Late Cenozoic fossil mammals from the Chapala rift basin, Jalisco, Mexico

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LATE CENOZOIC FOSSIL MAMMALS FROM THE CHAPALA RIFT BASIN, JALISCO, MEXICO

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Abstract—In the Mexican state of Jalisco, south of Guadalajara, Lake Chapala (Lago de Chapala) is the largest natural freshwater lake in Mexico and is located in the inner graben of the Chapala rift basin. Most of the outcrops in the Chapala rift basin are Miocene-Pleistocene volcanic rocks, but more than 600 m of lacustrine sediments are exposed on its northern flank. Some of these sediments also underlie Lake Chapala and indicate that a large, permanent and relatively deep lake was present since the early Pliocene and subsequently dismembered by tectonics and volcanism. Fossil vertebrates from the Chapala rift basin are fishes, reptiles, birds and (mostly) mammals. Those collected from the bottom of Lake Chapala or its shorelines are an extensive assemblage of late Pleistocene (Rancholabrean) age that includes xenarthrans (*Holmesina* sp., *Glyptotherium* sp., *Nothrotheriops shastensis*, *Paramylodon* cf. *P. harlani*), carnivores (*Canis* cf. *C. latrans*, *C.* ?*lupus*, *Panthera* cf. *P. onca*, ?P. *atrox*), small rodents (*Neotoma* sp., *Sigmodon* sp.), a capybara (*Neochoerus aesopi*), a lagomorph (*Lepus* sp.), proboscideans (*Cuvieronius hyodon*, *Mammuthus imperator*), horses (*Equus conversidens*, *E.* cf. *E. francisci*, *E.* ?*excelsus*, *E. niobrarensis*), a tapir (*Tapirus* sp.), a peccary (*Platygonus compressus*), camels (*Camelops hesternus*, *Camelops* sp. and an indeterminate llamine), deer (cf. *Navahoceras* sp., *Odocoileus* sp., *Cervus* sp.), an antelope (*Tetrameryx shuleri*), and a bison (*Bison* sp.). The Chapala Formation, exposed north of Lake Chapala, yields some fossil mammals, particularly *Nannippus*, indicative of a Blancan age, and a skeleton of *Stegomastodon rexroadensis* from the lake bottom is also of Blancan age. Some other fossils from the lake bottom (e.g., *Cuvieronius*) may be of Irvingtonian age. Thus, the Chapala basin yields a succession of mammal-dominated vertebrate fossil assemblages of Blancan, Irvingtonian? and Rancholabrean age.

INTRODUCTION

Located in southern Jalisco, south of Guadalajara, Lake Chapala (Lago de Chapala) is the largest natural freshwater lake in Mexico (Fig. 1). Sitting at an elevation of 1535 m, the lake is 70 km long and 30 km wide, with an average water depth of 10 m. Lake Chapala is fed by the Rio Lerma, which flows into its eastern end, and the outlet is the Rio de Santiago, also at its eastern end, which flows to the Pacific. The lake is located in a late Cenozoic basin, the Chapala rift.

The Chapala rift extends east-west about 110 km and is 35-60 km wide north-south. It has an inner graben bounded by block faults that is 10-30 km wide and contains Lake Chapala. Most of the outcrops in the Chapala rift are Miocene-Pleistocene volcanic rocks (e.g., Allan, 1986; Allan et al., 1991; Delgado et al., 1995; Rosas-Elguera et al., 1997; Ferrari et al., 2000). However, more than 600 m of lacustrine sedimentary rocks are exposed on the northern flank of the Chapala basin. These strata and their diatom floras indicate a large, permanent and relatively deep lake since the early Pliocene that was subsequently dismembered by tectonics and volcanism (Michaud et al., 2000).

Fossil vertebrates from the Chapala basin first came to scientific attention during the 1950s, and have been published on sporadically since then. Here, I review the fossil mammal assemblages from the Chapala basin to conclude that they are of Blancan, Irvingtonian? and Rancholabrean age. This review is based on both the published and unpublished literature as well as study of the Chapala fossil collections housed in Guadalajara, Mexico.

Institutional abbreviations: CIT = California Institute of Technology (collection now at LACM); INAH-MRG = Instituto Nacional de Antropologia e Historia-Museo Regional de Guadalajara; LACM = Los Angeles County Museum of Natural History; MPG = Museo de Paleontologia de Guadalajara.

STRATIGRAPHY

The current Lake Chapala (Fig. 1) is a remnant of a much larger Plio-Pleistocene lake that Clements (1963) and Mitchell (1965) referred to as Lake Jalisco. Thus, the current lake sits in an extensional basin in which there have been lakes since at least the late Pliocene. Strata exposed on the northern flank of the Chapala rift basin are volcaniclastic to clastic fluvial and lacustrine deposits interbedded with volcanic ash beds and are referred to as the Chapala Formation (Palmer, 1926; Downs, 1958a; Clements, 1959; Delgado et al., 1995; Rosasa-Elquera et al., 1997; Ferrari et al., 2000).

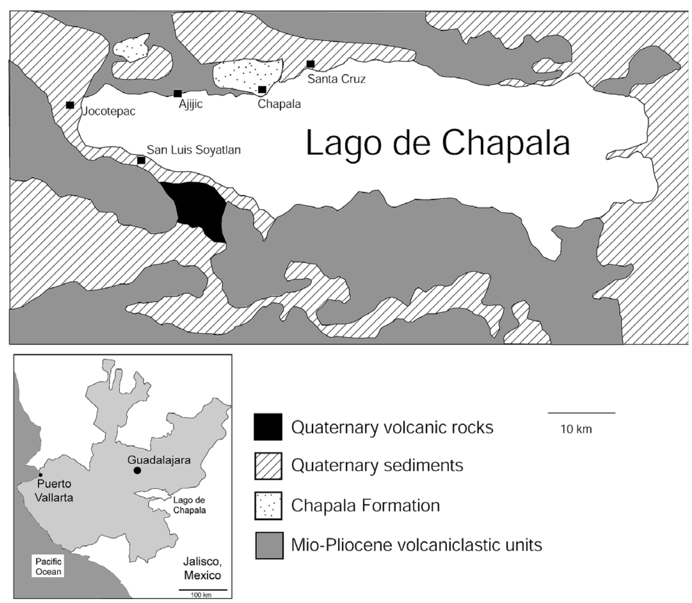

FIGURE 1. Geologic map around Lake Chapala (modified from Rufolo, 1998, fig. 3). Most of the fossil vertebrate localities are in the vicinity of the villages near/at the lake shore.

Palmer (1926, p. 127) introduced the term “Chapala beds” to refer to the shale-dominated strata that crop out north of Lake Chapala and dip ~20° to the northeast. He indicated the section at the village of Chapala should be considered the type section of the lithostratigraphic unit.

Clements (1959) described the Chapala Formatiion as "several hundred feet" of mostly claystone and shale, with minor sandstone, fine conglomerate, marl, diatomite and volcanic ash beds. He stated that the formation has a basal conglomerate that rests on Miocene rhyolite of the Chapala Group. Clements (1959) assigned the Chapala Formation a Plio-Pleistocene or early Pleistocene age based on the fossil mammals reported by Downs (1958a). However, he noted that the fossil vertebrates found on the lake floor are younger and not necessarily from the Chapala Formation.

Rosas-Elguera et al. (1997) identified the Chapala Formation on the northern side of Lake Chapala as lacustrine and fluvial sediments with some interbedded pyroclastic ash and pumice beds. The Chapala Formation overlies andesitic lava K/Ar dated at 3.4 ± 0.2 Ma (Delgado et al., 1995; Rosasa-Elquera et al., 1997; Ferrari et al., 2000). This places a maximum age on the Chapala Formation consistent with its fossil vertebrate record, which indicates an age that could be as old as late Blancan (~ 3 Ma).

