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Quaternary International

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Forum communication

## Quaternary gomphotheres (Mammalia: Proboscidea: Gomphotheriidae) from the continental shelf, Pearl Islands, Panama

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## ARTICLE INFO

## Article history:

Available online xxx

## Keywords:

Pearl Islands  
Panama  
Pleistocene  
Gomphothere  
*Cuvieronius*

## ABSTRACT

Fishermen have recovered four Quaternary proboscidean teeth from the continental shelf in the vicinity of the Pearl Islands, about 50–80 km offshore from the southern coast of Panama. Two upper third molars (M3) and one lower third molar (m3) are similar to comparable teeth of the Pleistocene gomphothere *Cuvieronius* based on the presence of 4½ to 5½ loph/lophids that are either horizontal or slightly inclined to long axis of the tooth and rather complicated enamel with single trefoils, incipient double trefoils, and numerous small accessory cusps. *Cuvieronius* is also known from the Pleistocene El Hatillo and La Triniáita sites from the Azuero Peninsula in Panama. The teeth of *Cuvieronius* from the Pearl Islands are referred to *C. hyodon* following recent taxonomic revisions indicating a single pan-American species of this genus was present in both North America and South America. The oldest records of *Cuvieronius* are from early Pleistocene (early Irvingtonian) faunas in El Salvador, Florida, and New Mexico. *Cuvieronius* dispersed to South America in the early Pleistocene during the Great American Biotic Interchange, with the earliest record of *C. hyodon* on that continent from the early to middle Pleistocene (Ensenadan) Tarija fauna in Bolivia. The two late Pleistocene populations of *C. hyodon* in the Neotropical region have a disjunct biogeographic distribution, with the population from southern Mexico and Central America separated from the second population in the Andean highlands of Ecuador, Peru, and Bolivia by a distance of about 1000 km. The intervening region comprising the lowland tropics of northern South America was populated by the gomphothere *Notiomastodon* during the late Pleistocene, although *Notiomastodon* is also known from Andean localities in Ecuador and Peru. Two of the *Cuvieronius* teeth from the Pearl Islands were recovered in nets by shrimp fisherman from depths of about 90 m, likely indicating they date to the Last Glacial Maximum between 30 and 15 ka, when sea level was as much as 120 m lower than present and the Gulf of Panama was dry land. These teeth represent the first record of late Pleistocene fossils of terrestrial mammals from the continental shelf in Central America.

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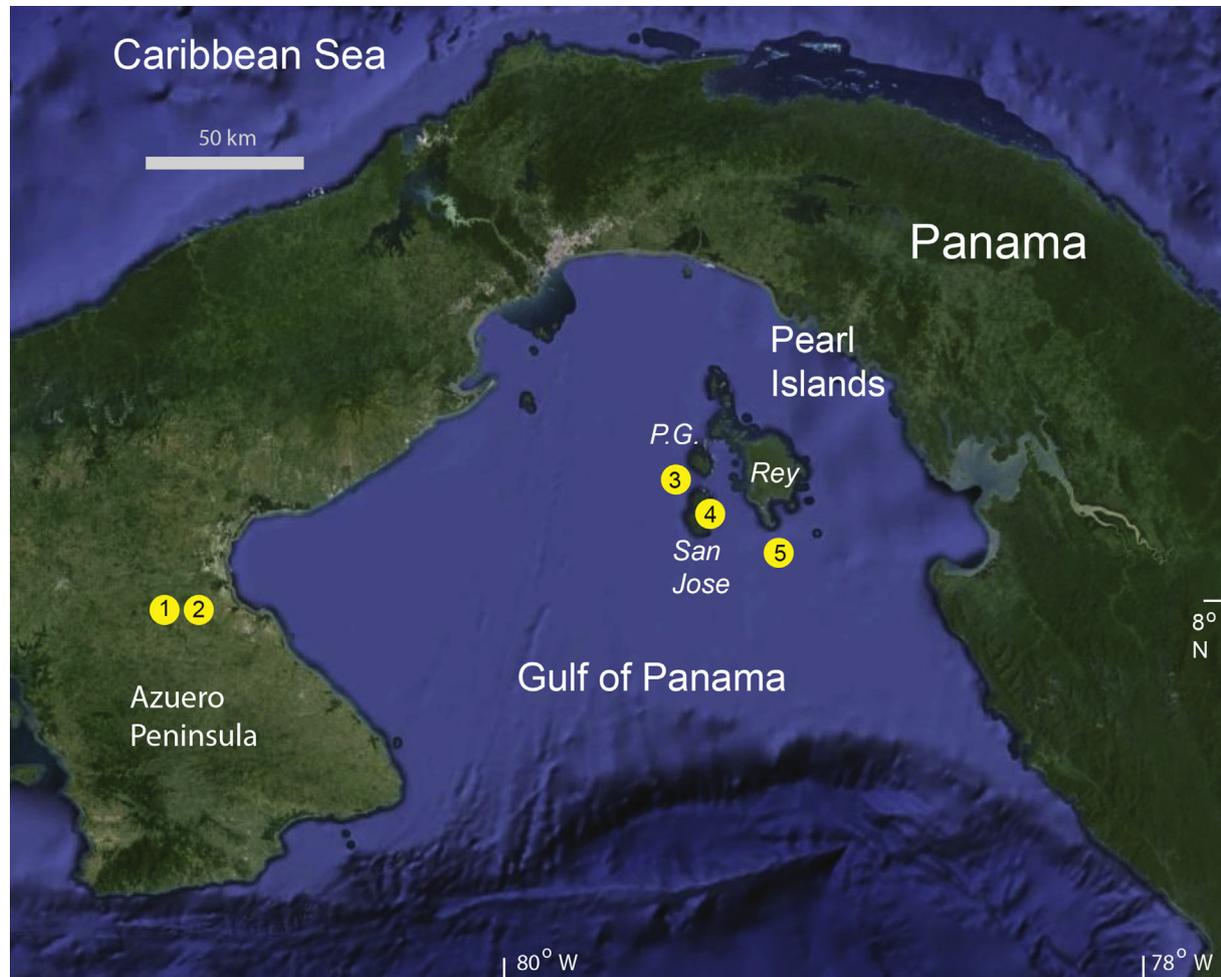
## 1. Introduction

