the Middle Pleistocene Tarija deposits in southern Bolivia, differ mainly in being significantly larger than *P. mirifica* from the Lower Pleistocene Leisey Shell Pits of Florida, USA. When comparing measurements of 1SSAP6-144 with figured metapodials from both species (in Boule & Thevenin, 1920; Webb & Stehli, 1995), the Río Tomayate material shows to be much larger than *P. mirifica*, and even larger than *P. weddelli*. Nevertheless, the Río Tomayate metapodials are shorter than those of the North American *Alforjas*, a llama that also possesses robust limbs, and is restricted to the Miocene and Pliocene. Río Tomayate materials can be assigned to the genus *Palaeolama*, but their specific identification remains uncertain, and it is possible that they represent a new species.

Hemiauchenia Gervais & Ameghino, 1880

Hemiauchenia cf. *H. seymourensis* Hibbard & Dalquest, 1962

(Figure 7L)

Referred material. 2SSAP30-875, right third upper molar.

Description. Maximum measurements: meso-distal length, 26.1 mm; labio-lingual length, 21 mm. This molar is distinguished from *Palaeolama* due to its prominent hypsodonty, a typical character of *Hemiauchenia* (Webb & Stehli, 1995). The tooth is larger than the average M3 of *H. macrocephala*, indicating

TABLE 1. Maximum measurements (in mm) of *Mazama* left mandibular ramus (1SSAP6-23) from Río Tomayate.

		MESO-DISTAL LENGTH	LABIO-LINGUAL LENGTH
mandibular ramus	m3	19	8.7
	m2	14.5	8.5
	m1	13	8
	p2	11	7.4
	p2-m3	73	

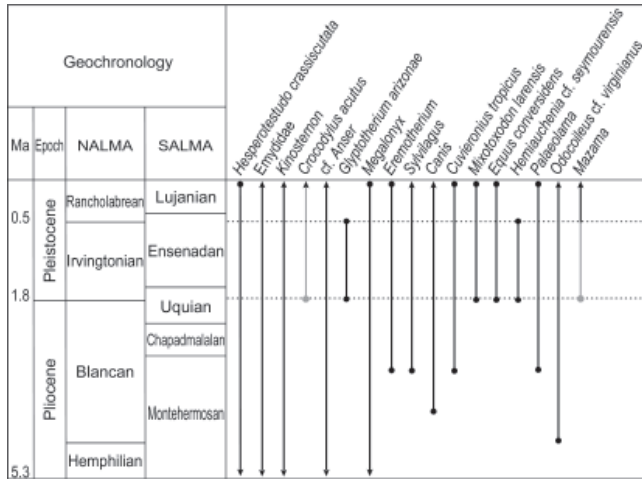


Figure 8. Chronological range in North America of vertebrates from Río Tomayate (from Tedford *et al.*, 1987; Meylan, 1995; Cartelle & de Iuliis, 1995; McKenna & Bell, 1997). The range of *Mazama* is based on its fossil record from South America (Webb, 2000). Gray lines represent proposed extended lineages for *C. acutus* and *Mazama* based on this study. Dashed lines delimit the age proposed for the Río Tomayate local fauna, Irvingtonian NALMA.

affinities with *H. seymourensis* or *H. blancoensis*. Although it may be difficult to differentiate between the Blancan *H. blancoensis* and the Irvingtonian *H. seymourensis* on the basis of a single molar, 2SSAP30-875 is comparable to *H. seymourensis* specimens from the Leisey Shell Pits, both in measurements and in the possession of a heavy layer of cementum that gives *H. seymourensis* “a distinctively blackened and roughened surface” Webb & Stehli (1995). The presence of Pleistocene-restricted taxa at Río Tomayate (see discussion below) also suggests that *H. seymourensis* rather than *H. blancoensis* is present at the site. The validity of the species *H. seymourensis*, however, has been recently questioned (Hulbert Jr., 2001), thus, the specific identification of the single tooth from Río Tomayate is provisional.

Remarks. This tooth represents the first record of the genus *Hemiauchenia* in Central America. Additional isolated teeth as well as postcranial remains found at Río Tomayate may be referable to either *Hemiauchenia* or *Palaeolama*.

