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FOSSIL PROBOSCIDEA FROM THE UPPER CENOZOIC OF CENTRAL AMERICA: TAXONOMY, EVOLUTIONARY AND PALEOBIOGEOGRAPHIC SIGNIFICANCE

PROBOSCIDEOS FÓSILES DEL CENOZOICO SUPERIOR DE AMÉRICA CENTRAL: TAXONOMÍA, EVOLUCIÓN Y SIGNIFICADO PALEOGEOGRÁFICO

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ABSTRACT: Fossils of proboscideans from Central America are assigned to four genera: *Gomphotherium*, *Cuvieronius*, *Mammut* and *Mammuthus*. Previous reports of *Stegomastodon*, *Rhynchotherium* and *Haplomastodon* from Central America are based on incorrect taxonomic identifications or on fossils not definitely diagnostic of these genera. The oldest proboscidean records from Central America (Guatemala, El Salvador, Honduras, and Costa Rica) are Late Miocene (early Hemphillian, ~ 7 Ma) records of *Gomphotherium*, and this suggests that gomphotheres dispersed from North America to Central America about nine million years after they dispersed from Asia to North America. However, there is no conclusive evidence that they dispersed into South America, where there are no records of *Gomphotherium*, so the Miocene Panamanian seaway apparently was a barrier to proboscidean dispersal. During the Late Pliocene, *Cuvieronius* arose from a gomphothere ancestor in North America (~ 3 Ma) and during the Late Pliocene (late Blancan) dispersed southward through Central America to South America. *Mammuthus* is known from two species in Central America, an Early Pleistocene species (*M. meridionalis*) and a more common Late Pleistocene species (*M. columbi*). *Mammut* has a single Central American record (Honduras), which is probably of Late Pleistocene age. Neither *Mammuthus* nor *Mammut* have records in South America. Central America was not a center of evolution of proboscideans during the late Cenozoic, instead, it was a pathway across which the Proboscidea migrated. There was a single immigration of *Cuvieronius* from Central America to South America during the Late Pliocene (~ 2.5 Ma). All South American proboscideans are Plio-Pleistocene *Cuvieronius*, or its descendants *Notiomastodon* and *Haplomastodon*.

Keywords: Proboscidea, Central America, *Gomphotherium*, *Cuvieronius*, *Rhynchotherium*, *Haplomastodon*, *Stegomastodon*, *Notiomastodon*, *Mammuthus*, *Mammut*.

RESUMEN: Los fósiles de proboscídeos de América Central se asignan a cuatro géneros: *Gomphotherium*, *Cuvieronius*, *Mammot* y *Mammuthus*. Los trabajos previos de *Stegomastodon*, *Rhynchotherium* y *Hapломastodon* para la región se basaron en identificaciones taxonómicas desactualizadas o en fósiles no diagnósticos para estos géneros. El proboscídeo más antiguo para Centroamérica (Guatemala, El Salvador, Honduras y Costa Rica) es el registro de *Gomphotherium* del Mioceno (Hemphiliano, ~ 7 Ma), sugiriendo que los gonfoterios se dispersaron desde Norteamérica a Centroamérica aproximadamente hace 9 millones de años después de que ellos se dispersaran desde Asia a Norteamérica. Sin embargo, no existe evidencia de que se dispersaran a Sudamérica, donde no existen registros de *Gomphotherium*, así que el canal interoceánico panameño del Mioceno debió de haber representado una barrera para su dispersión. Durante el Plioceno Tardío, el *Cuvieronius* evolucionó de un ancestro del *Gomphotherium* norteamericano y subsecuentemente se dispersó hacia el sur a través de América Central a Sudamérica (Plioceno Tardío). El *Mammot* posee un único registro en América Central (Honduras), posiblemente del Pleistoceno Tardío. Se conoce dos especies de *Mammuthus*, una del Pleistoceno Temprano (*M. meridionalis*) y una más abundante del Pleistoceno Tardío (*M. columbi*). Significativamente, ni el *Mammot* o el *Mammuthus* poseen registros en Sudamérica. América Central no funcionó como un centro de evolución u origen de algún nuevo taxón de proboscídeo durante el Cenozoico Tardío, pese a ello, si fue un lugar de paso o tránsito migratorio. El *Gomphotherium* arribó a Centroamérica durante el Mioceno Tardío, el *Cuvieronius* durante el Plioceno Tardío, *Mammuthus* durante el Pleistoceno Temprano y el *Mammot* hasta el Pleistoceno Tardío. Existió una única emigración de *Cuvieronius* desde América Central a Sudamérica durante el Plioceno Tardío (~ 2,5 Ma). Todos los proboscídeos sudamericanos son *Cuvieronius*, o sus descendientes directos *Notiomastodon* y *Hapломastodon* durante el Plio-Pleistoceno.

Palabras clave: Proboscídea, América Central, *Gomphotherium*, *Cuvieronius*, *Rhynchotherium*, *Hapломastodon*, *Stegomastodon*, *Notiomastodon*, *Mammuthus*, *Mammot*.

INTRODUCTION

Proboscidea is an order of mammals popularly referred to as elephants and their allies. Proboscideans originated in Africa during the Paleocene (Gheerbrant, 2009). They subsequently spread to Eurasia during the Early Miocene after Africa docked with Eurasia via the Arabian Peninsula (Shoshani et al., 1996; Tassy, 1996). By middle Miocene time, about 16 Ma, proboscideans crossed Beringia into North America and spread rapidly through the continent (Tedford et al., 2004; Prothero et al., 2008). Proboscideans first appeared in Central America during the Late Miocene, about 7 Ma, and they persisted there until their extinction at about the end of the Pleistocene. During the Pliocene, soon after the closure of the Panamanian isthmus, proboscideans continued to spread southward, into South America as far south as Chile and Argentina.

Central America has a diverse and complex fossil record of proboscideans of Miocene-Pleistocene age. By our count, there are at least 74 localities in Central America that have yielded proboscidean fossils, about 43 of which are well documented (Fig. 1; Table 1; Appendix). Here, we

present a critical review of the Central American record of proboscideans, based in part on recent taxonomic revisions and on more than two decades of research on their fossil record. These taxonomic revisions are the primary reason for fundamental differences between our review of the Central American proboscidean record and that of Arroyo-Cabrales et al. (2007), who used a different approach to the taxonomy and apparently did not review some of the records listed here.

We evaluate also the evolutionary and paleobiogeographic significance of these records to conclude that Central America was an important pathway to a single immigration of proboscideans from North to South America. In this article, LMA = land-mammal "age," m = lower molar and M = upper molar. We emphasize that in several cases, particularly with incomplete and juvenile proboscidean specimens, the taxonomic classification is not easy and several genera have overlapping diagnostic criteria, particularly in their juvenile molars (i.e., *Gomphotherium*, *Rhynchotherium*, *Cuvieronius*, *Hapломastodon*). The ideal specimen for a certain identification is either a complete skull, lower jaw and/or tusks, but in a tropical area with heavy rainfall conditions such as Central America, such ideal preservation is rare.

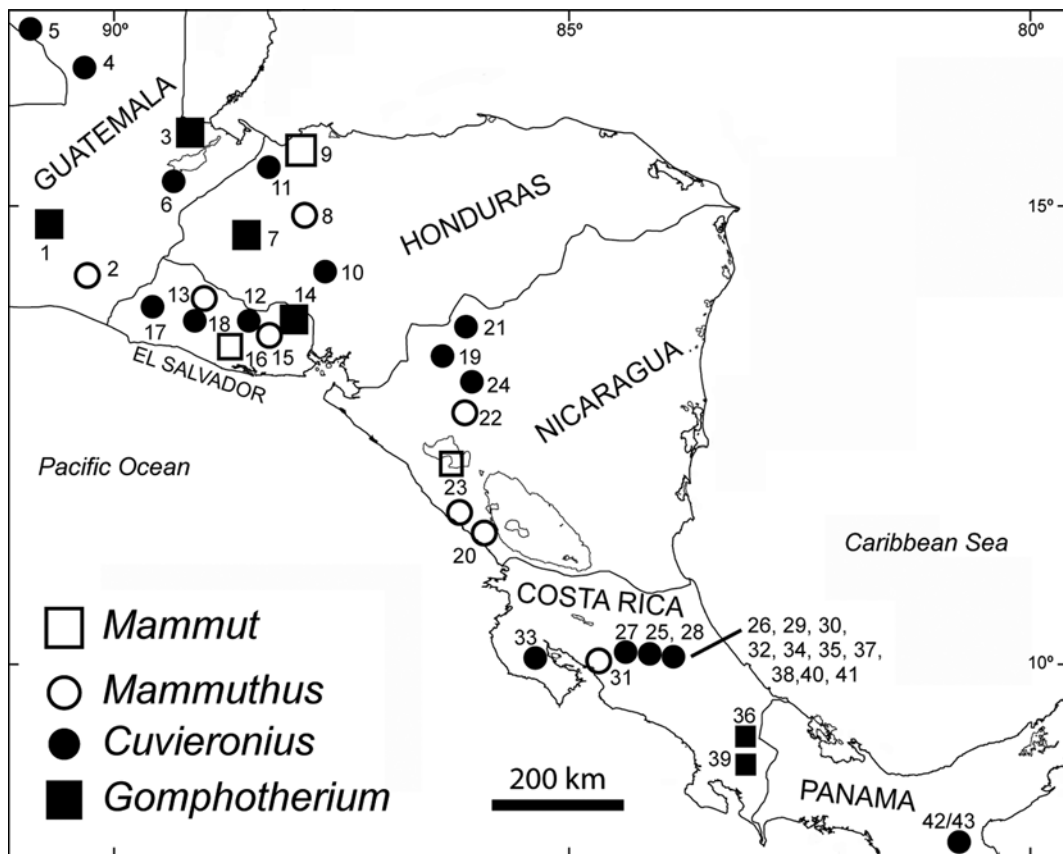


Fig. 1: Central American proboscidean localities. See Table 1 for locality list that matches numbers on the figure

GEOLOGICAL TIMESCALE

Ages were assigned to proboscidean fossils from Central America based primarily on the North American LMAs, characterized and correlated to the late Cenozoic epochs by Tedford et al. (2004) for the Miocene and by Bell et al. (2004) for the Pliocene-Recent. We thus use the traditional definition of the base of the Pleistocene at about 1.8 Ma, instead of the newly proposed definition, which lowers the Pleistocene base to about 2.6 Ma. Thus, the LMAs relevant to the Central American proboscidean record are: (1) Hemphillian: Late Miocene-Early Pliocene, ~ 4.7-9.0 Ma; (2) Blancan: Early Pliocene-Early Pleistocene, ~1.8-4.7 Ma; (3) Irvingtonian:

Early-Middle Pleistocene, ~ 200,000 years-1.8 Ma; and (4) Rancholabrean: Late Pleistocene, ~ 10,000-200,000 years. We also discuss the Marplatian South American LMA here, and based on Woodburne et al. (2006; also see Requero et al., 2007) its age is ~ 1.9-3.2 Ma.