We report four proboscidean teeth of Late Quaternary age from the continental shelf in the vicinity of the Pearl Islands (Archipiélago de las Perlas) in the Gulf of Panama (Golfo de Panamá), offshore from the southern coast of Panama in the eastern Pacific Ocean (Fig. 1). The Pearl Islands fossils consist of three complete teeth and a fourth partial tooth of gomphotheres (Proboscidea: Gomphotheriidae). Two of the teeth were collected in nets by

fisherman from the shallow waters of the Gulf of Panama. Although proboscideans of the gomphothere genus *Cuvieronius* are among the most common mammals from Pleistocene fossil sites elsewhere in Central America (Cisneros, 2005; Lucas and Alvarado, 2010), only two records of *Cuvieronius* were known previously from Panama, both from the Azuero Peninsula (Gazin, 1957; Pearson, 2005; Lucas, 2014). To our knowledge, the Pearl Islands gomphothere fossils represent the first records of Pleistocene mammals from the continental shelf in Central America or Mexico. These teeth almost certainly date to a glacial period, when sea levels were as much as 120 m below the present level and the shallow Gulf of Panama was mostly dry land. The two teeth from the Pearl Islands with the best

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**Fig. 1.** Map of Panama showing the location of late Pleistocene sites containing the gomphothere *Cuvieronius hyodon*. Sites 1–2 are on the Azuero Peninsula. Site 1. La Trinidadita. Site 2. El Hatillo. Sites 3–5 are in the Gulf of Panama in the vicinity of the Pearl Islands. Site 3. 8 km west of Isla de Pedro González (abbreviated P. G.) and 10 km northwest of Isla de San José. Site 4. Near Isla de San José. Site 5. South of Isla del Rey. The break in slope at the bottom of the map indicates the edge of the continental shelf at about 200 m depth.

provenance were recovered from a depth of about 90 m, suggesting they date to the late Pleistocene, probably during the Last Glacial Maximum between 30 and 15 ka. We provide descriptions and measurements of Pearl Islands gomphothere teeth, compare them to other gomphotheres from Central America, Mexico, Texas, Florida, and South America, and discuss their taxonomy, biogeography and provenance.

## 2. Materials and methods

The four teeth of gomphotheres from the vicinity of the Pearl Islands are housed in three museums. Two teeth are on display in the Museo de Ciencias Naturales, Panama City, Panama (MCNP); one tooth is on display in the Biomuseo, Panama City, Panama, but is originally from the paleontology collection of the Smithsonian Tropical Research Institute, Center for Tropical Paleontology and Archaeology (STRI/CTPA); and one tooth is in the vertebrate paleontology collection of the U. S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. We also examined comparative specimens of *Cuvieronius* in the vertebrate paleontology collection of the Florida Museum of Natural History at the University of Florida (UF) in Gainesville.