DISCUSSION

The Tomayate local fauna substantially increases the record of Salvadorian fossil vertebrates. The large concentration of *Cuvieronius* material so far recovered matches the well known deposits of Tarija, Bolivia, and the seventeen taxa unearthed at Río Tomayate make this new local fauna more diverse than any other vertebrate locality of Central America (Table 2). The potential of the site is high, considering that only a small part of the visible bonebeds has been excavated. In spite of the richness of the new locality, it is remarkable that no small bones have been recovered, even though screen washing was attempted repeatedly. Proboscideans and megatheriids, the largest individuals recorded in the outcrop, are the dominant taxa at Río

Tomayate. In contrast, only one lagomorph bone has been identified, and no rodents or lizards so far have been found. Webb & Perrigo (1984) suggested a preservational bias against small vertebrates in Central American outcrops. This may be due to the high-energy nature of the depositional environment, perhaps related to the action of tropical storms, which could act as a selective mechanical control over the preservation of vertebrates in the region. Further work on the taphonomy of deposits such as this is needed to better understand this phenomenon.

Several taxa recovered at Río Tomayate occur across the Plio-Pleistocene boundary and, consequently, cannot be used for a precise correlation. The locality, however, includes taxa whose only confirmed records are in the Pleistocene (Figure 8); these are *Glyptotherium arizonae*, *Mixotoxodon larensis*, *Equus conversidens* and *Mazama* (Gillette & Ray, 1980; Reynoso Rosales & Montellano Ballesteros 1994; McKenna & Bell, 1997; Lucas *et al.*, 1999; Webb, 2000). A Pleistocene age is also supported indirectly by the presence of *Crocodylus acutus*, an extant taxon with no previously confirmed fossil record. At present, no typical Rancholabrean taxa have been recovered at Río Tomayate. On the other hand, the presence of *Hemiauchenia* cf. *H. seymourensis* and *Glyptotherium arizonae* points to Irvingtonian NALMA (Webb & Stehli, 1995; Gillette & Ray, 1980). As discussed above, the distinction between the species *H. seymourensis* from *H. blancoensis*, based on a single molar, may not be conclusive. However, none of these llamas reaches the Rancholabrean NALMA, and consequently they support an older age for Río Tomayate, which cannot be Blancan due to the presence of taxa restricted to the Pleistocene.

The recognition of an Irvingtonian NALMA for the Río Tomayate fauna leads to a comparison with the neighboring Río Sisimico fauna (see location in Figure 1B), the only other relatively well-known Central American fauna for which this age has been proposed (Webb & Perrigo, 1984, 1985). The main argument these authors used for assigning an Early to Middle Pleistocene age to Río Sisimico was the primitive morphology of the endemic megalonychids *Meizonyx salvadorensis* and *Megalonyx obtusidens*. As discussed above, *Megalonyx* molariforms found at Río Tomayate cannot be assigned to *M. obtusidens*; consequently, they are not useful for establishing a correlation between these local faunas. If the faunas of Río Tomayate and Río Sisimico were contemporaneous, the resultant assemblage would represent an unusual case of three megalonychid species living closely (the sites are some 50 km from each other). Río Sisimico and Río Tomayate share the presence of *Hesperotestudo*, *Eremotherium*, *Mixotoxodon larensis* and *Cuvieronius tropicus*. All four taxa are present in several Pleistocene Central American faunas (Table 2). Furthermore, the three mammals *Eremotherium*, *Mixotoxodon* and *Cuvieronius tropicus* are also found in association at El Hormiguero, El Salvador and El Chorro, Nicaragua; both are Rancholabrean localities (Stirton & Gealey, 1949; Leidy, 1886). There is insufficient evidence to assess whether the local faunas of Río Sisimico and Río Tomayate were strictly contemporaneous.

Table 2. The most representative Pleistocene local faunas of continental vertebrates in Central America (sites with four or more identified taxa) based on literature (Álvarez & Aguilar, 1957; Czaplewski *et al.*, 2003; Espinoza Estrada, 1976; Gazin, 1956; Leidy, 1886; Lucas *et al.*, 1999; Mook, 1959; Page, 1978; Reshetov, 1982; Rosen & Bailey, 1967; Seiffert, 1977; Stirton & Gealey, 1949; Webb, 1991; Webb & Perrigo, 1984, 1985; Woodburne, 1969) and this study. **Abbreviations:** C, Cebada Cave, Belize, Late Pleistocene-Holocene; SA, Santa Amelia, Guatemala, Late Pleistocene; S, Río Sisimico (also Barranca del Sisimico or Sisimite), El Salvador, Early-Middle Pleistocene; T, Río Tomayate, El Salvador, Early Pleistocene; H, El Hormiguero, El Salvador, Late Pleistocene; Y, Yeroconte, Honduras, Late Pleistocene, Honduras; HU, Río Humuya, Honduras, Late Pleistocene; B, El Bosque, Nicaragua, Late Pleistocene; CH, Río El Chorro, Nicaragua, Pleistocene; BH, Barra Honda, Costa Rica, Pleistocene; HA, El Hatillo, Panama, Late Pleistocene. Except for *Dicotyles tajacu* and *Crocodylus moreletti*, that were formally described, the faunal list from Santa Amelia must be considered provisional. The genus name *Stegomastodon* is used here instead of *Haplomastodon* following Prado *et al.* (2003, 2005).