CENTRAL AMERICAN PROBOSCIDEAN TAXONOMY

We recognize four genera of fossil proboscideans from Central America: *Gomphotherium*, *Cuvieronius*, *Mammut* and *Mammuthus*. Other workers (including ourselves, and most recently Arroyo-Cabres et al., 2007) have previously identified three other proboscidean

Table 1

List of the well documented proboscidean localities in Central America (see Fig.1 and the Appendix)

Number (Fig.1)	Locality	Age	Proboscidean
Guatemala			
1	Chinautla	Hemphillian?	<i>Gomphotherium</i>
2	Estanzuela	Pleistocene	<i>Mammuthus</i>
3	Río Carboneras	Hemphillian?	<i>Gomphotherium</i>
4	Río de la Pasión	Rancholabrean	<i>Cuvieronius</i>
5	Río Usmanita	Pleistocene?	<i>Cuvieronius</i>
6	Zacapa	Pleistocene?	<i>Cuvieronius</i>
Honduras			
7	Gracias	Hemphillian	<i>Gomphotherium</i>
8	Orillas de Humaya	Rancholabrean	<i>Mammuthus</i>
9	San Pedro Sula	Pleistocene?	<i>Mammut</i>
10	Tambla (Humuya)	Pleistocene?	<i>Cuvieronius</i>
11	Yeroconte	Rancholabrean	<i>Cuvieronius?</i>
El Salvador			
12	Barranca del Sisimico	Irvingtonian	<i>Cuvieronius</i>
13	Chaltenango	Irvingtonian	<i>Cuvieronius/Mammuthus</i>
14	Corinto	Hemphillian	<i>Gomphotherium</i>
15	El Hormiguero	Rancholabrean	<i>Mammuthus</i>
16	Río de Jerusalén	Pleistocene	<i>Mammuthus</i>
17	Santa Ana	Pleistocene	<i>Cuvieronius</i>
18	Tomayate	Irvingtonian	<i>Cuvieronius</i>
Nicaragua			
19	El Bosque	Rancholabrean	<i>Cuvieronius</i>
20	El Palmar	Pleistocene	<i>Mammuthus</i>
21	Jalapa	Rancholabrean	<i>Cuvieronius</i>
22	Las Banderas	Pleistocene	<i>Mammuthus</i>
23	Masachapa	Pleistocene	<i>Mammuthus</i>
24	Matagalpa	Pleistocene?	<i>Cuvieronius</i>
Costa Rica			
25	Agua Caliente	Late Pleistocene	<i>Cuvieronius</i>
26	Bajo Barrantes	Late Pliocene-Early Pleistocene?	<i>Cuvieronius</i>
27	Buenos Aires de Palmares	Middle Pleistocene	<i>Cuvieronius</i>
28	Cachí	Pleistocene?	<i>Cuvieronius</i>
29	Candelaria	Pleistocene?	<i>Cuvieronius</i>
30	Claros de Guayabo de Mora	Pleistocene?	<i>Cuvieronius</i>
31	Hacienda del Silencio	Pleistocene	<i>Mammuthus</i>
32	Paseo Colón	Late Pleistocene	<i>Cuvieronius</i>

Table 1 (continuation)

Number (Fig. 1)	Locality	Age	Proboscidean
33	Península de Nicoya	Pleistocene?	<i>Cuvieronius</i>
34	Quebrada Rivera (Tibás 3)	Late Pleistocene	<i>Cuvieronius</i>
35	Río María Aguilar	Late Pleistocene	<i>Cuvieronius</i>
36	San Gerardo de Limoncito	Middle-Late Miocene (Late Miocene?)	<i>Gomphotherium</i>
37	Santa Ana	Middle Pleistocene	<i>Cuvieronius</i>
38	Santa Domingo	Middle or Late Pleistocene	<i>Cuvieronius</i>
39	Santa Rita	Middle-Late Miocene (Late Miocene?)	<i>Gomphotherium</i>
40	Tibás 1	Late Pleistocene	<i>Cuvieronius</i>
41	Tibás 2	Late Pleistocene	<i>Cuvieronius</i>
Panama			
42	El Hatillo	Rancholabrean	<i>Cuvieronius</i>
43	La Trinidaíta	Rancholabrean	<i>Cuvieronius</i>

genera from Central America---*Rhynchotherium*, *Stegomastodon* and *Haplomastodon*---but, based on revised taxonomy, there are no demonstrable records of these proboscidean genera in Central America (below, we briefly review this revised taxonomy).

Gomphotherium

Gomphotherium (Fig. 2) is an Old World and New World gomphothere with a long stratigraphic range through most of the Miocene and Pliocene. One of the first proboscideans to reach the New World, *Gomphotherium* is considered to have been ancestral to the more derived New World gomphotheres *Stegomastodon*, *Rhynchotherium* and *Cuvieronius* (e.g., Tobien, 1973; Lambert & Shoshani, 1998). *Gomphotherium* is characterized by its low and long skull with upper tusks with enamel bands, lower jaw with two elongate lower tusks in an elongate mandibular symphysis and last molars with 3-5 lophs/lophids that wear to single trefoils (e.g., Tobien, 1973; Lambert & Shoshani, 1998).

Gomphotherium was common in North America during the Miocene (Barstovian-early Hemphillian), but rare during the Pliocene (late

Hemphillian). Its records in North America extend as far south as southern Mexico (e.g., Ferrusquia-Villafranca, 1984, 1990; Lambert & Shoshani, 1998). A large number of species of *Gomphotherium* have been recognized, but Tobien (1978) argued that only one North American species is valid, *G. productum*. However, we believe the genus is more speciose in the New World (cf. Heckert et al., 2000) and that there are at least two species known from North America, and another is known from Central America. Thus, we accept the conclusion of Lucas & Morgan (2008) that the Central American species *Gomphotherium hondurensis* (= *Aybelodon hondurensis*, = *Blickotherium blicki*) (Fig. 3) is not a species of *Rhynchotherium*, but instead a derived species of *Gomphotherium*.

Cuvieronius

Cuvieronius (Fig. 2) is a New World gomphothere known from the Pliocene-Pleistocene of North America and the Pleistocene of Central and South America (e.g., Dudley, 1996; Lambert, 1996; Lambert & Shoshani, 1998; Prado et al., 2005; Lucas, 2008a; Ferretti, 2008). *Cuvieronius* is generally considered closely related to or derived

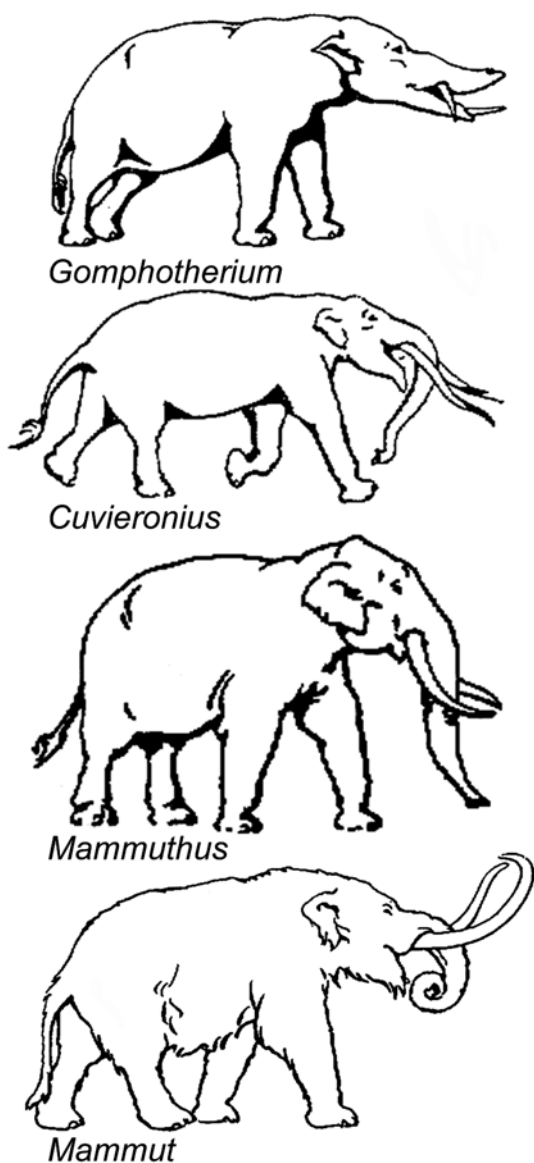


Fig. 2: Outline restorations of the four genera of Central American proboscideans; not to scale (after Osborn, 1936)

from the Pliocene gomphothere *Rhynchotherium* in North America and to have spread to Central and South America during the Pliocene (e.g., Tobien, 1973; Kurtén & Anderson, 1980; Webb & Perrigo, 1984; Miller, 1990; Dudley, 1996). In

North America, *Cuvieronius* records are known across Mexico (e.g., Montellano-Ballesteros, 2002; Alberdi & Corona-M., 2005) and in the southern United States in Arizona, New Mexico, Texas and Florida (e.g., Kurtén & Anderson, 1980; Dalquest & Schultz, 1992; Webb & Dudley, 1995; Lucas et al., 1999, 2000; Hulbert, 2001; Vance, 2002; Bell et al., 2004; Lucas & Morgan, 2005; Lucas, 2008a).

Characteristic features of *Cuvieronius* include its relatively long and low vaulted skull, large upper tusks with spiral enamel bands, lack of lower tusks, short mandibular symphysis that is not strongly downturned and bunolophodont third molars that have 4-5 lophs/lophids with slightly alternating cusps between them (Fig. 4). The twisted upper tusk, with its spiral band of enamel, is a derived feature shared by *Cuvieronius* and *Rhynchotherium*.

Most recent workers have generally regarded two species of *Cuvieronius* as valid, the type species *C. hyodon* (Fischer, 1814) and *C. tropicus* (Cope, 1884) (cf. Shoshani & Tassy, 1996). Indeed, it became traditional to refer all North American (from Mexico northward) specimens of *Cuvieronius* to *C. tropicus*, and to refer all South American specimens to *C. hyodon*. Some authors referred Central American (especially specimens from Honduras, Costa Rica and El Salvador) specimens to *C. hyodon* (e. g. Laurito, 1988) whereas others referred them to *C. tropicus* (e. g., Webb & Perrigo, 1984). A few authors remained undecided as to any species-level assignments pending a revision, or simply fell back on using the type species *C. hyodon* (e.g., Lambert, 1996; Lambert & Shoshani, 1998; Vance, 2002). However, as Lucas (2008a) concluded, extensive revision of the South American specimens of *Cuvieronius* (see especially Frassinetti & Alberdi, 2000; Prado et al., 2002, 2003, 2005; Alberdi et al., 2004) has established a range of variation in molar morphology for *C. hyodon* that encompasses the type specimen of *C. tropicus*.

Thus, Montellano-Ballesteros (2002) discussed the possible distinctiveness of *Cuvieronius*