In addition to the museum acronyms listed above, other abbreviations used in this paper are: ka (kilo-anna = thousands of years); Ma (Mega-anna = millions of years); GABI (Great American

Biotic Interchange); LF (Local Fauna); LGM (Last Glacial Maximum); NALMA (North American land mammal age); SALMA (South American land mammal age). The abbreviations for tooth positions are standard for mammals, with upper case letters for upper teeth and lower case letters for lower teeth. For example, M3 is an upper third molar and m2 is a lower second molar. Descriptions of the teeth follow the dental terminology for gomphotheriid proboscideans (Savage, 1955; Tobien, 1973; Lambert, 2007). In discussing gomphotheres from Mexico and Central America, we use the geographic names Mesoamerica, Middle America, and tropical North America interchangeably to refer to this geographic region. We prefer the term “gomphothere” for members of the proboscidean family Gomphotheriidae, rather than the terms “mastodon” or “mastodont” which are used for members of both the Gomphotheriidae and Mammutidae. We restrict usage of mastodon to the Mammutidae, including the American mastodon *Mammut americanum*.

We follow current usage in recognizing the Pliocene/Pleistocene boundary at 2.58 Ma, corresponding to the onset of Northern Hemisphere glaciation and the boundary between the Gauss and Matuyama geomagnetic chrons (Gibbard et al., 2010). The ages, boundaries, and faunal characterizations of the Pliocene and Pleistocene land mammal ages follow Bell et al. (2004) for the Blancan, Irvingtonian, and Rancholabrean NALMA in North America and Marshall et al. (1984) and Cione and Tonni (1995) for the

Uquian (= Marplatan), Ensenadan, and Lujanian SALMA in South America.

### 3. Regional setting

Three complete teeth and one partial tooth of gomphotheres are reported from the shallow waters of the Gulf of Panama near the Archipiélago de las Perlas or Pearl Islands, about 75–100 km southeast of Panama City, Panama (Fig. 1). Based on the available provenance, all four teeth are derived from the continental shelf from depths as great as 90 m. At least two of teeth, and probably all four teeth, were found by fishermen in shrimp nets that were dragged along the sea floor. For the two teeth known to have been caught in fisherman's nets, the depths should be considered approximations since we do not know the exact distances or depths over which the nets were dragged. Not surprisingly, considering the conditions of their discovery, these specimens have imprecise localities and lack geological data or other associated faunal remains. One tooth was found south of Isla del Rey, the largest of the Pearl Islands, two teeth were found near Isla de San José, and a fourth tooth was found west of Isla de San José and Isla de Pedro González (Fig. 1). The area of the Pearl Islands and continental shelf circumscribed by the localities for these fossils is between approximately 8° 10' and 8° 21' North latitude and 78° 40' and 79° 12' West longitude. These sites range from 50 to 80 km offshore from the southern coast of Panama. The latitude of the Pearl Islands proboscidean teeth would make them among the southernmost Quaternary fossils known from Central America. Specimens of *Cuvieronius* and other mammals from Late Quaternary sites on the Azuero Peninsula of Panama were found slightly farther south, between 7° and 8° North latitude, about 200 km southwest of the Pearl Islands (Gazin, 1957; Lucas, 2014).

#### 3.1. Previous records of Quaternary proboscideans from Panama

There are three published records of Pleistocene proboscideans from Panama. Gazin (1957) described the giant ground sloth *Eremotherium* from the El Hatillo site (Fig. 1, site 2), located about 2 km west of Pesé in Herrera Province on the Azuero Peninsula in south-central Panama (7° 55' N, 80° 38' W), and also discussed an associated vertebrate fauna of about 10 species, including a proboscidean. Gazin (1957) tentatively identified the El Hatillo proboscidean as *Cuvieronius hyodon*, recognized at that time as a South American species. Pearson (2005) identified a tooth fragment, three vertebrae, and tibia of *Cuvieronius* from the La Triniáita site (Fig. 1, site 1), located just west of El Hatillo about 9 km west of Pesé (7° 54' N, 80° 42' W). Pearson referred the gomphothere material from La Triniáita to *C. tropicus*, generally recognized as the North American species of *Cuvieronius* (see taxonomic discussion below). Lucas (2014) reexamined the late Pleistocene mammalian fauna from El Hatillo. He described and illustrated the gomphothere teeth previously mentioned by Gazin (1957), referring these specimens to *C. hyodon*. The El Hatillo and La Triniáita sites are located at an elevation of about 100 m on the Azuero Peninsula about 30 km inland from the Bahía de Parita, a bay in the western Gulf of Panama. Brief descriptions of the gomphotheres from El Hatillo and La Triniáita are presented below, after the description of the *Cuvieronius* teeth from the Pearl Islands.