The stratigraphic context of the vertebrate fossils from the bottom of Lake Chapala (Fig. 2) remains problematic. No lithostratigraphic name is applied to the bedrock under the lake, though it is most likely Chapala Formation on one or more fault blocks. Most of the mammal fossils from the lake bottom are obviously late Pleistocene (Rancholabrean) and probably derive from the youngest bedrock on the lake bottom and/or have been reworked from old shoreline deposits of the lake. However, at least one fossil from the lake bottom, a skeleton of *Stegomastodon rexroadensis*, is older than Rancholabrean, and some of the other fossils (for example, the gomphothere *Cuvieronius*) could also be older than Rancholabrean. I lack the data to resolve these stratigraphic uncertainties, so: (1) fossils from the Chapala Formation north of the lake are treated as a biostratigraphic assemblage separate from the lake-bottom fossils; (2) almost all the lake-bottom fossils are regarded as a single assemblage of Rancholabrean age; (3) the *Stegomastodon* skeleton from the lake bottom is of likely Blancan age; and (4) it is possible that some of the fossils from the lake bottom are of Irvingtonian age.

FIGURE 2. Photograph of dry lake bottom of Lake Chapala near Ajijic, Vertebrate fossil are derived from the clay-dominated sediments of the former lake bottom in the foreground.

PREVIOUS PALEONTOLOGICAL STUDIES

During the 1950s, fossil vertebrates from the Chapala basin first came to scientific attention. This was largely because the drainage of water from Lake Chapala for irrigation during 1951-1954 exposed hundreds of fossil bones on the emergent lake bottom. Thus, in 1955-1956, the LACM, with the collaboration of Mexican scientists (especially Federico Solorzano of Guadalajara) made an extensive effort to collect vertebrate fossils from Lake Chapala and its shores. Downs (1958a, b) summarized these efforts and reported catfish (cf. *Ictalurus*), giant armadillo (cf. *Holmesina* sp.), sloth (*Nothrotherium* sp.), capybara (cf. *Neochoerus* sp.), dog (*Canis* sp.), cat (*Felis* cf. *F.* (*Jaguarius*) sp.), gomphothere (*Cuvieronius* sp.), mammoth (*Mammuthus* sp.), horse (*Equus* sp. near *E. mexicanus*, *E.* cf. *E. conversidens*), peccary (*Platygonus* sp.), camel (*Camelops* sp.), antelope (*Tetrameryx* sp. near *T. shuleri*), deer (cf. *Cervus* sp., cf. *Odocoileus* sp.) and bison (*Bison* (*Platycerobison*) cf. *B.* (*P.*) *cheneyi*) based on fossils collected on the lake bottom. He also reported fish, turtle, crocodile, probable Mexican cormorant and flamingo, *Cuvieronius*, *Equus*, *Nannippus* and a large peccary from the Chapala Formation north of the lake. The lists of fossil mammals from Lake Chapala of Silva (1969) and Silva-Barcenas (1969) are based on Downs (1958a).

Downs (1958a) noted that the black bones collected from the lake bottom are probably the same age as the lighter-colored fossil bones (with the exception of the fossils of *Nannippus*) from the outcrops north of the lake. He assigned the lake bottom bones a late Pleistocene age. He noted that their black color is due to impregnation of the bones by colloidal manganese, a process still occurring at present (Downs, 1958b). Clements (1963) reviewed Downs' conclusions, stressing that fossil vertebrates from the Chapala Formation found on the northern shore of the lake include *Nannippus*, indicative of a Pliocene age.

During the 1960s-1980s, various articles were published on the fossil fishes and fossil birds of the Chapala basin (see below). However, little further discussion of the fossil mammals (other than Alvarez, 1971) appeared until the unpublished masters thesis of Rufolo (1998).

Rufolo (1998) described and illustrated fossil mammals from the Chapala basin in the collection of the LACM, documenting taxa of xenarthrans (cf. *Holmesina* sp., *Glyptotherium* sp., *Nothrotheriops shastensis*, *Paramylodon* cf. *P. harlani*), carnivores (*Canis* cf. *C. latrans*, *C.* ?*lupus*, *Panthera* cf. *P. onca*, ?P. *atrox*), a lagomorph (*Lepus* sp.), a capybara (*Neochoerus* ?*pinckneyi*), horses (*Nannippus* cf. *N. peninsulatus*, *Equus conversidens*, *E.* cf. *E. francisci*, *E.* ?*excelsus*, *E. niobrarensis*), a tapir (*Tapirus* sp.), a peccary (?*Platygonus* sp.), camels (*Camelops* sp. and an indeterminate llamine), deer (cf. *Navahoceras* sp., *Odocoileus* sp., *Cervus* sp.), an antelope (*Tetrameryx shuleri*), a bison (*Bison* sp.) and proboscideans (*Cuvieronius* sp., *Mammuthus* cf. *M. columbi*). Rufolo (1998) recognized the stratigraphic mixture of this assemblage and posited that it includes some late Blancan, possible Irvingtonian and mostly Rancholabrean taxa.

Lucas (2003) reviewed the proboscidean record from the Chapala basin based largely on collections in the INAH-MRG and MPG. He reported three proboscideans from the lake bottom: *Stegomastodon rexroadensis*, *Cuvieronius tropicus* and *Mammuthus imperator*. He concluded that Blancan, Irvingtonian and Rancholabrean taxa are mixed in the Lake Chapala vertebrate assemblage, and that among the proboscideans, only the *Cuvieronius* and *Mammuthus* records are coeval.

Alberdi and Corona-M. (2005) documented gomphotheriid proboscideans from Lake Chapala, also based on the INAH-MRG and MPG collections. They identified *Rhynchotherium*, *Cuvieronius* and *Stegomastodon* from the lake bottom assemblage.

FOSSIL LOCALITIES

One of the greatest limitations of the collections of fossil vertebrates from the Chapala basin is the general lack of detailed locality and stratigraphic provenance. This is because most of the specimens were collected from the lake bottom, often in fisherman's nets, and many were purchased from local residents (Downs, 1958a, b; Clements, 1963; Rufolo, 1998). Almost all of the fossils collected in this way lack detailed geographic provenance, and their stratigraphic origin cannot be more precisely determined than from the lake bottom, where they may be autochthonous to submerged sediment or may have been transported and redeposited within the lake. Nevertheless, as most previous workers concluded, almost all of the fossil vertebrates from the bottom of Lake Chapala represent a single biostratigraphic assemblage of Rancholabrean age. However, some of the fossils from the lake bottom as well as some of the fossils collected north of Lake Chapala, in the Chapala Formation outcrops, represent taxa that suggest older, Blancan, and possibly Irvingtonian, ages as well.

With a few exceptions (indicated below), all of the vertebrate fossils from the Chapala basin in the INAH-MRG and the MPG collections are simply labeled as "Chapala" or "Lago de Chapala." The LACM collection has somewhat more detailed provenance, which was discussed at length by Rufolo (1998). Thus, most of the LACM localities (Fig. 1) are for specimens from the lake bottom: 1130 (lake bottom and shore between Chapala and Ajijic), 1133 (= CIT locality 485, which is the former lake bottom 3.5 km west of San Luis Soyatlan), 1135 (a general locality for the lake bottom), 1135a (the lake bottom near Santa Cruz) and 65111 (the lake bottom between Chapala and Santa Cruz).

Two localities (LACM 1129 and 1176) are from the Chapala Formation about 2 km north of the town of Chapala. They yield the characteristically late Blancan horse *Nannippus peninsulatus*. However, LACM records also indicate the following taxa from LACM locality 1129 (based on Rufolo's identifications): *Canis* cf. *C.latrans*, Proboscidea, *Equus conversidens*, *Equus* sp., Tayassuidae, and a llamine camel. Locality 1176 also yields *Equus* sp. and *Canis* cf. *C. lupus*. It seems doubtful that all of these taxa are co-eval (*Nannippus* and *Equus conversidens*, for example), so the fossils collected from the Chapala Formation north of the lake also appear to represent a temporally mixed assemblage.