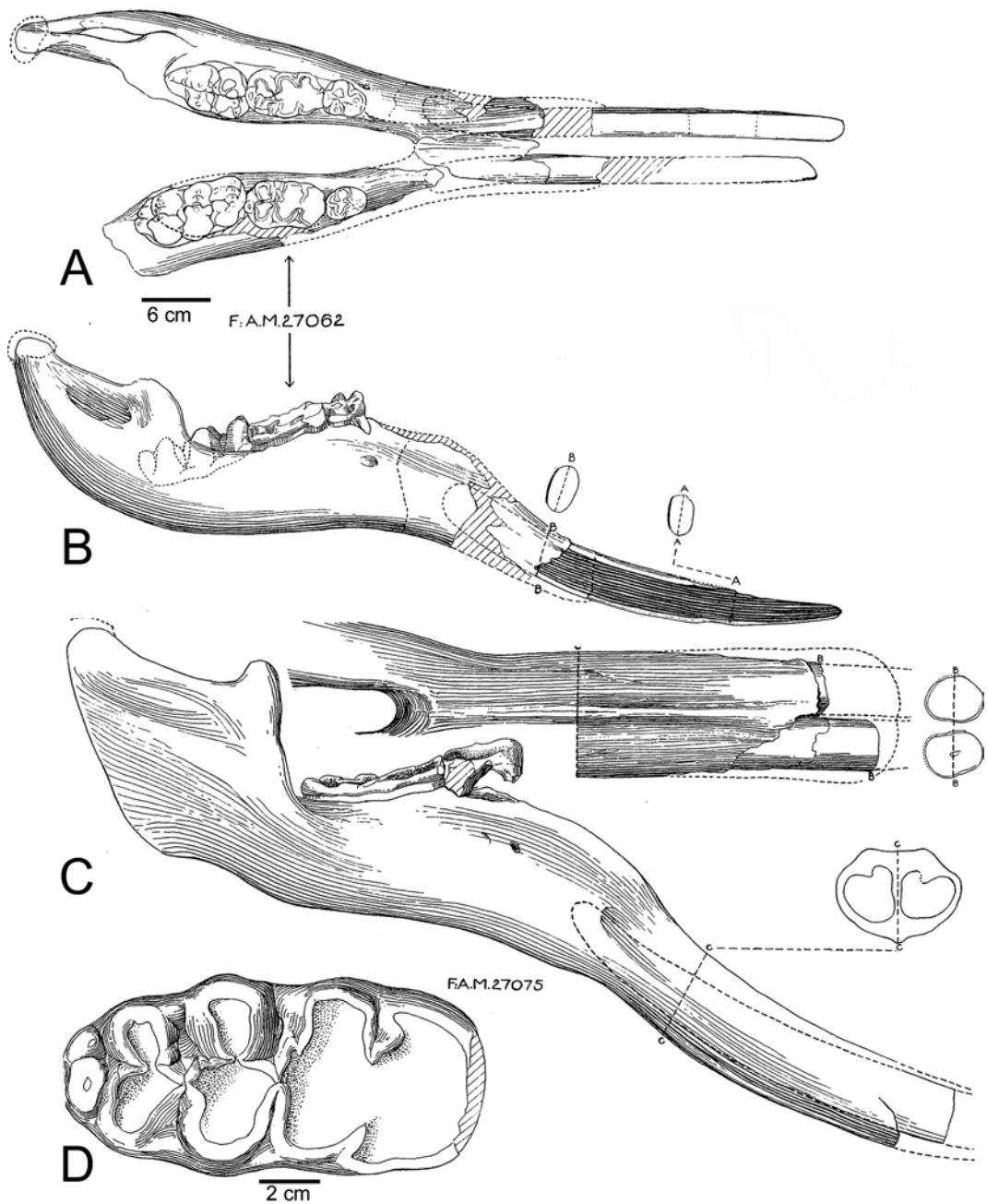


Fig. 3: Selected *Gomphotherium hondurensis* from the Late Miocene (Hemphillian) of Honduras--holotypes of *Blickotherium blicki* and *Aybelodon hondurensis* from the Gracias local fauna. A-B, Holotype of *Blickotherium blicki*, in occlusal (A) and right lateral (B) views. C-D, Holotype of *Aybelodon hondurensis*, lower jaw in ventral and lateral views (C) and right m3 in occlusal view (D). Modified from Frick (1933, figs. 4-5). One scale bar for A-C, separate scale bar for D

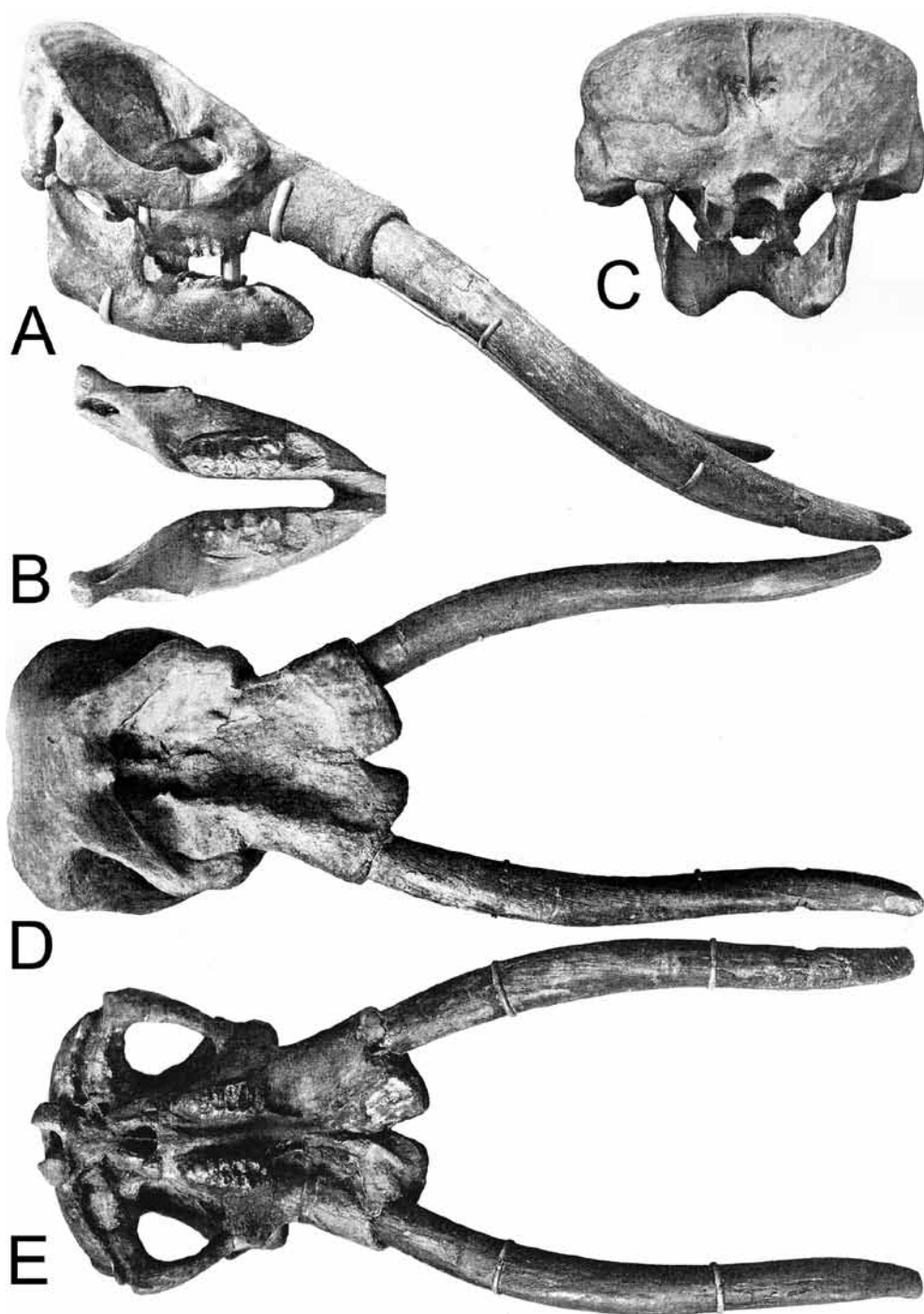


Fig. 4: Characteristic skull and lower jaw of *Cuvieronius hyodon*. MNHN (Musée Nationale d'Histoire Naturelle, Paris) TAR 1270, from Tarija, Bolivia, proposed as neotype of *Mastotherium hyodon* Fischer, 1814 by Lucas (2009b). A, Right lateral view of skull and lower jaw. B, Occlusal view of lower jaw. C, Occipital view of skull and lower jaw. D, Dorsal view of skull. E, Ventral view of skull. For scale, maximum length of skull (including tusks) = 210 cm. Modified from Boule & Thevenin (1920, pls. 1-3)

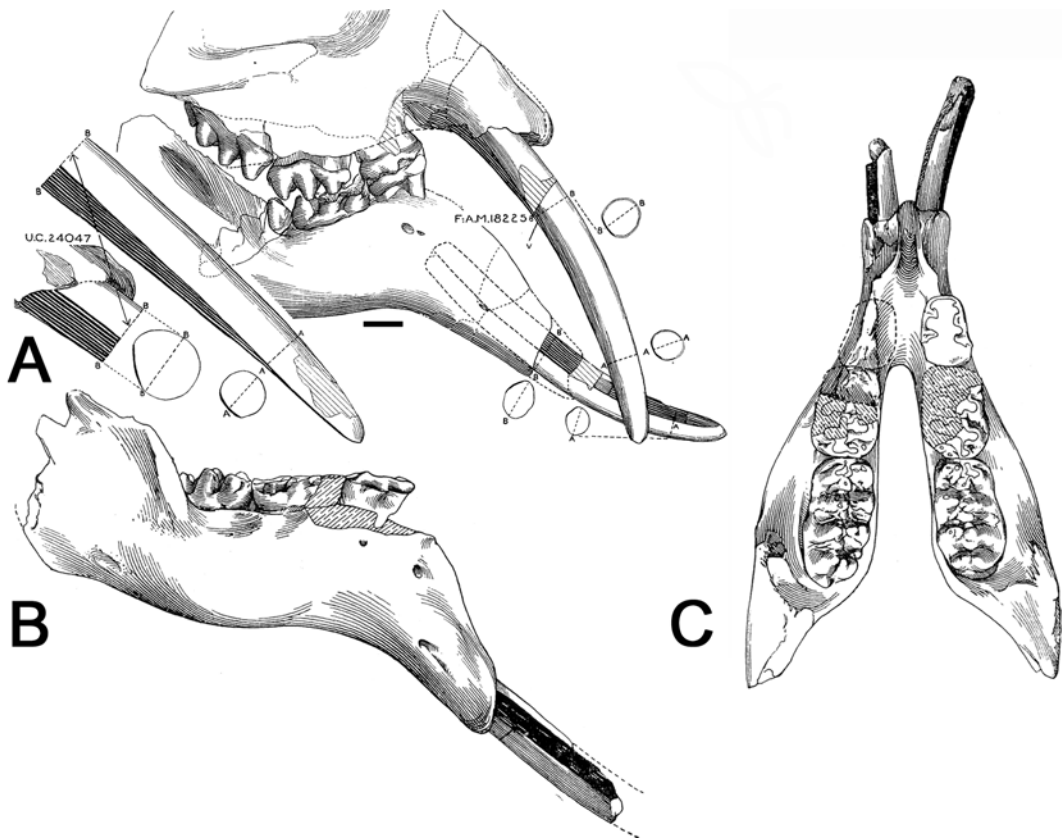


Fig. 5: Skull, tusk, lower jaw and cheek tooth morphology of *Rhynchotherium tascalae*. A, Comparison of upper tusk of *Rhynchotherium edensis* syntype (UCMP [University of California, Museum of Paleontology] 24047) on left, and juvenile skull and lower jaws (F:AM [Frick Collection, American Museum of Natural History] 18225; modified from Frick, 1933, fig.1). B-C, Type lower jaw of *Rhynchotherium browni* (from Osborn, 1936) in right lateral (B) and occlusal (C) views. For scale, m3 length = 174 mm in A, and m3 length = 180 mm for B-C

tropicus, which was based on a right dentary with m2-3 from Mexico that Cope (1884) named *Dibelodon tropicus*. Montellano-Ballesteros (2002) noted that the only feature of the type of *C. tropicus* that may diagnose it from *C. hyodon* is its possession of five lophids on the m3, although she concluded that the variability of this feature had not been fully established. In part, this is because some authors call a fifth lophid on a *Cuvieronius* m3 the talonid, depending on its overall width and height. However, a survey of some of the South American specimens referred to *C. hyodon* reveals five-lophid m3s very similar to that of the holotype of *C. tropicus* (e.g., Nordenskiöld, 1903, pl. 3; Pompeckj, 1905, pl. 3, fig. 1a). The Salvadoran specimens of *Cuvieronius* that Cisneros (2005,

fig. 6) assigned to *C. tropicus* have 4.5 or 5 lophids. Indeed, Prado et al. (2003, 2005; also see Lambert & Shoshani, 1998) diagnosed *C. hyodon* as having “four to four and half or five angular lophids” (Prado et al., 2003, p. 23). The m2 and m3 lengths and widths of the type specimen of *C. tropicus* also fall within the range of metric variation of the South American *C. hyodon* (see Frassinetti & Alberdi, 2000; Prado et al., 2002, 2003, 2005; Alberdi et al., 2004 for the molar metrics of South American *C. hyodon* specimens). It is thus impossible to maintain *C. tropicus* as a valid species distinct from *C. hyodon*. Therefore, Lucas (2008a) argued that *Cuvieronius* is monospecific, with *C. tropicus* a junior subjective synonym of *C. hyodon*. We accept the conclusion that