#### 3.2. Pearl Islands gomphothere localities

The Pearl Islands proboscidean tooth with the most complete data is a right M3 (USNM 421665), dredged from a depth of 50 fathoms (about 300 feet or 90 m) by a shrimp trawler belonging to a Mr. Earnist. A cast of this tooth was donated to the U. S. National

Museum of Natural History through Robert N. Stewart, formerly a geologist with the U. S. Panama Canal Zone. Although the locality data with the specimen state that the tooth was found "... south of the Pearl Islands of Panama" the coordinates associated with the fossil (8° 21' North latitude, 79° 12' West longitude) place the locality on the continental shelf just west of the Pearl Islands, about 8 km west of Isla de Pedro González and 10 km northwest of Isla de San José (Fig. 1, site 3).

Two teeth on display in the Museo de Ciencias Naturales, Panama City, Panama (MCNP 1 and MCNP 2) were collected by J. V. Delgado from "Isla de San José, Archipiélago de las Perlas" according to the specimen label associated with these teeth (Fig. 1, site 4). Although the locality information does not specify that the fossils were recovered by fisherman, the two MCNP teeth from Isla de San José were collected underwater in a marine environment based on the presence of marine epiphytic invertebrates adhering to the ventral surface of each tooth, including oysters, gastropods, small solitary corals, and bryozoans. The occurrence of the marine epiphytes only on the ventral or underside of the tooth (the roots are broken away) suggests that the teeth were both resting with the occlusal or crown surface facing down on the sea floor. The teeth are a grayish black in color and are heavily mineralized, whereas the attached invertebrates are white and appear to be modern, not fossil.

A fourth gomphothere tooth from the Pearl Islands, a right m3, was originally donated to the collection of Smithsonian Tropical Research Institute/Center for Tropical Paleontology and Archaeology (STRI/CTPA) in Panama in about 2008. The tooth is now on display in the recently opened Biomuseo in Panama City, Panama. On the basis of information provided by the collector to Richard Cooke, an anthropologist with STRI/CTPA, the tooth was recovered by the captain of a shrimp boat trawling in about 50 fathoms of water south of Isla del Rey (Fig. 1, site 5). This is about the same depth (about 300 feet or 90 m) from which the tooth west of Isla de Pedro González and Isla de San José was recovered.

## 4. Results

### 4.1. Descriptions of gomphothere teeth from Panama

#### 4.1.1. Right m3 from Isla del Rey, STRI/CTPA Collection (now on display in the Biomuseo)

A right m3 from south of Isla del Rey in the Pearl Islands, originally in the STRI/CTPA Collection (STRI/CTPA 1) and now on display in the Biomuseo, is very well preserved with an intact crown, but with the roots broken off (Fig. 2). The fossil tooth is black in color and heavily mineralized. It is completely unworn and lacks an interdental wear facet on its anterior margin where the tooth presumably would have contacted the m2. The enamel on the basal half of the crown is highly striated or crenulated, whereas the proximal half of each major cusp is essentially smooth. The tooth also has numerous small to very small, rounded, accessory cusps or cuspids distributed throughout the crown. The total number of all major and accessory cusps on this tooth is about 60 (after Mothé and Avilla, 2015). Cement is absent. The tooth can be identified as a lower m3 on the basis of the presence of more than three complete lophids and the gentle labial curvature from anterior to posterior. Upper M3s also have four or more lophids but are essentially straight from anterior to posterior, not curved. As in mammalian dental terminology in general, lower teeth have dental terms ending in -id whereas upper teeth do not. For instance, a loph on an upper tooth would be a lophid on a lower tooth.

The m3 has five complete lophids and several small cuspids on the posterior edge of the tooth that could be considered a sixth lophid, but generally are regarded as a partial or half lophid, for a