	C	SA	S	T	H	Y	HU	B	CH	BH	HA
Teleostei											
<i>Poeciliopsis maldonadoi</i>			X								
<i>Poecilia sphenops</i>			X								
Anura											
<i>Rana sickenbergi</i>			X								
Cryptodira											
<i>Hesperotestudo</i> sp.			X		X						
<i>H. crassiscutata</i>				X							
Testudinidae indet.							X				
<i>Rhinoclemmys</i> sp.							X				
<i>Pseudemys</i> sp.										X	
Emydidae indet.				X							
<i>Kinosternon</i> sp.				X							
Chelonia indet.							X				
Crocodylomorpha											
<i>Crocodylus acutus</i>				X							
Anseriformes											
cf. <i>Anser</i> sp.				X							
<i>Cairina moschata</i>										X	
Xenarthra											
<i>Glyptotherium arizonae</i>				X							
<i>Glyptotherium</i> sp.					X	X					
<i>Glyptodon</i> sp.	X								X	X	
Hoplophorini indet.										?	
<i>Dasypus</i> sp.	X										
<i>Pampatherium</i> sp.	?										
<i>Mylodon</i> sp.	?										
<i>Paramylodon</i> sp.	?										
cf. <i>Glossotherium</i> sp.									X		
<i>Scelidotherium</i> sp.									?		
<i>Megalonyx obtusidens</i>			X								
<i>Mezonyx salvadorensis</i>			X								
<i>Megalonyx</i> sp.	X		X				X				
Megalonychidae indet.								X			
<i>Eremotherium laurillardii</i>	X				X	X	X	X	X		X
<i>Eremotherium</i> sp.			X	X							
Chiroptera											
<i>Pteronotus parnelli</i>			X								
<i>Desmodus draculae</i>	X										
<i>Tonatia saurophila</i>	X										
<i>Carollia</i> sp.	X										
<i>Artibeus lituratus</i>	X										
Chiroptera (cont.)											
<i>Centurio cenex</i>	X										
<i>Sturnira</i> sp.	X										
<i>Lasiurus blossevillii</i>	X										
<i>Lasiurus ega</i>	X										
Carnivora											
<i>Felis concolor</i>								X			
<i>Felis</i> sp.		X									
<i>Smilodon</i> sp.					X						
aff. <i>Canis</i>					X						
<i>Canis latrans</i>											X
<i>Tremarctos floridanus</i>	X										
Proboscidea											
<i>Cuvieronius tropicus</i>		?	X	X	X					X	X
<i>Stegomastodon waringi</i>											X
Gomphotheriidae indet.							X		X		
<i>Mammuthus</i> sp.										X	
<i>Mammuthus</i> cf. <i>columbi</i>								X			
Notoungulata											
<i>Mixotoxodon laevis</i>		?	X	X	X	X	X	?	X		
Perissodactyla											
<i>Equus</i> sp.					X	X	X		X	X	X
<i>E. conversidens</i>					X						
Equidae indet.	X								X		
<i>Tapirus</i> sp.	X										
Artiodactyla											
<i>Camelops</i> sp.							X				
<i>Palaeolama</i> sp.					X						
<i>Hemiauchenia</i> cf. <i>seymourensis</i>					X						
Camelidae indet.	X				X						
<i>Odocoileus</i> sp.							X	X			X
<i>O.</i> cf. <i>virginianus</i>					X						
<i>Mazama</i> sp.		?		X							
Cervidae indet.			X								
<i>Tayassu tajacu</i>	X										
Tayassuidae indet.											
<i>Bison</i> sp.		?			X					X	
Rodentia											
<i>Nechoerus pinckneyi</i>					X				X		X
<i>Hydrochoerus</i> sp.	X							X			
Lagomorpha											
<i>Sylvilagus</i> sp.				X				X			

No other local fauna in Central America or in the neighbouring Mexico and Colombia resembles that of Río Tomayate. For instance, the record of *Palaeolama* represents an isolated record between southern USA and Venezuela (alleged *Palaeolama* remains from central Mexico were transferred to *Hemiauchenia* sp. by Montellano, 1989). Likewise, the molar of *Hemiauchenia* reported from the new site represents the sole report of this genus between central Mexico and Bolivia. Some of the North American taxa present at the new site did not apparently cross the Panamanian isthmus during the GAFI, as was the case for *Equus*

conversidens and *Glyptotherium arizonae*, with their southernmost record at Río Tomayate. These taxa have not yet been found at other Central American localities. *Megalonyx*, also present at Río Tomayate, has no confirmed records in South America. On the other hand, there are no confirmed fossil discoveries of *Mazama* and toxodontids north of El Salvador and Guatemala, respectively (but see Polaco *et al.*, 2004 for a preliminary toxodontid report in central Mexico). No South American faunas, Ensenadan or Uquian, seem to be comparable to the new site. Only Irvingtonian local faunas resemble Río Tomayate. For the Irvingtonian