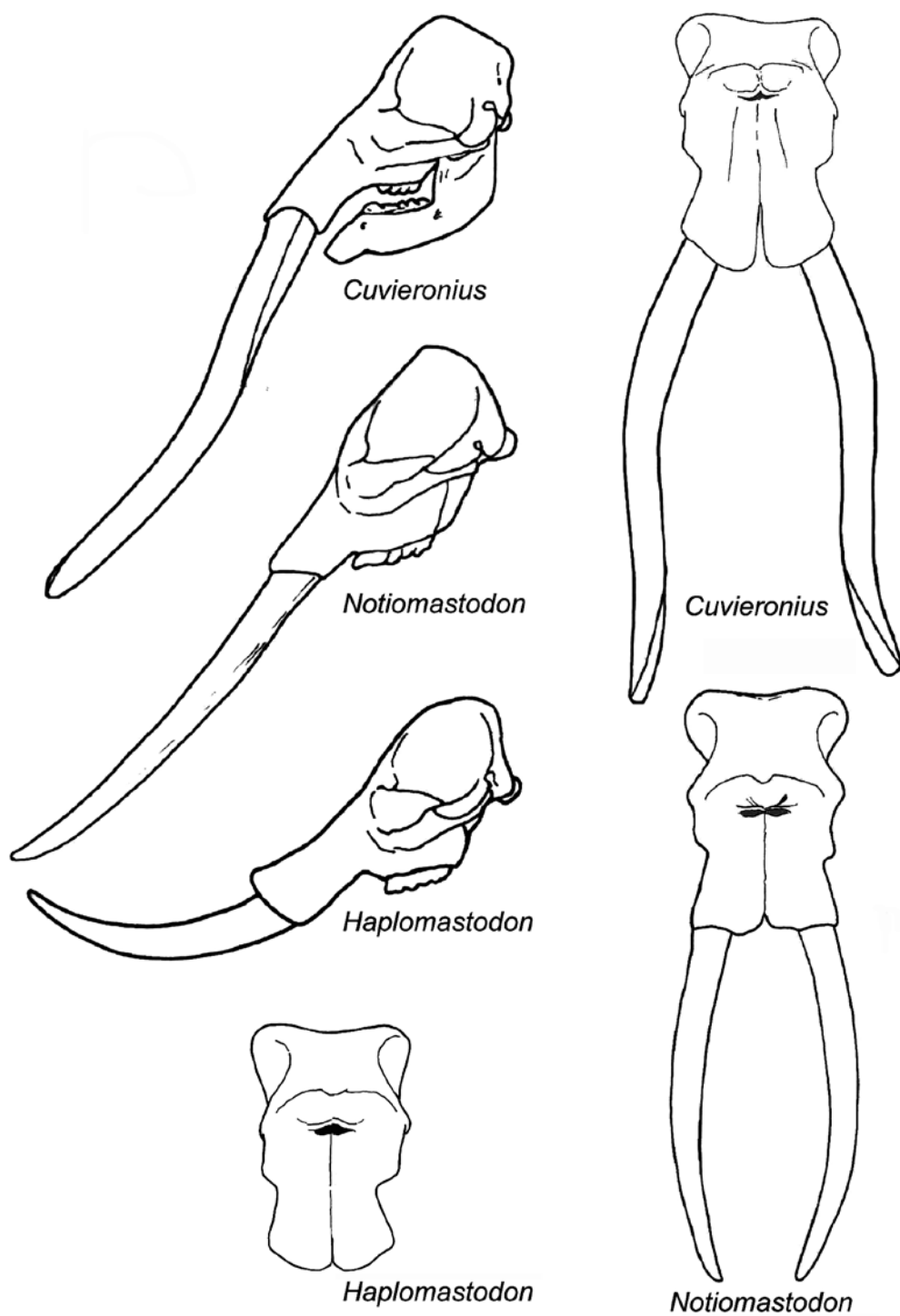


Fig. 6: Skulls of South American gomphotheres: *Cuvieronius hyodon*, *Notiomastodon platensis* and *Haplomastodon waringi*; not to scale. Modified from Ferretti (2008)

there is one valid species of *Cuvieronius* (which was also advocated by Laurito, 1988), and refer all Central American specimens of *Cuvieronius* to *C. hyodon*, which is the most abundant proboscidean in Central America. Also, the few reported Central American specimens with associated molars, tusks and, in some cases, the lower jaw, are readily assigned to this species (i.e. for example, specimens from Santa Ana and Tibás 2 in Costa Rica: Lucas et al., 1997).

Rhynchotherium

Rhynchotherium is a genus of advanced gomphotheres known from Hemphillian-Blancan strata of the New World. It is part of the derived clade of New World gomphotheres that includes *Cuvieronius* and that is united by the spiral enamel bands on the upper tusks, relatively simple (though variable) cheek-tooth crown morphology and short lower jaws. *Rhynchotherium* is diagnosed by its upper tusks with spiral enamel bands, M3/m3 with 4-4.5 relatively simple lophs/lophids, lower jaw with two tusks with flat medial sides and on the lateral sides straight external enamel bands that extend to their tips, a low and blunt coronoid process, deep and thick horizontal ramus below the cheek tooth row, short horizontal symphysis and sharply downturned symphyseal region in which the symphyseal angle is 45° or more (Fig. 5). This diagnosis indicates that isolated molars and tusk fragments are not diagnostic of *Rhynchotherium* instead of *Cuvieronius*, though most *Rhynchotherium* tend to have less complex and less hypsodont molars than most *Cuvieronius*. A lower jaw (particularly the symphyseal region) is needed to definitively diagnose specimens of *Rhynchotherium* from *Cuvieronius*. Thus, for example, the recent reports of *Rhynchotherium* from San Gerardo and Santa Rita in Costa Rica based only on upper molars (Laurito & Valerio, 2005; Valerio & Laurito, 2008) are of specimens that more likely belong to *Gomphotherium* and certainly cannot be assigned with confidence to *Rhynchotherium* (see Lucas & Morgan, 2008; present paper).

Lucas & Morgan (2008) presented a comprehensive revision of the taxonomy of *Rhynchotherium*, and re-assigned the two supposed *Rhynchotherium* species from Honduras--*Blickotherium blicki* Frick, 1933 and *Aybelodon hondurensis* Frick, 1933--to *Gomphotherium*. Only one species of *Rhynchotherium* is valid, *R. tlascalae* (= *R. edense*, = *R. falconeri*, = *R. browni*, = *R. simpsoni*), and the isolated tooth records assigned to *Rhynchotherium* are not diagnostic of the genus (Lucas & Morgan, 2008). Verified records of *R. tlascalae* thus are from North America—Mexico, California, Arizona, New Mexico, Texas and Florida. Therefore, there are no confirmed Central American records of *Rhynchotherium*, and it is unlikely that *Rhynchotherium* originated in Central America (as some have claimed, such as Webb & Perrigo, 1984 and Woodburne et al., 2006), and more likely that it originated in North America, given that its entire fossil record is in North America.

Stegomastodon

Stegomastodon was the last North American gomphothere, with a stratigraphic range of Blancan to Irvingtonian (Lucas et al., 1999, 2000). It has a tall and short skull with large, uniformly curved upper tusks that lack enamel, no lower tusks and molar teeth that wear to a double trefoil.

Kurtén & Anderson (1980) argued that only a single species of *Stegomastodon* is valid, *S. mirificus* (Leidy). However, we believe that a more primitive species is recognizable, which is smaller and has simpler trefoiling. These are Pliocene (Blancan) specimens to which some workers have applied Woodburne's (1961) name *S. rexfordensis*, but the name *S. primitivus* has priority (Lambert & Shoshani, 1998). Thus, we envision two species of North American *Stegomastodon*---primitive *S. primitivus* and the advanced *S. mirificus*. *Stegomastodon* records are confined to North America and extend as far south as Jalisco in Mexico (Lucas, 2003; Alberdi & Corona-M, 2005).

Stegomastodon has been reported from Central America at the El Bosque locality in northern Nicaragua (Espinoza, 1976). However,

Reshetov (1982) pointed out that this record should be revised, and as Laurito & Valerio (2005) and Lucas et al. (2008) noted, there has been no documentation of this record. The Late Pleistocene (Rancholabrean LMA) age of the El Bosque fossil assemblage makes it highly unlikely that *Stegomastodon* was found at the locality. Instead, *Cuvieronius* is present at the El Bosque locality (Lucas et al., 2008), and it is likely that the report of *Stegomastodon* was based on misidentification of a cheek tooth of *Cuvieronius*. Thus, there are no records of *Stegomastodon* in Central America (Lucas et al., 2007).

Haplomastodon

Among the South American gomphotheres, the taxonomy of *Haplomastodon* (Figs. 6-7) has been particularly problematic (e.g., Hoffstetter, 1950, 1952, 1955; Simpson and Paula Couto, 1957; Parodi-Bustos, 1962; Ficarrelli et al., 1993, 1995; Lucas et al., 1997; Lucas, 2008c, 2009a). Some workers regard it as a synonym of *Stegomastodon* (e.g., Alberdi et al., 2002; Prado et al., 2002, 2003, 2005), others treat it as a distinct genus (e.g., Ficarrelli et al., 1993, 1995; Lucas et al., 1997), whereas others regard it as a synonym of *Notiomastodon* (Madden, 1984; Ferretti, 2008). We continue to regard *Haplomastodon* as a distinct taxon. The distinction between *Haplomastodon* and the very similar genus *Cuvieronius* is skull shape (relatively tall and short in *Haplomastodon*, low and long in *Cuvieronius*) and tusk morphology (upwardly curved and lacking enamel in adult *Haplomastodon*, not upwardly curved with spiral enamel bands in *Cuvieronius*) (Figs. 6-7). We distinguish *Haplomastodon* from *Notiomastodon* primarily by the more complex molar crowns of *Notiomastodon* (cf. Cabrera, 1929).

Only one record of *Haplomastodon* has been claimed in Central America--a subadult lower jaw, isolated molars and tusk fragment from Barra Honda in Costa Rica (Lucas & Alvarado, 1991b; Lucas et al., 1997, fig. 7). Identification as *Haplomastodon* was based on the relatively straight tusk with a straight enamel

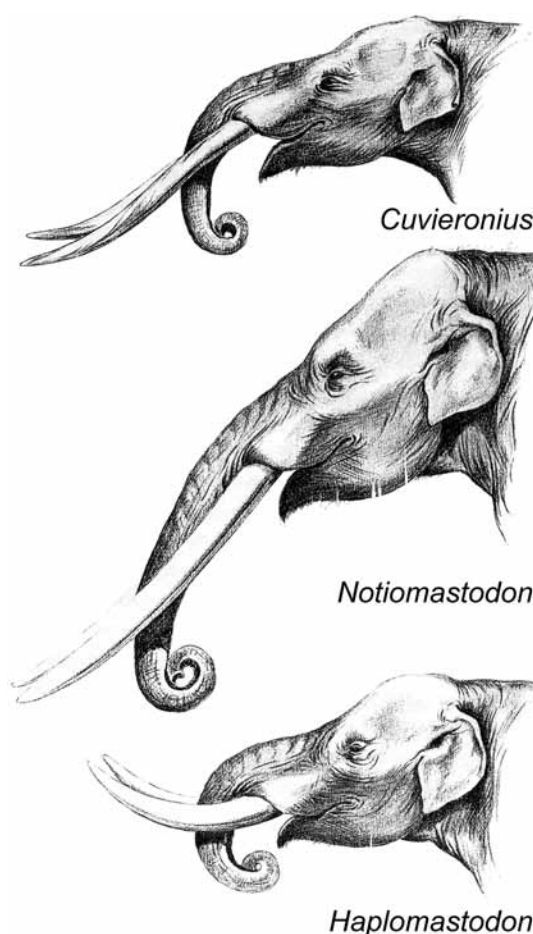


Fig. 7: Restorations of the heads of the three South American gomphotheres: *Cuvieronius hyodon*, *Notiomastodon platensis* and *Haplomastodon waringi*. Modified from Simpson & Paula Couto (1957)

band, supposedly characteristic of juvenile *Haplomastodon* (Simpson & Paula Couto, 1957). However, we now conclude that the tusk fragment of the Barra Honda gomphothere is too short (too incomplete) to document the curvature and enamel band morphology of the specimen, and, in the absence of more conclusive evidence, it is better identified as *Cuvieronius hyodon* (cf. Laurito, 1990). Thus, although *Haplomastodon* is very abundant in northern South America (i.e. Colombia), at the moment there are no definitive Central American records of *Haplomastodon*.