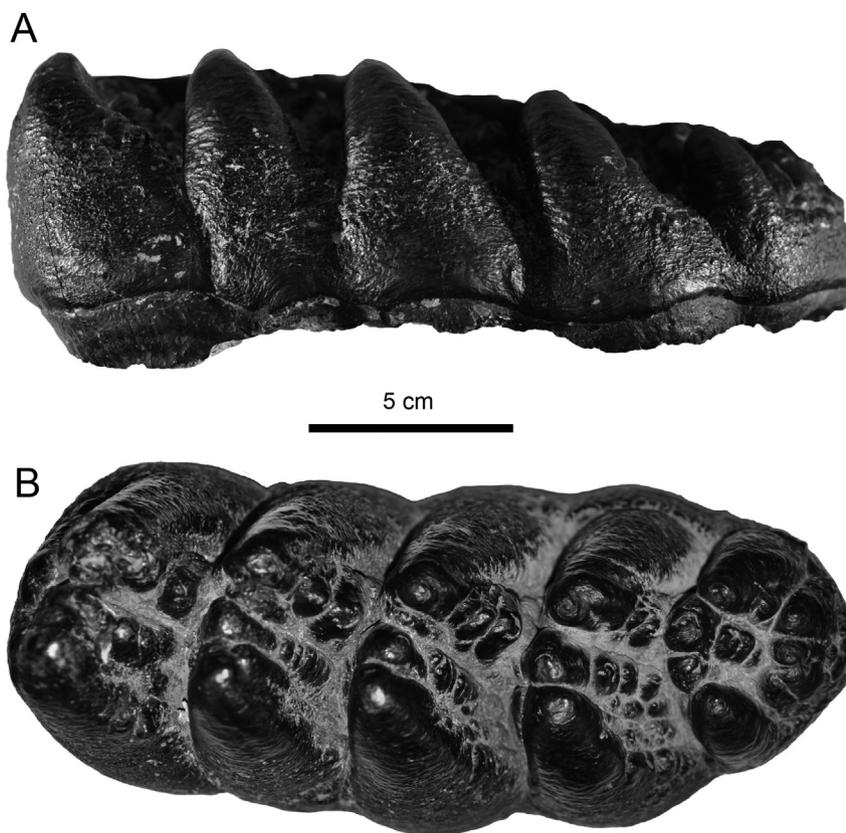


Fig. 2. Right m3 of *Cuvieronius hyodon* from south of Isla del Rey, Pearl Islands, Panama (STRI/CTPA 1). A. Lingual view, B. occlusal view.

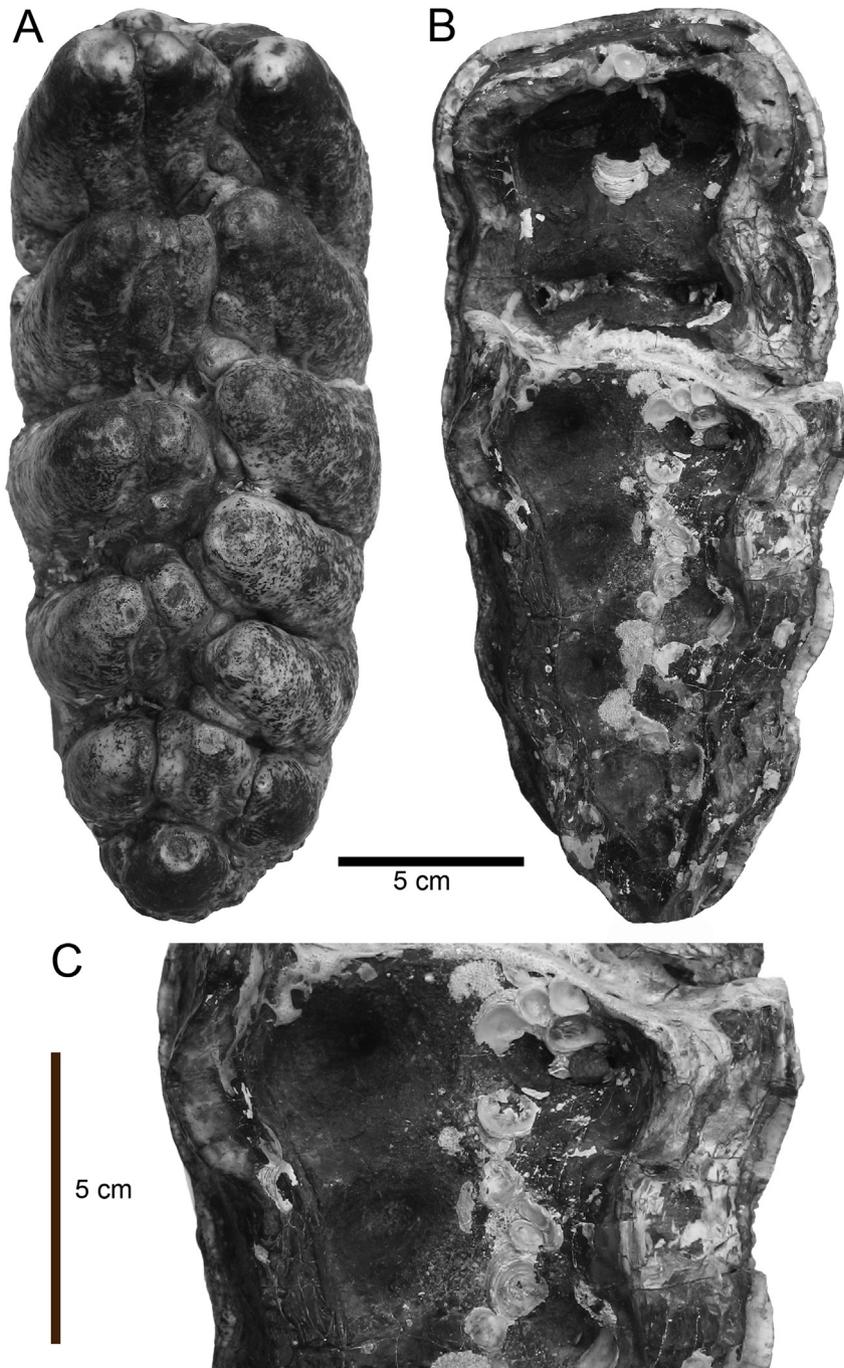
total of  $5\frac{1}{2}$  lophids. The lack of an interlophid between the fifth lophid and the small cuspids on the posterior edge of the m3 suggests that these cuspids could also be considered the distal or posterior cingulum, rather than a partial lophid. The four anterior lophids extend across the entire width of the tooth and are angled slightly posteriorly from the lingual to the labial margin. Each of these four lophids consists of two large conical conids, one lingual, one labial, connected at the midline by from one to three small, rounded, accessory conulids. On each lophid, the lingual conid is located somewhat anterior to the posterior conid. Lophid 5 is different in size and shape from the anterior four lophids. It is much narrower and strongly curved rather than essentially straight, convex anteriorly, concave posteriorly. The larger lingual and labial conids are positioned posteriorly to the two small rounded midline conulids. Posterior to lophid 5, on the posterior margin of the tooth, is a small half lophid consisting of four tiny cuspids that are essentially horizontal in orientation. These cuspids could also be considered the posterior cingulum.