VERTEBRATE TAXA

Fishes

Alvarez (1966), Alvarez and Arriola (1972), Barbour (1973), Smith et al. (1975), Cavender and Miller (1982) and Smith (1987) documented the fossil fishes from the Chapala basin (Table 1). Most of them came from a gravel pit ~5 km west of Jocotopec on Highway 15. The majority of fossil fish taxa from the Chapala basin are still extant in the lake. However, Cavender and Miller (1982) drew attention to the fossil salmon they described (*Salmo australis*) from a sandy bed near Ajijic as an indicator of previous colder water conditions.

Amphibians and Reptiles

Fossils of frogs, snakes, turtles and crocodiles are present in the Chapala vertebrate fossil collections but have not been studied and published in detail. The list presented here (Table 1) is from Solorzano (2002).

Birds

Howard (1969) and Alvarez (1977) described fossil birds from the Chapala basin (Table 1). Howard (1969) described the fossil birds collected by the LACM, primarily from the lake bottom. Alvarez (1977) described fossil birds found in the gravel pit near Jocotopec that yielded the fossil fishes described by Smith et al. (1975). The Chapala avifauna (Table 1) is dominated by water birds, especially by foot-propelled diving birds, including anhingas, cormorants and ducks.

Mammals

Rufolo (1998) provided the most extensive documentation to date of fossil mammals from the Chapala basin. His work was based on 414 catalogued specimens in the LACM collection, mostly collected or purchased by T. R. Downs and associates during the 1950s (e.g., Downs, 1958a, b). I have not restudied this collection, so my comments on it are a summary of Rufolo's excellent but unpublished work. Here, I also document fossil mammals from the Chapala basin in the INAH-MRG and the MPG collections (Figs. 3-6) to arrive at a complete list of mammal taxa from the bottom of Lake Chapala (Table 1).

Holmesina

Rufolo (1998, fig. 4) tentatively identified a single osteoderm of the movable band of the carapace as a pampathere, cf. *Holmesina*. This osteoderm has a distinct marginal band, a raised central keel and has a complex surface texture, as in *Holmesina* osteoderms (Edmund, 1985a, b, 1987).

Glyptotherium

Rufolo (1998, fig. 5) assigned a single astragalus to the glyptodont *Glyptotherium*, as it resembles astragali of this genus (Gillette and Ray, 1981) and is not *Holmesina* (Hulbert and Morgan, 1993).

Sloths

Rufolo (1998, fig. 6) assigned a left dentary with molariforms 2 and 3 to the Shasta ground sloth, *Nothrotheriops shastense*. This dentary lacks canininform teeth and has vertically aligned grooves on both the lateral and medial surfaces of the teeth, justifying the assignment (Stock, 1925; Miller, 1971). An incomplete tibia and fibula were assigned to *Paramylodon* cf. *P. harlani* by Rufolo (1998). Sloths are thus rare in the Chapala collections.

Canids

Nowak (1979, p. 106, 115) suggested that the taxon Downs (1958a) identified as "*Canis* sp., large wolf" might be the dire wolf, *C. dirus*. Dundas (1999) took this to be a confirmed record of *C. dirus* at Lake Chapala, but it is not (Rufolo, 1998).

An incomplete canine and left M2 were identified by Rufolo (1998) as *Canis*, possibly the coyote *C. latrans*. More complete specimens—a left dentary with p2-m2 and phalanx—of a larger canid were tentatively assigned by him to *Canis* ?*lupus*.

Felids

As with the canids, Rufolo (1998) had meager material of cats available to him in the LACM collection. Thus, he assigned an incomplete dentary with part of the canine and roots of p3-4 to *Panthera* cf. *P. onca*, and a humerus of a larger cat to ?*Panthera atrox*.

Small rodents

Barbour (1973) and Smith et al. (1975), in documenting the fossil fishes from the gravel pit ~5 km west of Jocotopec on Highway 15 (see above), also listed fossil records of *Neotoma* sp. and *Sigmodon* sp. from this site, but these remain to be documented.

Neochoerus

Fossils of capybaras from the Chapala basin were originally assigned to the extant species *Hydrochoerus magnus* by Peters (1951). Alvarez (1971) documented premolar variation in a sample of capybara fossils from Lake Chapala. He assigned them to *Hydrochoerus* sp., but Mones (1991, p. 62) identified the Chapala caybaras as *Neochoerus aesopi*.

Rufolo (1998, fig. 8) only had a single left dentary fragment with p4-m1 of a capybara available to him in the LACM Chapala collection, and he identified it as *Neochoerus* ?*pinckneyi*. I follow Mones (1991) in assigning the Chapala capybaras to *N. aesopi* (Table 1), though *N. pinckneyi* may be the appropriate name (G. S. Morgan, written commun., 2008).

Leporid

A single calcaneum identified as cf. *Lepus* sp. by Rufolo (1998) is one of the rare fossils of a small mammal in the LACM Chapala collection.

Cuvieronius

Downs (1958a) first reported *Cuvieronius* sp. from the Chapala lake bottom collections. Rufolo (1998) referred various tusk fragments with spiral enamel bands and isolated cheek teeth in the LACM collec-

TABLE 1. Fossil vertebrate taxa from the Lake Chapala assemblage, late Pleistocene (Rancholabrean). These are the taxa based on fossils collected in the lake bottom or along its margins.

OSTEICHTHYES

Cyprinidae:
- *Algansea tincella*
- *Algansea popoche*
- *Yuriria alta*

Catostomidae:
- *Moxostoma robustum*

Ictaluridae:
- *Ictalurus dugesi*
- *Ictalurus spodius*
- *Alloophorus robustus*
- *Ameca splendens*
- *Chapalichthys encaustus*
- *Goodea atripinnis*
- *Xenotoca* sp.

Atherinidae:
- *Chirostoma lucius*
- *Chirostoma promelas*
- *Salmo australis*

Centrarchidae:
- *Micropterus relictus*

AMPHIBIA
- *Rana* sp.

REPTILIA

Testudines:
- *Terrapene culturatus*
- *Kinosternon hirtipes*
- *Kinosternon integrum*
- *Pseudemys* sp.

Ophidia:
- *Thamnophis* sp.
- *Trimorphodon tau*
- *Colubridae*

Crocodylia:
- *Crocodylus* sp.

AVES

Podicipeididae:
- *Aechmophorus occidentalis*
- *Podiceps caspicus*
- *Podylimbus podiceps*

Ardeidae:
- *Tigrisoma*(?) sp.

Phalacrocoracidae:
- *Phalacrocorax chapalensis*
- *Phalacrocorax olivaceus*
- *Phalacrocorax goletensis*
- *Phalacrocorax* sp.

Anhingidae:
- *Anhinga anhinga*

Anatidae:
- *Aythya americana*
- *Aythya marila*
- *Aythya* sp.
- *Oxyura zapatanima*

Scolopacidae:
- *Calidris fuscollis*

Icteridae:
- *Sturnella*(?) sp.

MAMMALIA

Edentata:
- *Holmesina* sp.
- *Glyptotherium* sp.
- *Nothrotheriops shastense*
- *Paramylodon* cf. *P. harlani*

Carnivora:
- *Canis latrans*
- *Canis* ?*lupus*
- *Panthera* cf. *P. onca*
- ?*Panthera atrox*

Rodentia:
- *Sigmodon* sp.
- *Neotoma* sp.
- *Neochoerus aesopi*

Lagomorpha:
- cf. *Lepus* sp.