Gilliland Local Fauna, Texas, USA, Hibbard & Dalquest (1966) report six taxa that are present at Río Tomayate: a "large" *Hesperotestudo* (presumably *H. crassiscutata*), *G. arizonae*, *Cuvieronius tropicus*, *Sylvilagus*, *Hemiauchenia seymourensis* and *Odocoileus*. The local fauna most readily comparable to Río Tomayate, however, is probably the Leisey Shell Pits in Florida, USA (early Irvingtonian NALMA, Morgan & Hulbert Jr., 1995). The taxa common to Río Tomayate include *Kinosternon*, *Hesperotestudo crassiscutata*, *Glyptotherium arizonae*, *Eremotherium*, *Cuvieronius tropicus*, *Sylvilagus*, *Odocoileus*, *Hemiauchenia seymourensis* and *Palaeolama*. This faunal similarity supports an Irvingtonian NALMA for Río Tomayate.

The record of *Mazama* at Río Tomayate is significant. Except for an unconfirmed report in the Upper Pleistocene of Guatemala (Woodburne, 1969; see Table 2), there are no fossil records of *Mazama* in Central America or elsewhere in North America. However, this genus is present in the Upper Pleistocene of Brazil (de Paula Couto, 1980). Besides being the only non-dubious fossil record of *Mazama* outside South America, the material from Río Tomayate is also the oldest, supporting a Central American origin for this genus, a hypothesis previously proposed by Webb (2000).

The current absence of both *Palaeolama* and *Hemiauchenia* in the fossil record of other Central American countries is notorious. This may be considered a result of the lack of systematic prospecting in the area. However, isolated Pleistocene records are common in the region, specially those of Late Pleistocene age. Lardé-y-Larín (1950) reported some 30 such sites for El Salvador, and Lucas *et al.* (1999) listed a similar number of these sites for Costa Rica. A more intriguing hypothesis would be that *Palaeolama* and *Hemiauchenia* may have become extinct in Central America in the Late Pleistocene, explaining, thus, the current absence of fossils of these llamas from sites of younger age than Río Tomayate in the region. Except for Río Sisimico in El Salvador, and the small locality of Bajo Barrantes in Costa Rica that only yielded *Mixotoxodon larensis* (Laurito Mora, 1993; Lucas *et al.*, 1999), all well correlated Pleistocene sites in Central America are younger than Río Tomayate. Clearly more prospecting in the region is necessary to assess this hypothesis. At present, it is not clear if *Palaeolama* is a taxon that evolved in North America or in South America. The first appearance datum on both continents has a similar age, early Irvingtonian NALMA (Webb & Stehli, 1995) and Uquian SALMA (Marshall *et al.*, 1984; Mones, 1988) respectively. The record of this genus at Río Tomayate raises a third possibility, that *Palaeolama* evolved in Central America and dispersed in both directions.

The presence of large tortoises such as *Hesperotestudo crassiscutata*, is usually seen as an indicator of more xeric environments than at present (Preston, 1979; Hulbert Jr. & Pratt, 1998), a possibility also supported by the record of camelids in Río Tomayate. In El Salvador, a dry environment would be more likely during a glacial stage.

CONCLUSIONS

Río Tomayate is so far the richest vertebrate locality known in Central America and probably the largest known concentration of *Cuvieronius* in America. *Crocodylus acutus* has now fossil record, whereas *Equus conversidens* and *Glyptotherium arizonae* have their geographical ranges extended to Central America. The records of *Palaeolama* and *Hemiauchenia* eliminate "gaps" in the distribution of these fossil mammals in America. The age of the fauna is probably Early to Middle Pleistocene, as suggested by the overall similarity with North American Irvingtonian faunas, as well as the presence of *H. cf. H. seymourensis* and *G. arizonae*. A precise correlation with the nearby Río Sisimico local fauna, however, remains uncertain, due to the lack of shared index taxa. The first appearance datum of *Mazama* from Río Tomayate provides support to the hypothesis that this genus evolved in Central America and dispersed to South America. Some taxa, in particular *Hesperotestudo crassiscutata*, are indicative of an arid, perhaps colder environment for El Salvador at the time of accumulation of these fossils.

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