Trefoiling is present on lophids 1–4, consisting of a well-developed ridge extending posteriorly from the primary labial cusp, just labial to the midline of the tooth. The individual trefoils consist of two to three small rounded cuspids that would have coalesced with wear. There is minor secondary or double trefoiling, consisting of one or two small cuspids extending posteriorly from the primary lingual conid. The valleys separating lophids 1–5 are deep, extending two-thirds of the distance to the base of the crown, interrupted only by the trefoils extending posteriorly from the labial conid of each lophid. The valleys are not impeded by the smaller lingual trefoils, except between lophids 4 and 5. The m3 has several weak cingula, the most prominent of which is located along the anterior margin of the tooth. The anterior cingulum consists of an elliptical cuspid at the midline connected to a beaded ridge of

tiny cuspids that extends almost to the labial edge of the tooth. A fairly well-developed cingulum is located on the labial edge of lophid 4 near the base of the crown. It has an anteroposterior orientation and consists of a beaded ridge of tiny cuspids. There is also a very weak cingulum near the base of the crown on the labial margin of lophid 3 that could probably be considered an anterior extension of the better developed cingulum labial to lophid 4.

#### 4.1.2. Right M3 and partial right m2/m3 from Isla de San José, MCNP Collection

A right M3 from the vicinity of Isla de San José in the Pearl Islands in the MCNP Collection (MCNP 1) is well preserved (Fig. 3). The crown is intact but the roots have been broken off. This tooth is nearly unworn, except for a slight hint of wear on the anterolabial cone on loph 1. The enamel on the proximal half of the crown is relatively smooth, whereas the enamel is more heavily striated on the basal portion of the crown. The tooth is a right upper M3 composed of five complete lophs and a sixth partial loph for a total of  $5\frac{1}{2}$  lophs. The total number of all major and accessory cusps on this tooth is about 45 (after Mothé and Avilla, 2015). The first three lophs are essentially horizontal relative to the long axis of the tooth, whereas lophs 4 and 5 are angled noticeably posteriorly from the anterolingual to the posterolabial portion of the lophs. Although there is some variation, the four anterior lophs consist of a large conical lingual cone and a somewhat smaller rounded labial cone, joined at the midline by a third rounded accessory conule that is nearly as large as the labial cone. The midline conule is separated from the larger lingual cone by a noticeable valley but is more closely appressed to the labial cone of similar size, giving an almost “twinned” appearance. Loph 5 has a large conical lingual cone located anteriorly, separated by a valley from two small rounded midline accessory conules that are separated by a valley from a rounded labial cone. The labial cone is smaller than the lingual cone