Proboscidea:
- *Cuvieronius hyodon*
- *Mammuthus imperator*

Perissodactyla:
- *Equus conversidens*
- *Equus* ?*excelsus*
- *Equus* cf. *E. francisi*
- *Equus niobrarensis*
- *Tapirus* sp.

Artiodactyla:
- *Platygonus compressus*
- *Camelops* sp.
- *Camelops hesternus*
- Llamine
- *Cervus* sp.
- *Odocoileus* sp.
- ?*Navahoceras* sp.
- *Tetrameryx shuleri*
- *Bison antiquus antiquus*
- *Bison alaskensis*

tion to *Cuvieronius* sp. Based on Chapala specimens in the INAH MRG and MPG collections, Lucas (2003) identified *Cuvieronius tropicus,* and Alberdi and Corona-M. (2005) reported *Cuvieronius* sp.

I assign the Chapala *Cuvieronius* (e.g., Fig. 3, Table 2) to *C. hyodon* following Lucas (this volume), who argues that the genus is monospecific. The MPG has the following specimens of *C. hyodon* from the Chapala lake bottom: MPG 2, right dentary fragment with m2; 4, right m2; 5, right M3; 6, palate with left M1-2 and right M2; 8, incomplete left m2; 11, tusk fragments with spiral enamel bands; 12, palate with left and right M2-3; 720, left dentary fragment with dp2-3; and uncatalogued left dentary fragment with m2. The INAH-MRG collection has an uncatalogued palate with left and right M2-3 (Fig. 3A), an incomplete skull with left M2-3 and right M3 (Fig. 3B), dentary fragment with right m2-3 (Fig. 3C), an incomplete tusk, an ulna, and a right m3 (Fig. 3D). Note that the isolated teeth referred here to *Cuvieronius* could, strictly speaking, belong to *Rhynchotherium*. However, all lower jaws referred here are diagnostically *Cuvieronius*, so it seems unlikely *Rhynchotherium* is present in the Chapala collections.

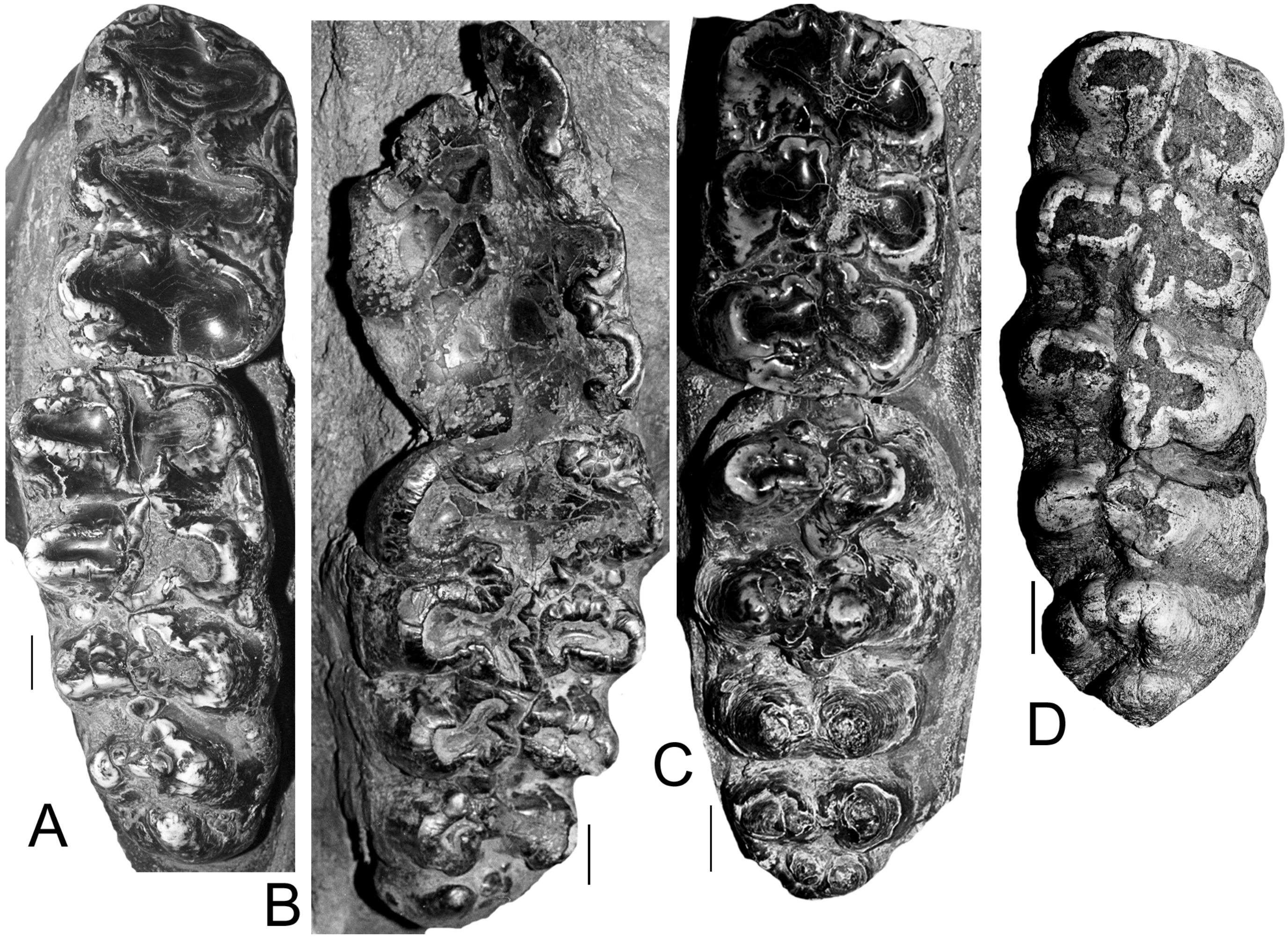

FIGURE 3. Selected specimens of *Cuvieronius hyodon* from the lake bottom sediments of Lake Chapala. All are uncatalogued specimens in the INAH-MRG collection. **A**, Left M2-3 (Ajijic). **B**, Right M2-3. **C**, Right m2-3. **D**, Right m3 (Ajijic). Bar scales = 2 cm.

TABLE 2. Measurements (in mm) of cheek teeth of *Cuvieronius hyodon* from the lake bottom sediments of Lake Chapala in the INAH-MRG and MPG collections.

Specimen	**m2l**	**m2w**	**m3l**	**m3w**	**M2l**	**M2w**	**M3l**	**M3w**
INAH uncat			198	82				
INAH uncat					126	84	173	85
INAH uncat	131	68	202	82				
MPG 2	110	67						
MPG 4	138	79						
MPG 5			199	94				
MPG 6					101	65		
MPG 712			193	87				
MPG 726			179	82				
MPG uncat					120	79	164	81
MPG uncat							201	91
Mean	126	71	194	85	116	76	179	86

Indeed, Alberdi and Corona-M. (2005) identified an isolated uncatalogued right M3 from Ajijic in the MPG collection as *Rhynchotherium* sp., and also assigned MPG 709 (a left m3) and MRG 10-295050 (Alberdi and Corona-M., 2005, fig. 2e) to *Rhynchotherium*. However, isolated molars cannot be used to distinguish *Rhynchotherium* from *Cuvieronius* (see Lucas and Morgan, this volume), and the tusk is more likely an upper tusk of *Cuvieronius*. Therefore, I do not identify *Rhynchotherium* in the Chapala collections in Guadalajara.

Stegomastodon

A nearly complete skeleton of *Stegomastodon* in the MPG was collected at Santa Cruz de la Soledad from sediment on the Chapala lake bottom (Alberdi et al., 2002; Lucas, 2003). The skull has long, nearly straight tusks that lack enamel bands. The m3 has five lophids with relatively simple trefoils. This is a primitive *Stegomastodon* assignable to *S. primitivus* (= *S. rexroadensis*), and thus arguably a Blancan fossil as it is much more primitive than Irvingtonian fossils of *Stegomastodon* (cf. Lucas et al., 1999, 2000). This fossil will be described elsewhere.