Mammuthus

Mammoths (*Mammuthus*) (Fig. 2) are probably the best known fossil proboscideans. They have a fossil record in the Plio-Pleistocene of Eurasia and in the North American Pleistocene. Our perception of the evolution and taxonomy of North American *Mammuthus* is that of Maglio (1973), Agenbroad and co-workers (Agenbroad, 1984, 1994, 2005; Agenbroad & Mead, 1996) and Lucas and collaborators (Lucas, 1996; Lucas & Effinger, 1991; Lucas et al., 1993, 1999, 2000). Thus, *Mammuthus* immigrated into North America via Beringia at or near the beginning of the Irvingtonian LMA, ~ 1.6-1.8 Ma. Indeed, its first appearance datum has traditionally been used to define the beginning of the Irvingtonian LMA (Bell et al., 2004). The founder population of North American *Mammuthus* is well represented by the lower jaw of *M. meridionalis* (= *M. hayi*) from Tijeras Arroyo, New Mexico (Lucas, 1996; Lucas & Effinger, 1991; Lucas et al., 1993).

Polymorphic populations of North American *Mammuthus* evolved gradually through the Pleistocene, much as did Old World *Mammuthus* (Lister, 1996). *M. imperator* (the Imperial mammoth) is the descendant of *M. meridionalis* in North America, and it co-occurs with mammoths with the morphology of *M. meridionalis* (older samples) and *M. columbi* (younger samples). *M. columbi* (the Columbian mammoth), the descendant of *M. imperator*, was the common Late Pleistocene mammoth in North America (Maglio, 1973; Agenbroad, 1984, 2005). Chronologically, *M. meridionalis* in North America is restricted to the Early Pleistocene (about 1.8 to 1.2 Ma), *M. imperator* is late Early and Middle Pleistocene (about 1.2 Ma to 130,000 years old), and most *M. columbi* are Late Pleistocene (about 130,000 to 10,000 years old).

Most *Mammuthus* records in Central America are of *M. columbi*, and are from Honduras, El Salvador, Nicaragua and Costa Rica (Fig. 1, Table 1, Appendix; Laurito & Aguilar, 2007). However, more primitive and older *Mammuthus* (*M. cf. M. hayi* of Cisneros, 2008, which we identify as *M. meridionalis*) are known from El Salvador. Clearly,

Mammuthus immigrated from North America into Central America during the Early Pleistocene.

Mammut

The American mastodont (*Mammut americanum*) (Fig. 2) is one of the most widely distributed Pleistocene proboscideans in North America. Records range in age from Blancan to Rancholabrean and extend from Alaska to Florida and to Puebla in central Mexico (e.g., Kurtén & Anderson, 1980; Shoshani, 1990; Saunders, 1996; Polaco et al., 2001; Green, 2002); the southernmost record of *M. americanum* is in Honduras (Lucas & Alvarado, 1991a). Characteristic features of the American mastodont include a low and long skull with long and curved tusks, no lower tusks and last molars with 4 or 5 lophs/lophids and no cusps (pillars) in the valleys. The single record of the American mastodont from Central America is of a M3 from San Pedro Sula, Honduras (Lucas & Alvarado, 1991a).

CENTRAL AMERICAN PROBOSCIDEAN RECORDS

Proboscidean fossils are known from all of the Central American countries except Belize (Fig. 1, Table 1, Appendix). In the Appendix to this article, we review all of these records and provide discussion of the taxonomy, age and reliability of the proboscidean records from Central America. Below, we present a brief synopsis based on the much more detailed information in the Appendix.

Guatemala

Well-documented Guatemalan proboscidean records are of *Gomphotherium* and *Cuvieronius*, and it is likely that the Guatemalan records of *Gomphotherium* are of the same age as the Honduran records from the Gracias Formation (early Hemphillian). Guatemalan

Cuvieronius records are most likely Late Pleistocene, whereas a single undocumented mammoth record (mentioned by Arroyo-Cabrales et al., 2007, p. 18) is also likely of Late Pleistocene age.

Honduras

Honduras has the most extensive record of Miocene proboscidean fossils in Central America and a less extensive Pleistocene record. *Gomphotherium* fossils in the Gracias Formation are numerous, well dated as early Hemphillian, and provide what we regard as the oldest reliably-dated proboscidean records in Central America. Other Honduran records are Pleistocene occurrences of *Cuvieronius*, *Mammuthus columbi* (Fig. 8) and the single Central American record of *Mammut*.

El Salvador

El Salvador has an extensive fossil record of proboscideans assigned to *Gomphotherium*, *Cuvieronius* and *Mammuthus*. Particularly significant is the Chalatenango record of the co-occurrence of primitive *Mammuthus* with *Cuvieronius*, which is confidently assigned an Early Pleistocene (Irvingtonian) age. This is the best evidence that both of these proboscidean genera were in Central America during the Irvingtonian, though it seems likely that *Cuvieronius* dispersed into Central America as early as the late Blancan. Other well-dated Irvingtonian records of *C. hyodon* are from Barranca del Sisimico and Tomayate in El Salvador (see Appendix). The well-dated Rancholabrean record of *C. hyodon* at El Hormiguero (see Appendix) helps also to establish the presence of *Cuvieronius* in Central America during the Rancholabrean.

Nicaragua

All fossil records of proboscideans from Nicaragua are of *Cuvieronius hyodon* (rare) and more common *Mammuthus columbi* and appear to be of Late Pleistocene age. Their greatest significance lies in the relative abundance of *M. columbi*, suggestive of the presence of grasslands/savannah in parts of Nicaragua during the Late Pleistocene.

Costa Rica

Costa Rica has an extensive proboscidean fossil record dominated by fossils of *Cuvieronius hyodon*. One of them, the Santa Ana (Oviedo) site is well dated because the ignimbrite deposits that bracket the alluvial-palustrine strata that yield *C. hyodon* are dated by $^{40}\text{Ar}/^{39}\text{Ar}$ to ~ 0.32 Ma (Pérez et al., 2006). The *Cuvieronius* found at Bajo Barrantes appear to be, by stratigraphic correlations, Upper Pliocene to Lower Pleistocene (see the Appendix). The southernmost record of *Mammuthus* (*M. columbi*) is from Hacienda El Silencio in central Costa Rica. Miocene records of *Gomphotherium* are from San Gerardo de Limoncito and Santa Rita (see Appendix).

Panama

Only two fossil records of proboscideans are known from Panama, both of *Cuvieronius hyodon*, and these are relatively young, circa 45,000 years old (see Appendix).

CENTRAL AMERICA AS THE PROBOSCIDEAN PATHWAY

We divide the history of Central American proboscideans into three immigrations: (1) ar-

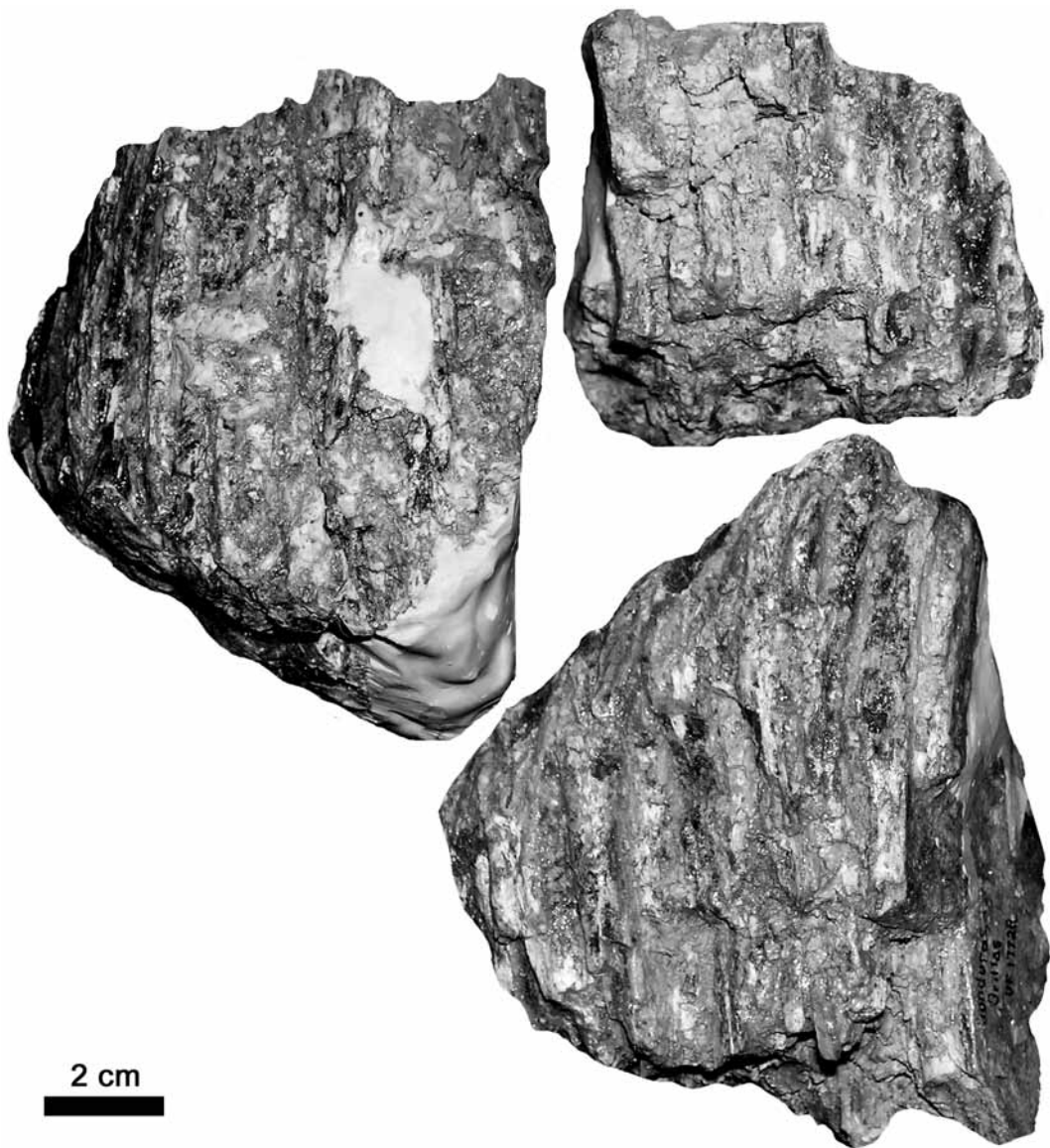


Fig. 8: Molar fragments of *Mammuthus columbi* from the Late Pleistocene Orillas del Humaya locality in Honduras. Fragments are catalogued as UF (Florida State Museum) 17728

rival of *Gomphotherium* during the Late Miocene (early Hemphillian); (2) arrival of *Cuvieronius* during the Pliocene (?) and *Mammuthus* during

the Early Pleistocene (Irvingtonian); and (3) arrival of *Mammut* during the Late Pleistocene (Rancholabrean). We see no evidence for endemic

evolution or a center of origin of proboscideans in Central America, as was most recently advocated by Woodburne et al. (2006), based largely on the supposed presence of *Rhynchotherium* in the Miocene of Honduras. Indeed, reassignment of the Honduran record of *Rhynchotherium* to *Gomphotherium* eliminates the only known evidence for the origin of a proboscidean taxon in Central America. All proboscidean genera known from Central America are also known from North America, which is where they apparently originated. Central America acted as a one way dispersal route for proboscideans from North America to Central America and, in one case, onward to South America (Fig. 9). We therefore refer to Central America as the “proboscidean pathway”.