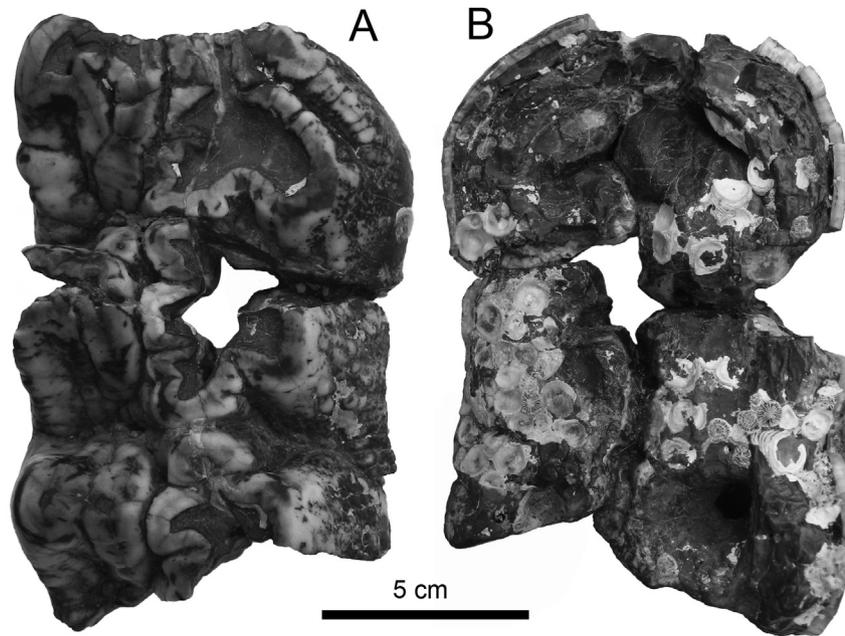
**Fig. 3.** Right M3 of *Cuvieronius hyodon* from Isla de San José, Pearl Islands, Panama (MCNP 1). A. Occlusal view, B. ventral view, C. enlarged view of a portion of the ventral surface showing attached specimens of modern marine invertebrates.

and positioned considerably farther posteriorly. The lingual cone is positioned progressively more anteriorly relative to the labial cone from the front to the back of the tooth, especially on lophs 4 and 5. The last half loph consists of a rather large, conical midline conule located almost on the posterior margin of the tooth and a smaller rounded conule located in a more anterolingual position on the lingual margin.

The valleys between the lophs are deep and wide between the labial halves of the lophs, but are shallower and much narrower lingually. There are small cusps located at the base of the valleys, on the posterior surfaces of the lophs, and on the posterior margin at the base of the crown. The primary trefoils extend posteriorly from the large lingual cone on each loph just lingual to the midline, and

consist of from one to three small cusps that are unworn. The trefoils are most prominent on lophs 1 and 2, weak on lophs 3 and 4, and absent on loph 5. An anterior cingulum consisting of a low beaded ridge composed of very small cusps extends from the base of the primary lingual cone to the labial margin of the tooth.

A second tooth from near Isla de San José in the MCNP Collection (MCNP 2) is the anterior half to two-thirds of a right m2 or m3 (Fig. 4). The posterior portion of the tooth is broken off, and thus it is not possible to determine the exact number of lophids present or the tooth position. The two anterior lophids are complete, the posterior lophid or lophid 3 is broken along its posterior face. This is the only tooth in the Pearl Islands sample that shows a substantial