Mammuthus

Rufolo (1998) assigned tusk fragments and cheek teeth in the LACM collection to *Mammuthus* cf. *M. columbi*. Lucas (2003) assigned mammoth fossils from Lake Chapala in the INAH-MRG and MPG collections to *M. imperator*.

The most abundant mammal fossils from the Chapala lake bottom in the MPG collection are isolated teeth of *Mammuthus imperator* catalogued as MPG VF-3, 4, 5(Fig. 4D), 6 (Fig. 4B), 7 (Fig. 4A), 8 (Fig. 4E), 9, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 113, 796, 797, 799, 800, 802, 806, 807, 810 and 12 uncatalogued molars. The INAH-MRG collection has three uncatalogued vertebrae and a rib as well as 10-295055, a right dentary fragment with m3 (Fig. 4C). Measurements of these molars (Table 3) are within the

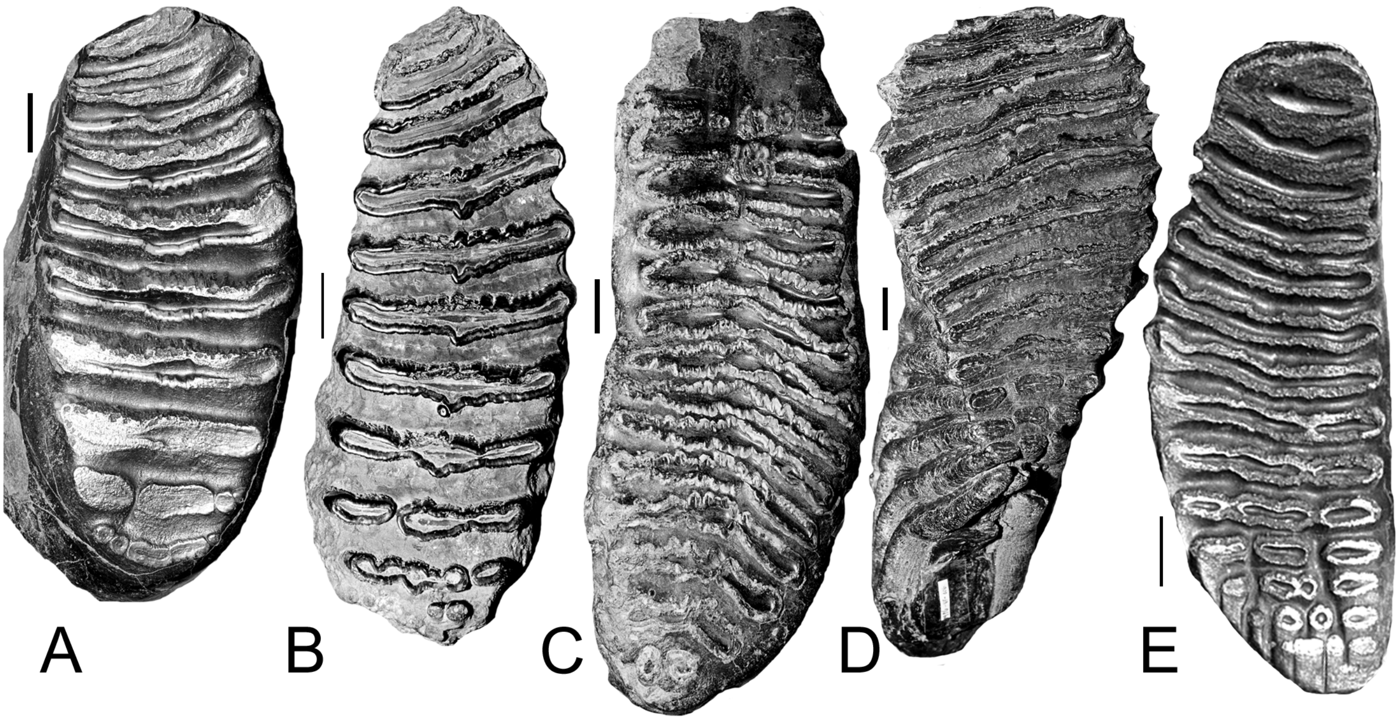

FIGURE 4. Selected specimens of *Mammuthus imperator* from the lake bottom sediments of Lake Chapala. **A**, MPG 7, left M2. **B**, MPG 6, left M3. **C**, INAH-MRG 10-295055, left m3. **D**, MPG 5, right m3. **E**, MPG 8, left M3. Bar scales = 2 cm.

TABLE 3. Measurements (in mm) of cheek teeth of *Mammuthus imperator* from the lake bottom sediments of Lake Chapala in the INAH-MRG and MPG collections. Abbreviations are: l = length, w = width, h = crown height, pl = plate number, plr = plate ratio, plt = plate thickness, et = enamel thickness.

M3 specimen	**l**	**w**	**h**	**pl**	**plr**	**plt**	**et**
MPG uncat		106	230			12.1	3.6
MPG 44	240+	115	170	13+	6	12.1	3.7
MPG uncat	260+	90		14+	6	11.1	3.7
MPG 807	190+	90	200	13+	8	8.7	2.7
MPG 800	230+	90		11+	6	9.8	3.2
Mean	230+	98	200	14+	6-8	10.8	3.4
m3 specimen	**l**	**w**	**h**	**pl**	**plr**	**plt**	**et**
MPG 29		87				10.8	3.6
MPG 9						8.9	2.8
MPG 49		95	260			9.1	2.6
MPG 3		75+	180+			8.2	2.6
MPG 12		87	230			9.1	
MPG 11		75	180			8.3	
MPG 8	155+	60+	130+	10+	7	8.7	2.3
MPG 5	245+	90	160+	14+	8	9.2	3.6
MPG uncat	160+	52+	120	13+	9	8.2	2.1
MPG uncat	230+	65		13+	8	8.1	2.2
MPG uncat	160+	65		13+	8	8.1	2.2
MPG uncat					7	8.3	2.2
MPG uncat						9.2	2.5
MPG uncat						10.1	2.2
MPG uncat						8.8	1.9
MPG uncat						9.1	2.8
MPG uncat	160	60		13+	8		
MPG 797	220+	82	150	15+	7	9.5	2.6
MPG 796	200+	75	155	15+	7	10	3.1
MPG uncat	220	85		15+	7	10	3.1
MPG 799		50	180	13+	8		
Mean	194+	74	175	15+	7-8	8.9	2.6

range of values of *M. imperator*, and the enamel thickness values and plate thicknesses of the Chapala mammoths are outside of the range of *M. columbi* (Madden, 1981, 1995; Agenbroad, 1994). Thus, given their relatively thick enamel and plates, I assign the Chapala mammoths to *M. imperator* (Lucas, 2003).

Nannippus

Rufolo (1998) assigned an upper molar, fragment of a scapula and a magnum to *Nannippus* cf. *N. peninsulatus*, which is a Blancan species. These fossils are from the Chapala Formation north of the lake.

Equus

Rufolo (1998) assigned numerous isolated cheek teeth, some mandibular material and assorted postcrania to *Equus conversidens*. This is a relatively small horse with moderately complex fossettes (e.g., Hibbard, 1955; Reynoso-Rosales and Montellano-Ballesteros, 1994). He assigned two relatively narrow lower molars and a radius to *E.* cf. *E. francisci*. A larger horse with more rectangular upper molars, elongate and broad protocones and plicated enamel was assigned to *Equus ?excelsus* based on isolated teeth and postcrania. A larger horse, also represented by isolated teeth and postcrania, was assigned to *E. niobrarensis*.