Arrival of *Gomphotherium*

The initial immigration of proboscideans into Central America apparently occurred during the Late Miocene (early Hemphillian), well documented and calibrated by the extensive record of *Gomphotherium* in the Gracias Formation of Honduras, and at the top of the Curré Formation in Costa Rica, the southernmost record of the genus. *Gomphotherium* records in El Salvador and Guatemala are also likely to be early Hemphillian records.

Prior to the Hemphillian, most of the Pacific slopes of Central America were covered by large shield ignimbritic volcanoes, yet North American mammals made it to Panama (Whitmore & Stewart, 1965; MacFadden, 2006). Nevertheless, no proboscidean fossils are known from the pre-Hemphillian Miocene (Barstovian) mammal assemblages of Panama (MacFadden, 2006). This suggests that proboscideans were confined to North America (including Mexico) for about nine million years, during the Middle and the early-Late Miocene (Barstovian, Clarendonian and part of the Hemphillian), barred from tropical Central

America. The existence of large seaway barrier(s) between Mexico and Central America during the Miocene (cf. Alvarado et al., 2007) may have been a factor in restricting -- but not necessary impeding -- proboscidean immigration, though the Panamanian record of Miocene mammals indicates it was not an impenetrable barrier to the dispersal of North American mammals southward.

Arrival of *Cuvieronius* and *Mammuthus*

The oldest North American records of *Cuvieronius* are late Blancan, and the origin of the genus from *Gomphotherium* (or *Rhynchotherium*?) in North America was likely a late Blancan event (Lucas, 2008a). The co-occurrence of *C. hyodon* and a primitive *Mammuthus* (*M. meridionalis*) at Chaltenango in El Salvador is of Early Pleistocene (Irvingtonian) age, an age assignment indicated by similar co-occurrences in the southern United States (Lucas et al., 1999, 2000) and by the remainder of the Chaltenango fossil mammal assemblage (Cisneros, 2008). This is very significant because it indicates the presence of *Cuvieronius* and *Mammuthus* in Central America during the Early Pleistocene, though it is likely that *Cuvieronius* arrived earlier, in the Pliocene (Fig. 9). *Cuvieronius* evidently dispersed southward into South America soon after its arrival in Central America, because its oldest South American records are of Late Pliocene age (see below).

Mammuthus, however, never made it to South America (the only supposed South American records are very doubtful; see discussion and details in Alvarado, 1994 and Lucas et al., 2007). Thus, other than at Chaltenango, its Central American records are of *Mammuthus columbi* and extend from El Salvador and western Honduras through Nicaragua into central Costa Rica. They are likely all of Late Pleistocene age, and reflect the maximum geographic distribution of that species. All

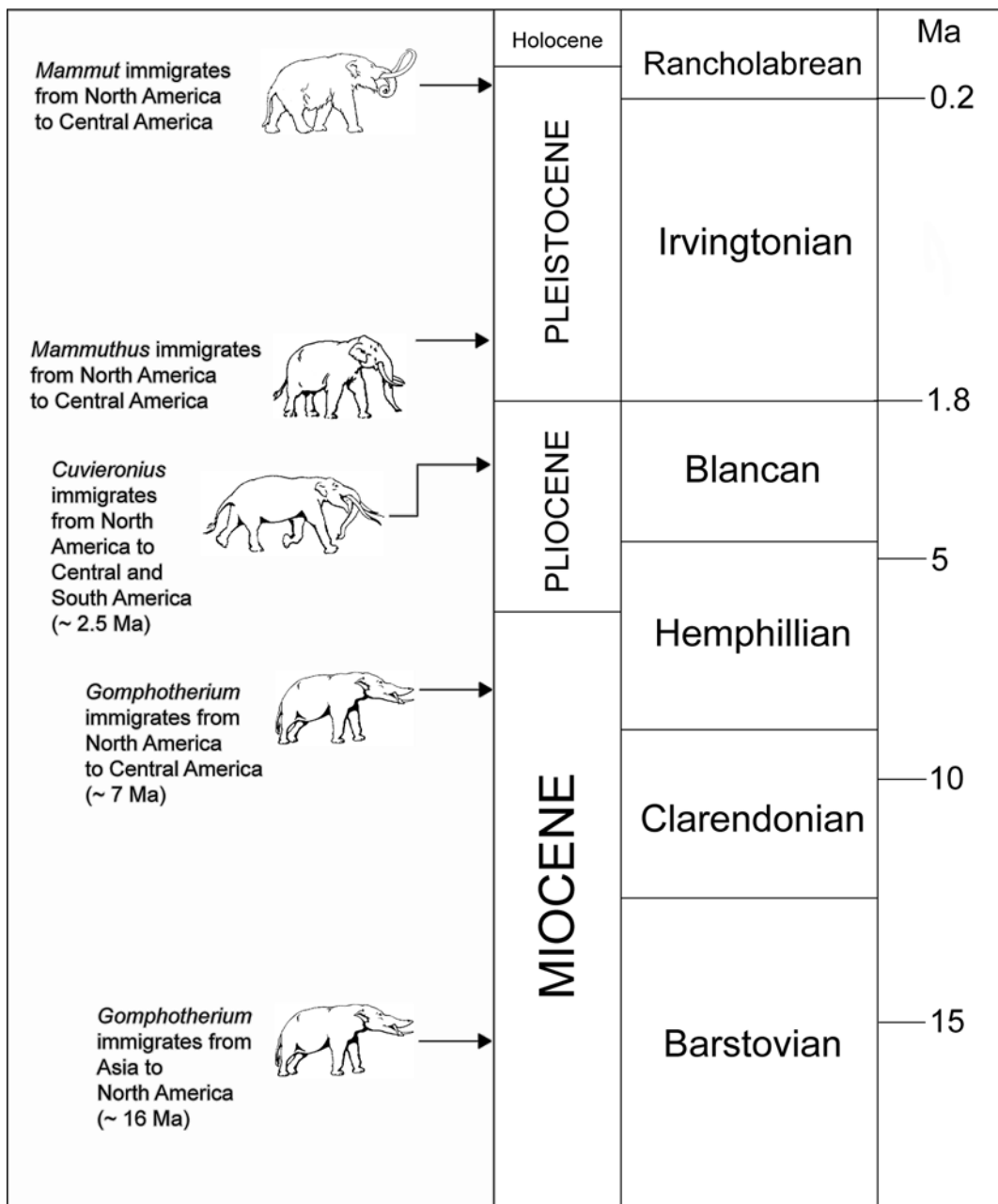


Fig. 9: Temporal distribution of key immigration events in the history of Central American Proboscidea

mammoth fossil localities are on the Pacific slope of Central America. Mammoths were grazing proboscideans, and this suggests the presence of dry woodlands or thorn-scrub savannahs, probably reflecting the rain shadow created by regional uplift (i.e., Talamanca range) and the Central American volcanic range, which accompanied the closing of the Bolivar trench. The idea that by Late Pleistocene time all of Central America was rainforest (Raven & Axelrod, 1975; Webb, 1991) is thus not well supported by the fossil distribution of *Mammuthus*, nor is it supported by the fossil record of *Equus*, *Bison* or by the vegetational history (Gómez, 1986). However, the absence of mammoths south of central Costa Rica is significant, indicating a barrier to their dispersal to the south—likely the tropical jungles of Panama and northern South America (the called “Darién plug”), which did not provide the vegetation necessary to the diet of mammoths (Prado et al., 2005). This barrier evidently also prevented *Haplomastodon* from entering Central America from northern South America.

Arrival of *Mammut*

Mammut, the American mastodont, has a single record in Central America from Honduras that lacks detailed provenance, so its precise age is uncertain. The maximum expansion of *Mammut* in North America was during the Late Pleistocene (Rancholabrean) (King & Saunders, 1984; Saunders, 1996), so it seems likely that the Central American record reflects that expansion (Fig. 9). Although *Mammut* is confidently interpreted as a forest-living proboscidean that browsed on sylvan vegetation, it apparently did not disperse southward to South America, possibly because of a dietary specialization on a particular type of vegetation (Prado et al., 2005).

Proboscidean extinction

The Late Pleistocene extinction of proboscideans in Central America was part of the global extinction of the Late Pleistocene mammalian mega-

fauna that is often attributed to overkill by human hunters or to climate change (warming) at the end of the last glacial age (e. g., Barnosky et al., 2004; Surovell et al., 2005; Koch & Barnosky, 2006). Unfortunately, there are few reliable data to precisely date the youngest proboscidean fossil records in Central America, though no data support an age younger than Late Pleistocene (for example, in Costa Rica, the *Cuvieronius* record at Santa Ana is Middle Pleistocene, and the *Cuvieronius* from Paseo Colón and Tibás are much younger, apparently Late Pleistocene). Despite some claims to the contrary, there are currently no demonstrable human-proboscidean associations in Central America (Hurtado de Mendoza & Alvarado, 1988; Lucas et al., 1997, 2008).

IMPLICATIONS FOR PROBOSCIDEAN EVOLUTION IN SOUTH AMERICA

There is no evidence that Central America acted as a center of evolution for proboscideans during the late Cenozoic. Instead, Central America was a pathway—another well trodden road across which the Proboscidea migrated to achieve a nearly global distribution during the Pleistocene. *Gomphotherium* arrived in Central America during the Late Miocene, *Cuvieronius* passed through during the Pliocene, *Mammuthus* arrived during the Early Pleistocene and *Mammut* arrived during the Late Pleistocene.

López et al. (2001) report proboscidean postcrania from the middle part of the Uquia Formation in northern Argentina, strata with a fission track age of ~ 2.5 Ma that have been correlated magnetostratigraphically to the upper part of the Gauss Chron (C2) (Reguero et al., 2007). This seems to us to be the most reliably dated, oldest record of proboscideans in South America, indicating their first appearance in the continent during the late Marplatense (Sanandresian) LMA (Alberdi & Prado, 1995; Woodburne et al., 2006). Alberdi & Prado (1995) have suggested that the oldest South American proboscidean records are of *Cuvieronius hyodon*, and, if correct, this indicates a rapid dispersal of *Cuvieronius* from North to South America very soon after the clo-

sure of the Panamanian isthmus. The Central American record of this passage appears to be undiscovered because no Central American records of *Cuvieronius* are demonstrably Pliocene. The oldest reliably dated record of *Cuvieronius* in Central America is early Irvingtonian, though perhaps Blancan records exist, and we suggest that *Cuvieronius* passed through Central America during the Pliocene (Blancan), but we have not yet captured its presence until strata of early Irvingtonian age (Fig. 9).

Available data thus suggest a single immigration of *Cuvieronius* from Central America to South America during the Pliocene, and that this is the first entry of proboscideans into South America. Note that we agree with Alberdi et al. (2004) and Ferretti (2008) that “*Amahuacatherium*” from the “Miocene” of Peru (Campbell et al., 2000a, b, 2009, 2010) is a specimen of *Haplomastodon* most likely from a deposit of Late Pleistocene age. However, if *Amahuacatherium* is accepted as a distinct proboscidean taxon from a Miocene (older than 9.5 Ma) deposit, then it could be argued that the late Hemphillian (~ 7 Ma) appearance of *Gomphotherium* in Central America postdates an earlier immigration of gomphotheres into South America. Nevertheless, there are no known South American gomphotheres between the putative age of *Amahuacatherium* (< 9.5 Ma) and their oldest reliably dated record (~ 2.5 Ma). Proboscidean immigrations into Eurasia and into North America during the Miocene were followed rapidly by diversification and proliferation, so that proboscidean fossils became common components of post-immigration fossil assemblages. If *Amahuacatherium* demonstrates a Miocene immigration of proboscideans into South America, why are there no proboscidean fossils for at least seven million years? This is another argument against the Miocene age of *Amahuacatherium*. Instead, we believe that the South American fossil record of proboscideans begins in the Pliocene (Marplatan) and is followed by an abundance and diversity of proboscideans in the Pleistocene. This is consistent with the single Pliocene immigration of *Cuvieronius* into South America followed by diversification into

Haplomastodon and *Notiomastodon*, and a rapid spread of proboscideans to as far south as Chile and southern Argentina.