An uncatalogued horse skull and lower jaw (not of the same individual or the same species) from the Chapala lake bottom are in the INAH collection (Fig. 5). The skull has been heavily restored and bears left I1-3, right I1 and left and right P2-4 with the left M1-2 erupting and the right M2 erupting. The lower jaw has the left and right i1-3, c and p2-m3. The upper and lower incisors have infundibuli. The upper cheek tooth crowns have a fairly simple pattern. Measurements are: P2 l = 42, w = 24; P3 l = 32, w = 26; P4 l = 31, w =23. The narrow teeth and relatively large size are outside the range of variation of *Equus conversidens* documented by Reynoso-Rosales and Montellano-Ballesteros (1994), and are very close to the morphology and size of specimens Rufolo (1998) assigned to *E. niobrarensis*.

The lower teeth conform well in size and morphology of *Equus conversidens* as documented by Reynoso-Rosales and Montellano-Ballesteros (1994). Lower tooth measurements are: p2 l = 29, w = 16; p3

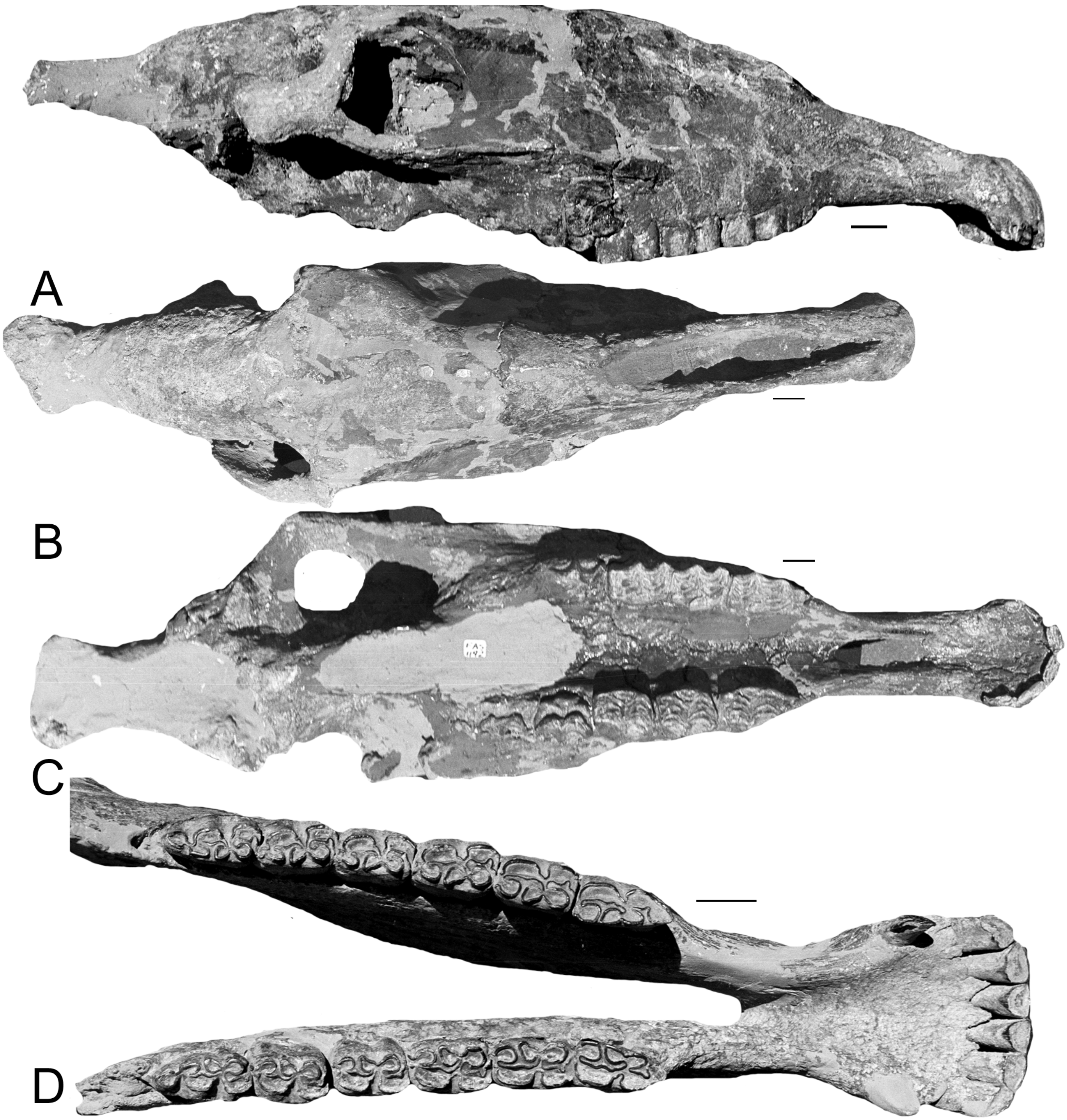

FIGURE 5. Skull and lower jaw of *Equus*, INAH MRG FAS 1192. Skull is heavily restored and is not the same individual as the lower jaw. **A-C**, *Equus* cf. *E. niobrarensis*, skull in right lateral (**A**), dorsal (**B**) and ventral (**C**) views. **D**, *Equus conversidens*, lower jaw in occlusal view. Bar scales = 2 cm.

l = 23, w = 17; p4 l = 24, w =18; m1 l = 23, w = 16; m2 l = 22, w = 17; m3 l = 23, w = 15. Clearly, at least two *Equus* species are present in the fossil assemblage from the Chapala lake bottom.

Tapirus

Rufolo (1998) assigned a single upper molar in the LACM collection to *Tapirus*. The MPG collection contains several isolated upper cheek teeth of *Tapirus* from the lake bottom: MPG 201, left DP4 (l = 25, w = 24) (Fig. 6H); 202, right M1 (l = 24, w = 30) (Fig. 6K); 203, right M1 (l = 26, w = 29); 204, right M2 (l = 30, w = 33) (Fig. 6I); 205, right M2 (l = 30, w = 34) (Fig. 6L); and 206, left M3 (l = 31, w = 33) (Fig. 6J). These isolated teeth (Fig. 6H-L) do not allow a species-level identification, but they are part of the large species complex of *T. merriami*, *T. hayesi* and *T. copei* (R. White, written commun., 2007).

Platygonus

The peccary ?*Platygonus* sp. was identified by Rufolo (1998) in the LACM collection based on teeth, dentaries and assorted postcrania.

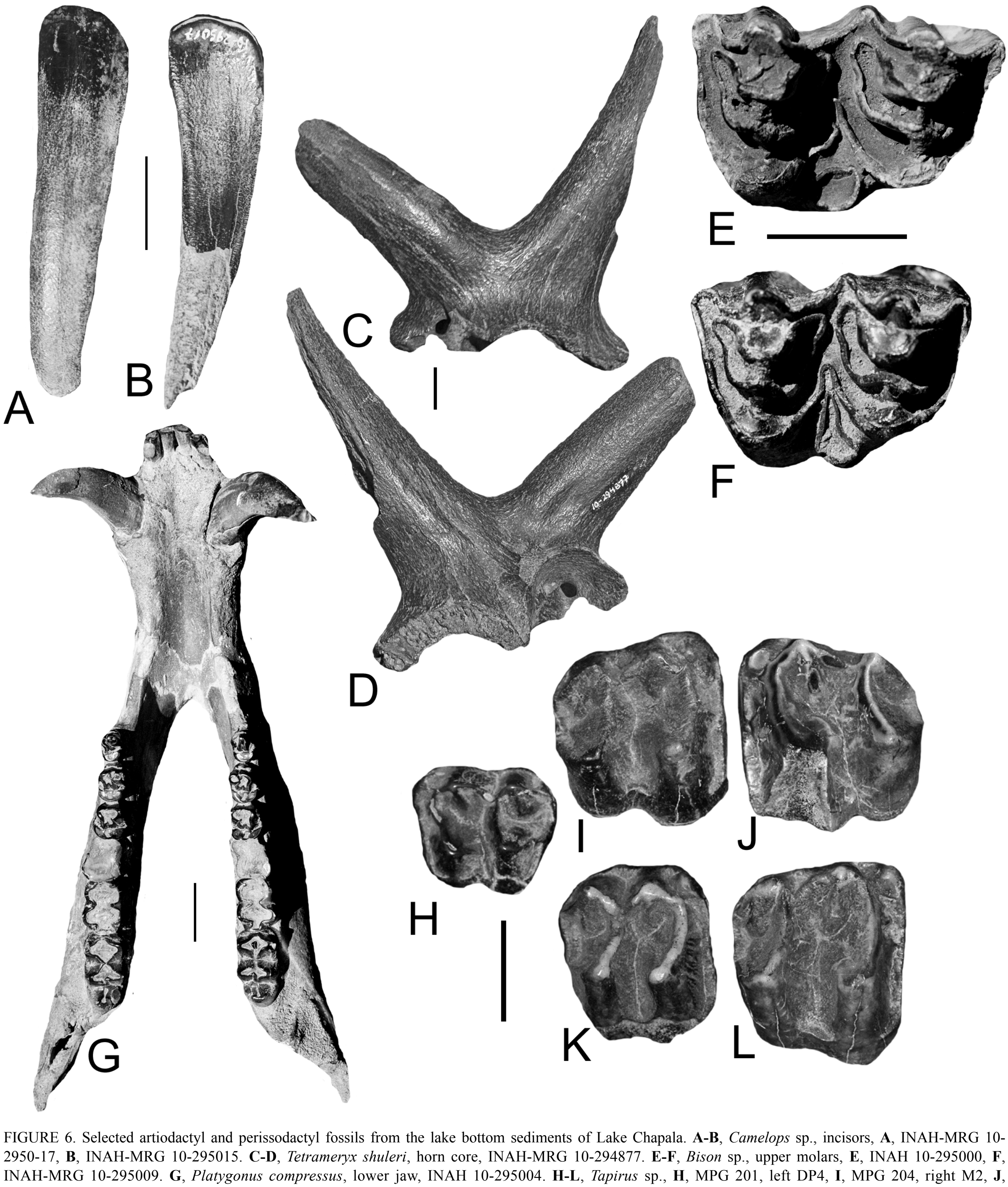

FIGURE 6. Selected artiodactyl and perissodactyl fossils from the lake bottom sediments of Lake Chapala. **A-B**, *Camelops* sp., incisors, **A**, INAH-MRG 10-2950-17, **B**, INAH-MRG 10-295015. **C-D**, *Tetrameryx shuleri*, horn core, INAH-MRG 10-294877. **E-F**, *Bison* sp., upper molars, **E**, INAH 10-295000, **F**, INAH-MRG 10-295009. **G**, *Platygonus compressus*, lower jaw, INAH 10-295004. **H-L**, *Tapirus* sp., **H**, MPG 201, left DP4, **I**, MPG 204, right M2, **J**, MPG 206, left M3, **K**, MPG 202, right M1, **L**, MPG 205, right M2. Bar scales = 2 cm (separate scales for **A-B**, **C-D**, **E-F**, **G** and **H-L**).

INAH-MRG 10-295004 is a lower jaw of a peccary with left and right i1-2, c and p2-m3 (Fig. 6G). Dental measurements are: p2 l = 10, w = 8; p3 l = 13, w = 9, p4 l = 12, w = 10; m1 l = 16, w = 12; m2 l = 17, w = 13; m3 l = 25, w = 15. The elongated lower jaw (indicative of an elongated snout), nonmolariform premolars and molars with two pairs of cusps connected by crests support assignment to *Platygonus*. Lack of i3 and size (compare dental measurements above to Slaughter, 1966, fig. 6) justify assignment to *P. compressus* (also see Simpson, 1949; Lucas and Smartt, 1995).

Camelops

Rufolo (1998) recognized a small species of *Camelops* (based on dental and postcranial material), a large species of *Camelops* (based on a P4 and m2) and an indeterminate llamine based on small and slender postcrania.

Specimens of *Camelops* in the INAH-MRG collection are: upper incisors (Fig. 6A-B), 10-295015 (l = 70, w = 20), 10-295017 (l = 63, w = 20); right dentary fragment with m3, 10-295016 (m3 l = 60, w = 20); and lower jaw with very worn right i1, c, p4-m3 and left c,p4-m2; measurements are: p4 l = 23, w = 14; m1 l = 23, w = 19; m2 l = 37, w = 22; m3 l = 57, w = 20. These specimens represent two different-sized species of *Camelops*, one within the size range of *C. hesternus* (cf. Webb, 1965).

Cervids

Antlers and postcrania allowed Rufolo (1998) to distinguish three cervids in the LACM Chapala collection: a large species he assigned to *Cervus* sp., a small species he designated *Odocoileus* sp. and an intermediate-sized form with stout limb elements that he assigned to ?*Navahoceras* sp. R. White (written commun., 2007) suggests, however, that the specimens Rufolo assigned to *Cervus* may better be assigned to *Odocoileus*.

Tetrameryx

An incomplete skull, horn cores, a M3 and an incomplete humerus were identified as *Tetrameryx shuleri* by Rufolo (1998). Characteristic horn cores of *T. shuleri* are INAH-MRG 10-294877 (Fig. 6C-D) and 294879.

Bison

McDonald (1981, p. 75, tables 19-20) listed *Bison latifr*ons from Chapala, but, as noted by R. White (written commun., 2007), the source of this record was cited as Skinner and Kaisen (1947), which makes no mention of *B. latifrons* from Chapala. McDonald (1981) also listed *B. antiquus antiquus* (tables 23-24) and *B. alaskensis* (tables 41-42) from Chapala. Rufolo (1998) identified *Bison* sp. based on a horn core, lower molars, a dentary and postcrania. Downs (1958a) had identified these as *B. cheneyi* (= *B. alleni*), but they are not complete enough for a species-level identification.

Similarly, specimens of *Bison* in the INAH-MRG collection are isolated teeth and bones not diagnostic at the species level: upper molars (Fig. 6E-F), 10-295009 (l = 36, w = 25), 10-295000 (l = 34, w = 24); two small horn core fragments, 10-295006 and 10-295007 (maximum diameter = 47); and a metapodial (canon bone), 10-295004 (l = 243, proximal w = 68, distal w = 78).

MAMMALIAN BIOSTRATIGRAPHY AND BIOCHRONOLOGY

Two mammal records from the Chapala basin are of Blancan age: (1) *Nannippus* from the Chapala Formation north of the lake; and (2) *Stegomastodon primitivus* from the lake bottom (Fig. 7). The possibility that some of the lake bottom fossils are of Irvingtonian age cannot be discounted; some of the specimens of *Cuvieronius hyodon* and *Mammuthus imperator*, taxa known to occur during the Irvingtonian to the north, may be of Irvingtonian age. However, these records could also be Rancholabrean, so I consider the presence of an Irvingtonian mammal assemblage in the Chapala lake bottom sediments possible but not certain (Fig. 7).