The absence of *Stegomastodon* in Central America does not support the immigration of this genus into South America advocated by Alberdi et al. (2002, 2004, 2007) and Prado et al. (2003). Recognition of *Notiomastodon* as a distinct genus to encompass specimens from South America previously assigned to *Stegomastodon* (Cabrera, 1929; Madden, 1984; Ferretti, 2008) also does not support the concept of an immigration of *Stegomastodon* from North to South America. South American proboscideans are thus a modest Plio-Pleistocene evolutionary radiation of *Cuvieronius hyodon* in the Andean Cordillera and its apparent descendants *Notiomastodon* and *Haplomastodon* in the Brazilian tropical lowlands and the Argentine pampas.

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APPENDIX

Proboscidean fossils are known from all of the Central American countries except Belize (Fig. 1, Table 1). In this Appendix, we review all of these records and provide discussion of the taxonomy, age and reliability of the proboscidean records from Central America. We do so by first discussing proboscidean records that we consider reliable—those based on fossil specimens that have been described (illustrated), or on fossils that we have examined or that have been reported by a reliable authority. Then, we also list less reliable records, which are numerous and often little more than reports without any documentation.

Guatemala

Chinautla: Osborn (1926, p. 12; also see Osborn 1936, p. 432) named the new species *Serridentinus guatemalensis* for an incomplete upper molar from Chinautla, but provided no more detailed provenance. This tooth clearly belongs to *Gomphotherium* (Lucas et al., 2007), and *S. guatemalensis* is likely a synonym of *G. hondurensis*. This is presumably a Miocene record.

Estanzuela: a tooth of *Mammuthus columbi* collected by Barnum Brown (we have seen this molar in the Museo Estanzuela in Zacapa) together with other Late Pleistocene mammal fossils.

Río Carboneras: Lucas & Alvarado (1995) reported isolated cheek teeth they assigned to “*Rhynchotherium blicki*” from the Herreria Formation along the Río Carboneras in eastern Guatemala (also see Mota-Vidaurre, 1989; Madden & Mota-Vidaurre, 1989). Based on this record, they suggested a Hemphillian age by correlation to the Gracias Formation in Honduras. We concur and consider this a likely Hemphillian record of *Gomphotherium hondurensis* (cf. Lucas & Morgan, 2008).

Río de la Pasión: Woodburne (1969) reported *Cuvieronius*? as part of an extensive Late Pleistocene (Rancholabrean) mammal assemblage from a playa of the Río de la Pasión near the town of Santa Amelia.

Río Usumancita: Vinson (1962) mentioned the presence of *Cuvieronius* in Pleistocene deposits in the vicinity of the Río Usumancita in the Petén-Chiapas frontier.

Zacapa: In the Museo Estanzuela in Zacapa we have examined molars and a mounted skeleton of *Cuvieronius hyodon* found in the vicinity of Zacapa. These are presumably Pleistocene fossils.

Other localities: Ibarra (1980) lists several proboscidean records from Guatemala that lack documentation: (1) Jutiapa—“pieza de mamut:” (2) Huehuetenango—a mastodont; (3) Chinautla—*Cuvieronius* or “*Haplomastodon*,” and (4) Tulumaje y Tulumajillo—a proboscidean.

Honduras

Gracias Formation: Various localities in the Gracias Formation, between Gracias and Las Flores in western Honduras, yield an extensive assemblage of Late Miocene (early Hemphillian) vertebrate fossils including the type material and other specimens previously assigned to *Aybelodon hondurensis* and *Blickotherium blicki* (Frick, 1933; Olson & McGrew, 1941; Webb & Perrigo, 1984; Lucas & Morgan, 2008) (Fig. 3). Assigning these proboscidean fossils to one taxon is well accepted (Webb & Tessman, 1968; Tobien, 1973; Webb & Perrigo, 1984; Lucas & Morgan, 2008), and they were long placed in the genus *Rhynchotherium*. However, revision of the genus excludes these species, which are regarded as derived specimens of *Gomphotherium* (Lucas & Morgan, 2008). This is a significant taxonomic conclusion because it eliminates the oldest supposed record of *Rhynchotherium* (North American records begin during the latest Hemphillian) and eliminates the principal *Rhynchotherium* record in Central America.

Orillas del Humaya: The cutbank of the Río Humaya, north of Comayagua, yields a Late Pleistocene vertebrate fossil assemblage that includes two broken molars of *Mammuthus*. Webb & Perrigo (1984, p. 252) report a plate frequency of 8/100 mm and identified the fossils as *Mammuthus*

cf. *M. columbi*. These molars are in the Florida State Museum catalogued as UFL 17728 (Fig. 8). Their relatively thin plates and thin enamel bands justify assignment to *M. columbi*.

San Pedro Sula: Lucas & Alvarado (1991a) documented a right M3 of the American mastodont, *Mammuthus americanum*, from San Pedro Sula in northern Honduras. Nothing is known about the geological provenance of this fossil, and we assume it is of Rancholabrean age.

Tambla: Leidy (1859) reported an isolated molar collected from Tambla (= present day Humaya: M. Bonta, written commun, 2010) that he identified as *Mastodon*, and later illustrated (Leidy, 1869, pl. 27, fig. 14) and referred to it as possibly belonging to "*Mastodon andium*". Osborn (1936, fig. 454C) also illustrated this tooth (it is a left M3), and we have examined it in the collection of the Academy of Natural Sciences in Philadelphia. Osborn (1936) assigned the Tambla molar to *Rhynchotherium*, but it is indistinguishable from *Cuvieronius hyodon*, to which we assign it (as did Lucas et al., 2007, fig. 16.2.a). Earlier, LeConte (1858, p. 7) mentioned the "Mastodon bed" near "Tambla", assigning the fossils to "*Mastodon giganteus*". Squier (1859, p. 610) also noted that "huesos grandes" are present "about a league from Tambla, in a sandstone formation, and consist of a large deposit of the fossilized bones of the mastodon....not simply the remains of a single skeleton, but of several...." Squier (1859, p. 610) also illustrated a molar in a dentary fragment from this bone bed that appears to us to be *C. hyodon*.

Yeroconte: The Yeroconte locality in northwestern Honduras yields a Late Pleistocene (Rancholabrean) vertebrate fossil assemblage dominated by remains of the giant ground sloth *Eremotherium laurillardi*. It includes the isolated humerus and ulna of a gomphothere, probably (but not demonstrably) *Cuvieronius* (McGrew, 1942; Webb & Perrigo, 1984; Lucas, 2008b, fig. 6).

Other localities: (1) Tamara-Sapper (1905, p. 12-13) reported bones of a "mastodont" from near Tamara as follows: "Según el Dr. Fritzgärtner, en el camino de Tegucigalpa a Támara afloran primero margas, areniscas y conglomerados y luego tobas blancas. Debajo de las tobas se descubrieron cerca

de Támara, maderas petrificadas y carneolos rojos así como también algunos huesos de mastodonte...." (2) Potrerillo--Sapper (1905, p. 12-13) also reported a mastodont skeleton "Cerca de Potrerillo, en el departamento de Paraíso, afloran rocas calcáreas, en Danlí en parte conglomerados de cuarzo y en parte sedimentos cuaternarios. El Dr. Fritzgärtner encontró en el cuaternario de Danlí, un esqueleto casi completo de mastodonte, el cual fue llevado al Museo Nacional de Tegucigalpa, que ahora no existe."

El Salvador

Barranca del Sisimico: *Cuvieronius* sp. has been reported from this locality, which is along the Río Sisimico, approximately 1.5 km SW of the 67 km mark on the Pan American Highway. The site is in the Cuscatlán Formation (Webb & Perrigo, 1984), and is considered to be Early Pleistocene (Irvingtonian) based on the primitive evolutionary stage of the two ground sloth species collected there (Webb & Perrigo, 1985).

Cantón Magdalena: Cisneros (2008) reported an indeterminate gomphotheriid from Caserio la Criva (Municipality of Chalchuapa).

Chalatenango: Cisneros (2008) documented *Mammuthus* and *Cuvieronius* specimens from the Department of Chalatenango. He assigned a partial left lower molar to *Mammuthus* cf. *M. hayi*, and a partial tusk to *Cuvieronius*. Based on the tentative identification of *Mammuthus* cf. *M. hayi*, he assigned the site an Irvingtonian age. We regard this as a primitive *Mammuthus* best assigned to *M. meridionalis* following the taxonomy of Maglio (1973) and Lucas et al. (1993, 1999, 2000). This new find of *Mammuthus* is remarkable for its co-occurrence with *Cuvieronius*, similar to several co-occurrences of these genera in the United States (Hibbard & Dalquest, 1966; Webb & Dudley, 1995; Lucas et al., 1999, 2000). These North American localities are of Irvingtonian age, which suggests *Mammuthus meridionalis* (= *M. hayi*) was the only mammoth species to co-exist with *Cuvieronius*. Webb & Dudley (1995) suggested that *M. meridionalis* and *Cuvieronius* formed mixed herds in coastal savannas.

Corinto: A series of exposures of alluvial sediments between ignimbrite units in the Río Torola Valley (Municipality of Corinto) yielded a Hemphillian mammal assemblage including "*Rhynchotherium blicki*" (Cisneros, 2008), which we assign to *Gomphotherium hondurensis* (cf. Lucas & Morgan, 2008). The Corinto mammal assemblage is correlated to the Hemphillian Gracias Formation assemblage in Honduras (Webb & Perrigo, 1984). Cisneros (2008) also correlated Corinto with the Río Carboneras site in eastern Guatemala (Herrería Formation) based on the specimens of "*Rhynchotherium blicki*" reported by Lucas & Alvarado (1995).

Río de Jerusalén: A molar of *Mammuthus "jeffersonii"* (Stirton & Gealey, 1949; Lardé-y-Larín, 1950), which we attribute to *M. columbi*.

San Juan del Sur (El Hormiguero): This long known locality (Stirton & Gealey, 1949; Lardé, 1950; Webb & Perrigo, 1984) is on San Juan del Sur farm, between the departments of Morazán and San Miguel, and yields a Rancholabrean-age mammal assemblage (*Bison* is present) that includes *Cuvieronius hyodon*.

Santa Ana: A complete mandible, incorrectly referred to *Titanotherium* (Lardé-y-Larín, 1950), is most likely a proboscidean (Cisneros, 2008); also, Laurito (1988) reported two *Cuvieronius hyodon* molars from Santa Ana.

Tomayate: This site, along the Río Tomayate (Apopa Municipality), is considered to be Irvingtonian by Cisneros (2005, 2008). In addition to other mammals, there is a large concentration of the proboscidean *Cuvieronius hyodon* within a stratum of unconsolidated ash. Assigning an Irvingtonian age to the locality is based mainly on the presence of the glyptodont *Glyptotherium arizonae* and the camel *Hemiauchenia* cf. *H. seymourensis*.