Most of the mammal fossils from the lake bottom sediments are Rancholabrean in age (Fig. 7). Thus, all of the LACM lake bottom sites yield assemblages with *Bison*, *Mammuthus*, *Camelops*, advanced species of *Equus*, *Odocoileus*, *Navahoceras*, *Tetrameryx* and *Cuvieronius*. Some include capybara (*Neochoerus*), sloth (*Nothrotheriops*,

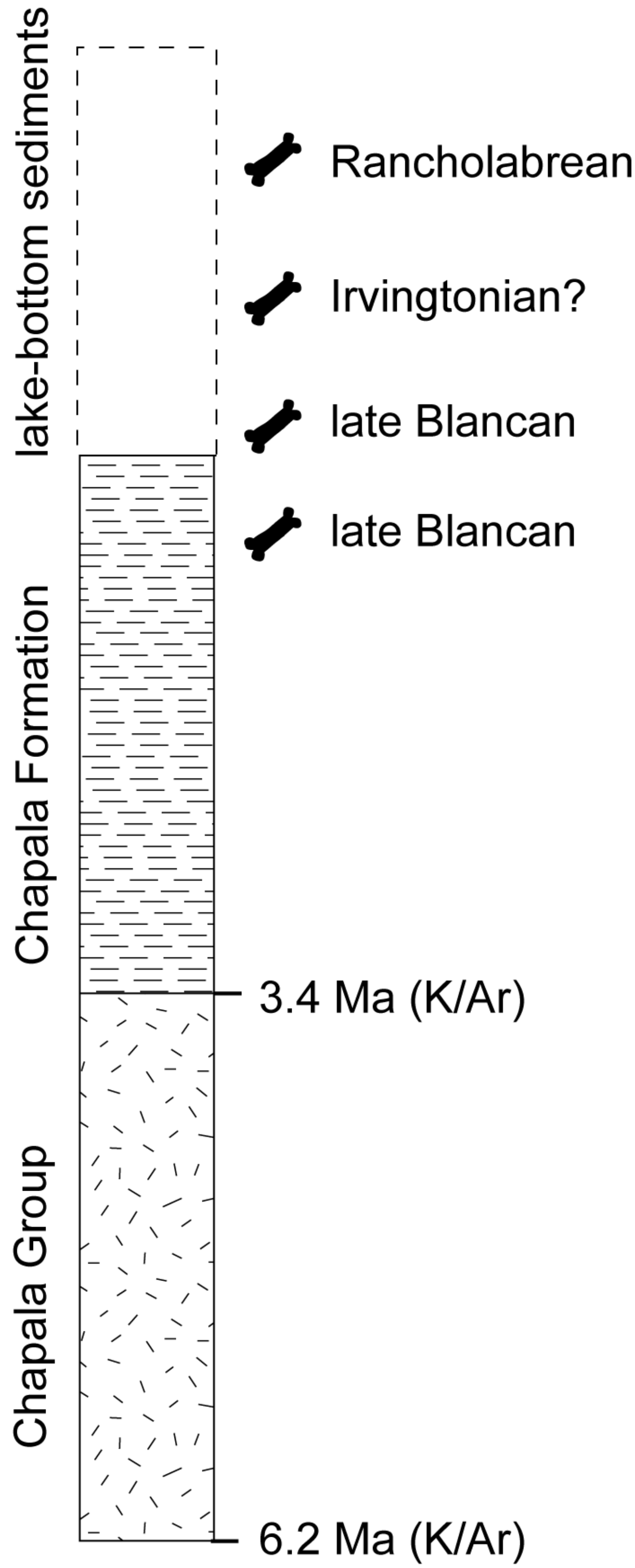

FIGURE 7. Summary of mammalian biostratigraphy and biochronology of the Chapala basin.

Paramylodon), glyptodont (*Glyptotherium*), carnivore (*Canis* and *Felis*) and tayassuid fossils as well. These sites are thus readily assigned a Rancholabrean age. The only possible argument against this is the presence of *Cuvieronius*, which disappears in the southern United States by the end of the Irvingtonian (Lucas et al., 1999, 2000). However, there may be a well-dated Rancholabrean record of *Cuvieronius* in northern Mexico (Mead et al., 2006), and in Central and South America, *Cuvieronius* persisted until the late Pleistocene (Lujanian), so its presence in the Rancholabrean of Jalisco is plausible.

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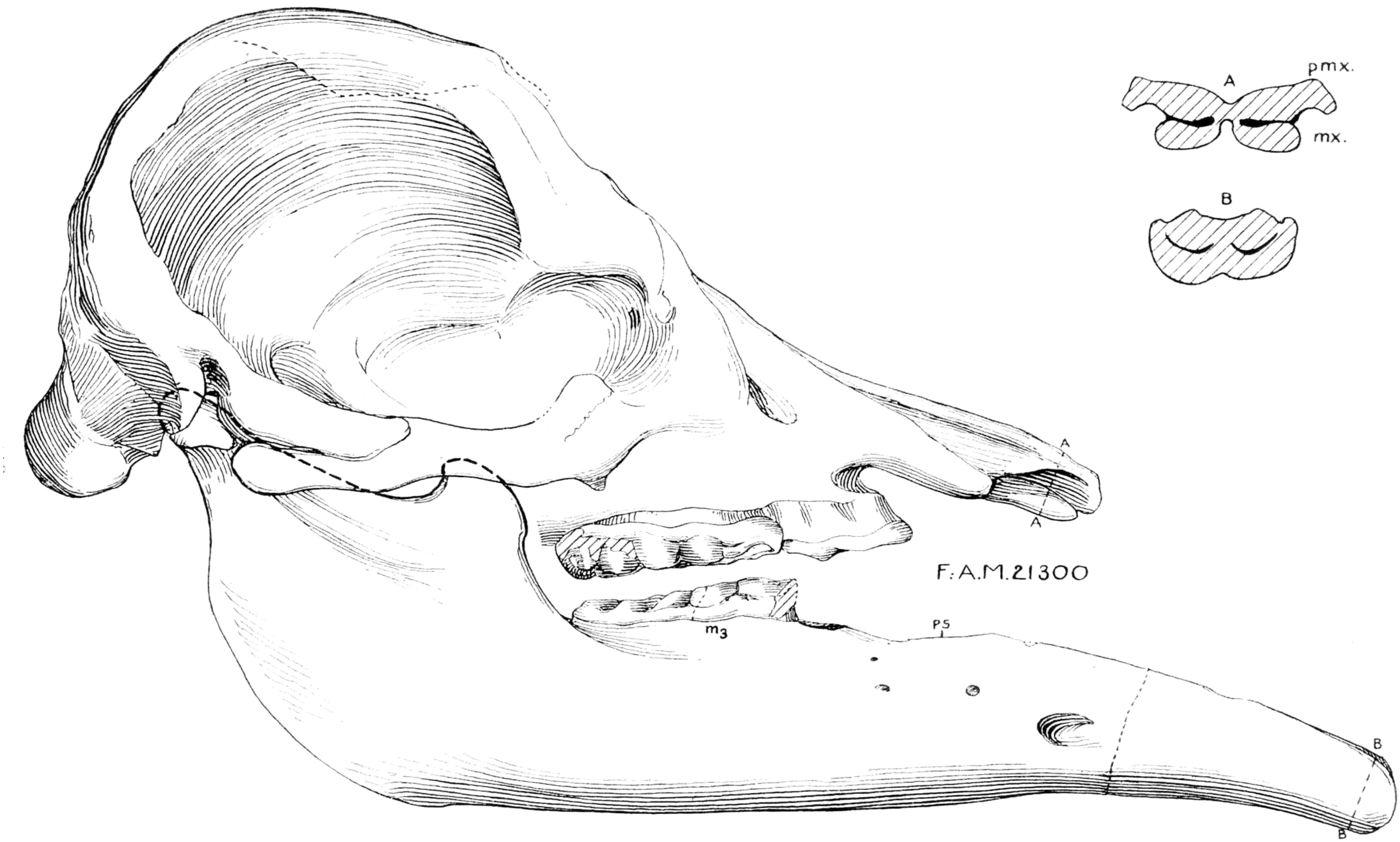

Fig. 10. F:A.M.21300, *Trilophodon cruziensis*, n.sp., type, from Santa Cruz, New Mexico.