Other localities: Less reliable proboscidean localities in El Salvador were reported by Lardé (1924, 1950) and Lardé y Larín (1950): (1) Acahuapa-Lempaa (proboscidean maxillary fragment: Lardé-y-Larín, 1950); (2) Gruta de Corinto (proboscidean molar: Lardé, 1924; Lardé, 1950; Lardé-y-Larín, 1950); (3) Chalchuapa (proboscidean molar: Lardé, 1924; Lardé-y-Larín, 1950); (4) Colinas de Jucuarán (probably a proboscidean skeleton, including an incomplete

tusk, vertebrae and fragments of femora: Lardé-y-Larín, 1950); (5) El Almendro (proboscidean mandibular ramus with molars: Lardé-y-Larín, 1950); (6) Ilobasco (proboscidean molars and unidentified fragmented bones: Guzmán, 1950; Lardé-y-Larín, 1950); (7) Jayaque (proboscidean molars and other bones: Lardé, 1924; Lardé-y-Larín, 1950); (8) Nueva Esparta (two proboscidean molars: Lardé-y-Larín, 1950); (9) Río Chula—in the stream bed of the Río Chula (a proboscidean molar and other fragmented bones: Stirton & Gealey, 1949); (10) Río de Los Frailes (a rather complete proboscidean skeleton: Guzmán, 1950); this find is unusual due to the mention of a lower mandible with a small tusk, which suggests it may belong to a sub-adult individual of *Mammuth americanum* (adults do not have tusks) or to a non-Pleistocene gomphotheriid (*Gomphotherium*); (11) San Agustín (incomplete upper proboscidean tusk and other associated bones: Lardé-y-Larín, 1950); and (12) San Juan Buenavista (several remains of a proboscidean, partially articulated: Jiménez, 1959); photographs of an incomplete molar (Jiménez, 1959: p. 12) suggest *Cuvieronius*.

Nicaragua

El Bosque: At the El Bosque locality, southwest of Pueblo Nuevo, Espinoza (1976) reported (but did not document) *Stegomastodon* and *Gomphotherium*. Reshetov (1982) pointed out that this record should be revised, and Laurito & Valerio (2005) said that such a preliminary determination was never confirmed and the specimen(s) could correspond to *Cuvieronius*. In fact, these identifications are highly unlikely given the Late Pleistocene age of the El Bosque fossil assemblage (Lucas et al., 2008). At El Bosque, only the presence of the proboscidean *Cuvieronius hyodon* can be verified based on an incomplete molar (Lucas et al., 2008).

El Palmar: Lucas et al. (2008) documented the partial skeleton of a mammoth (including a lower jaw) collected from volcanoclastic sands at the El Palmar (Las Moras) locality in southern Nicaragua, which is north of the highway

between Rivas and Tola in the drainage of the Río Chacalapa. The partial mammoth skeleton from El Palmar consists of the lower jaw, the glenoid portions of both scapulae, both humeral heads, the proximal ends of both ulnae, several vertebral centra, many rib fragments, some carpals and an incomplete femur. The lower jaw contains the left and right m3s. Morphology and metrics of the jaw and teeth are characteristic of *Mammuthus columbi* (Lucas, 2005; Lucas et al., 2008).

Jalapa: The Jalapa (El Chorro) locality is in a channel deposit of a Pleistocene river on the northeast bank of the small river called El Chorro, southwest of Jalapa, in northernmost Nicaragua (Lucas et al., 2008). Leidy (1886) first reported fossil mammals from Nicaragua at Jalapa, including "*Mastodon andium*". Some of the fossils Leidy described are still housed in the Academy of Natural Sciences, Philadelphia (Lucas et al., 2008), but we have not been able to locate the fossils that Leidy identified as "*Mastodon andium*", which most likely would be referred to *Cuvieronius hyodon* (Lucas, 2008a, c).

Las Banderas: Lucas et al. (2008) mentioned the presence of mammoth postcranial bones in alluvium at a stone quarry near Las Banderas in northern Nicaragua.

Masachapa: Lucas et al. (2008) documented molar and tusk fragments of *Mammuthus columbi* from the Masachapa locality. The locality is an alluvial deposit that forms a sea cliff near Masachapa in southwestern Nicaragua.

Matagalpa: At Matagalpa, numerous bones and a molar of the proboscidean *Cuvieronius* were collected from the bank of the Río Viejo. These fossils are documented in a photograph taken 27 February 1940 by Omas Medrano and stored in the Museo Nacional de Nicaragua archive, but the fossils are apparently lost, and we have not relocated the fossil site (Lucas et al., 2008).

Other localities: Two less reliable records of proboscidean fossils are known from Nicaragua: (1) Jinotepe—Lucas et al. (2008) noted that south of Lake Aranás (north of Jinotepe), some

proboscidean postcrania were discovered while digging a water well but were subsequently lost; and (2) Sébaco—Lucas et al. (2008) reported bones of a mammoth (now lost) from the Sébaco (Palo Verde) locality, which is a man-made well dug just west of the Río Grande de Matagalpa.

Costa Rica

Lucas et al. (1997) provided a detailed review of the fossil proboscidean record in Costa Rica, so we mostly present a synopsis based on their report.

Agua Caliente: Left M2 and dentary fragment with m2-3 of *Cuvieronius hyodon* (Laurito, 1988; Lucas et al., 1997).

Bajo Barrantes: A neural spine, probably of *Cuvieronius* (Lucas et al., 1997).

Buenos Aires de Palmares: Alvarado (1986) described the locality; Laurito (1988) and Lucas et al. (1997) assigned molars, a jaw fragment and a scapula to *Cuvieronius hyodon*.

Cachí: *Cuvieronius hyodon* (Laurito, 1988).

Candelaria (Quebrada Grande de Palmares): *Cuvieronius hyodon* (Laurito, 1988).

Claras de Guayabo de Mora: Left and right m3s of *Cuvieronius hyodon* (Alvarado, 1986; Laurito, 1988; Lucas et al., 1997).

Hacienda del Silencio: Incomplete lower molar of *Mammuthus columbi* (Gutiérrez, 1963; Lucas et al., 1997, fig. 8)

Península de Nicoya: Five localities (Hacienda las Ánimas, Nicoya, Quirimán, Barra Honda and San Fernando) yield proboscidean fossils from surficial alluvium, colluvium and/or swamp sediments (Alvarado, 1986; Lucas et al., 1997). From Hacienda las Ánimas, Alfaro (1911) and Segura (1938, 1942) reported "*Mammuthus andium*" "from Hacienda las Ánimas", and Laurito (1988, figs. 25-27) and Lucas et al. (1997) documented a right m2 of *Cuvieronius hyodon*. From the Nicoya 2 locality, Segura (1942) originally reported *Trilophodon* sp., but Lucas et

al. (1997) later documented molar fragments of *C. hyodon*. Lucas et al. (1997) also documented a m3 fragment of *C. hyodon* from the Nicoya 1 locality. Segura (1938, 1942) and Meléndez (1954) reported *Mastodon* sp. from Quirimán de Nicoya. At Barra Honda (Río Nacaome), *C. hyodon* is known from a left p4, incomplete right m3 and incomplete molar (Mora, 1981; Laurito, 1990; Lucas et al., 1997; Acuña-Mesén & García-Díaz, 1998), and from a lower jaw (Laurito et al., 1993). At San Fernando, vertebrae have been referred tentatively to *Cuvieronius* (Lucas et al., 1997).

Tibás 1: Tip of tusk, molar fragments and distal end of femur of *Cuvieronius hyodon* (Snarskis et al., 1977; Laurito, 1988; Lucas et al., 1997).

Tibás 2: Tusk and molars of *Cuvieronius hyodon* (Laurito, 1988; Lucas et al., 1997).

Quebrada Rivera (Tibás 3): Molar of *Cuvieronius hyodon* (Laurito & Valerio, 2004).

Río María Aguilar: Right m2 of *Cuvieronius hyodon* (Laurito, 1988; Lucas et al., 1997).

Paseo Colón: Incomplete molars of *Cuvieronius hyodon* (Alvarado, 1986; Laurito, 1988; Lucas et al., 1997).

Santa Ana (Sitio Oviedo): Tusk fragments and a right m3 of *Cuvieronius hyodon* (Alvarado, 1986; Laurito, 1988; Lucas et al., 1997).

Santo Domingo: Molar fragments of *Cuvieronius hyodon* (Alvarado, 1986; Laurito, 1988; Lucas et al., 1997).

San Gerardo de Limoncito: Valerio & Laurito (2008) documented two deciduous premolars and tusk fragments with enamel bands that they assigned to "*Rhynchotherium*" (= *Gomphotherium*) *blicki*. However, the deciduous premolars and tusk fragments are not easily distinguished from *Cuvieronius hyodon* (compare, especially, Valerio & Laurito, 2008, fig. 1 with Lucas, 2008a, fig. 6A). Particularly significant is the relatively broad anterior lophids of the Costa Rican deciduous premolars, which apparently distinguish them from the deciduous premolars of *Gomphotherium*, which have relatively narrow anterior lophids so

that the teeth have a more triangular occlusal outline than do the Costa Rican deciduous premolars (compare Valerio & Laurito, 2008, fig. 1 to Frick, 1933, figs. 33, 37). Thus, it is necessary to emphasize and clarify that there is an overlapping range of morphological variation in deciduous teeth of *Gomphotherium* and *Cuvieronius*.

The selachians (sharks and rays), such as *Isurus desori*, *Isogomphodon caunellensis*, and *Hemipristis serra*, from San Gerardo de Limoncito are Miocene taxa (Laurito & Valerio, 2008a). Other vertebrate and invertebrate fossils from San Gerardo de Limoncito have a longer chronological range (Oligocene to Pliocene), and the microforaminiferan *Orbulina universa* (Laurito & Valerio, 2008a, b) is present and has a temporal range from Middle Miocene to Holocene. Thus, the concurrent range zone age of the fossiliferous layer is Middle to Late Miocene. An inferred and more restricted age assignment of Late Miocene (Hemphillian) can be advocated because the fan delta deposits that contain the fossil layer are located at the top of the Curré Formation (Valerio & Laurito, 2008), also in agreement with regional stratigraphic correlations (i.e. Alvarado et al., 2009). An Early Pliocene age is more speculative. Therefore, based on its biostratigraphic position (Miocene, perhaps Upper Miocene), the proboscidean from San Gerardo de Limoncito is more likely *Gomphotherium*. We thus identify this as a Miocene record of *Gomphotherium* in Table 1.

Santa Rita: Laurito and Valerio (2005) identified a palate with M2-3s as "*Rhynchotherium*" *blicki*, with an estimated age of Early Pliocene, but later evaluation confirms that the fossiliferous conglomerate corresponds to the same conglomerate of the locality of San Gerardo de Limoncito, previously described (located 9.8 km to the west of Santa Rita), and therefore it is of probable Late Miocene age (Valerio & Laurito, 2008). But as noted by Lucas & Morgan (2008), this specimen lacks diagnostic features of *Rhynchotherium*, and based on its age is best identified as *Gomphotherium*.

Other localities: Lucas et al. (1997, table 1) listed various additional proboscidean records from Costa Rica that cannot be further documented: Quirimán de Nicoya, Nicoya 1, Nicoya 2, San Fernando, Quebrada Fierro, Cirri de Naranjo, San Miguel de Turrúcares, and Potrero Grande.

Panama

El Hatillo: On the Azuero Peninsula, Gazin (1957, p. 347) identified *Cuvieronius* associated with other Late Pleistocene

mammals, including *Equus*, *Eremotherium* and *Glossotherium*.

La Trinidaíta: Also on the Azuero Peninsula, this locality is about 9 km west of Pesé. Pearson (2005) reported *Cuvieronius tropicus* (tooth fragments, vertebrae, part of a rib and a tibia) associated with *Eremotherium*. He obtained radiocarbon ages of ~ 45, 000 14C yr. B. P. on charcoal associated with the bones. Pearson (2005) also inferred that this is a likely age for Gazin's nearby El Hatillo locality, which is to say that the Panamanian *Cuvieronius* records (which we assign to *C. hyodon*) date from the Marine Isotope Stage 3 interstadial.