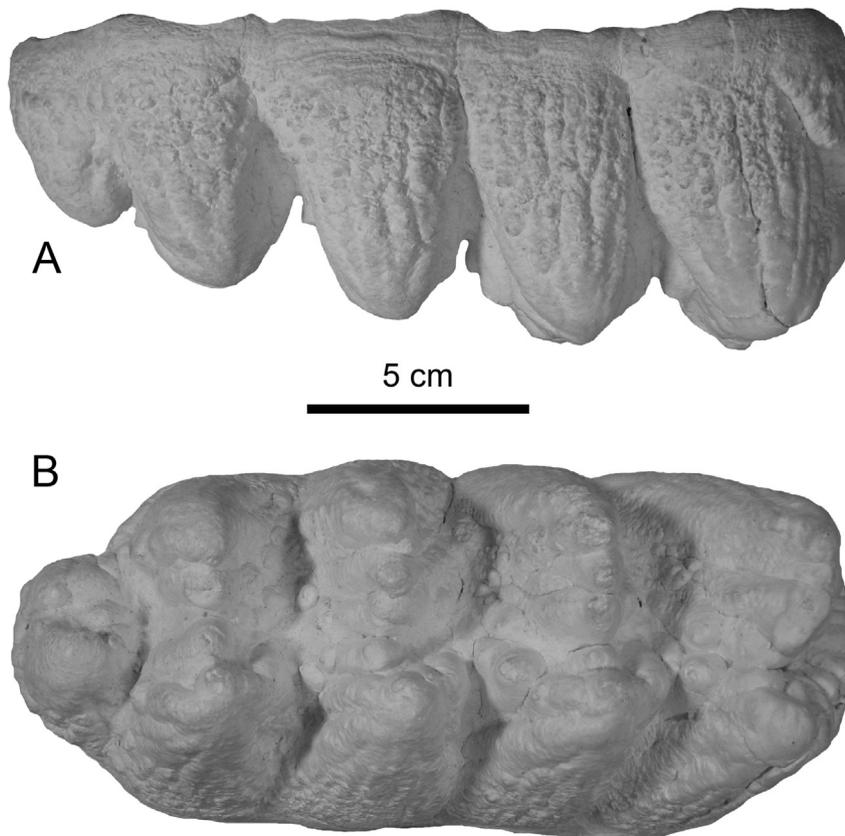


**Fig. 4.** Partial right m2/m3 of *Cuvieronius hyodon* from Isla de San José, Pearl Islands, Panama (MCNP 2). A. Occlusal view, B. ventral view. Note attached specimens of modern marine invertebrates on ventral surface.

amount of wear. There is a prominent interdental wear facet on the anterior margin of the tooth where it would have contacted the next tooth anterior (either m1 or m2). There is a well-developed anterior cingulum anterior to the labial portion of lophid 1, consisting of a large rounded cusp anterior and ventral to the main conid and then extending to the labial margin of the tooth as a low,

beaded ridge of tiny cusps. The labial edge of the tooth has numerous small cusps at the base of the crown. The enamel of this tooth is very thick, from 5 to 6 mm in thickness.

On each lophid the lingual conid is higher and the labial conid is more heavily worn. Lophids 1 and 2 each have large lingual and labial conids connected at the midline by two small, rounded



**Fig. 5.** Right M3 of *Cuvieronius hyodon* from near Isla de San José and Isla de Pedro González, Pearl Islands (USNM 421665). A. Labial view, B. occlusal view.

accessory conulids of similar size. Each lophid has a well-developed trefoil that extends posteriorly from the labial conid, just labial to the midline. The trefoils are “club-shaped” with the rounded portion oriented posteriorly. Lophids 2 and 3 also have smaller anterior extensions of the trefoils on the labial conids. There is also minor secondary or double trefoiling, consisting of single, small rounded cusps on the posterior face of the lingual portion of lophids 1 and 2, just lingual to the midline. These cusps would appear as small trefoils in later wear stages. The valleys between lophids 1 and 2 and 2 and 3 are deep both lingually and labially, but are interrupted along the midline by the primary and secondary trefoils.

#### 4.1.3. Right M3 from west of Isla San José and Isla de Pedro González, USNM collection

A right M3 in the U. S. National Museum of Natural History collection, Smithsonian Institution (USNM 421665) from near Isla San José and Isla de Pedro González in the Pearl Islands is complete and virtually unworn, with just a slight amount of wear on the labial portion of the first loph (Fig. 5). The tooth consists of four complete lophs and a half loph at the posterior edge of the tooth for a total of 4½ lophs. The four complete lophs, as well as the posteriormost half loph, are essentially horizontal to the long axis of the tooth. Lophs 1–4 consist of a large, rounded cone lingually and an anteroposteriorly compressed ridge composed of from three to six smaller rounded cusps labially. The large lingual cone comprises about 40% the width of each loph, whereas the labial ridge comprises the remaining 60% of the width. The posteriormost portion of the M3 containing loph 5 (or half loph) is constricted transversely. This loph is about half the width of the four anterior lophs, and consists of two rather large, rounded cusps of similar size, one lingual, one labial.

The enamel on the labial and lingual edges of the lophs of USNM 421665 is heavily striated or crenulated from the base of the crown almost to the tips of the crowns. Besides the major lophs and cones, the crown of the tooth possesses numerous tiny cusps, concentrated in the valleys between the lophs and on the posterior faces of the labial portions of the lophs. The total number of all major and accessory cusps on this tooth is about 48 (after Mothé and Avilla, 2015). One or two small, rounded cusps extending both anteriorly and posteriorly from the lingual cone on lophs 2–4, just lingual to the midline, would have worn into trefoils. Loph 1 has only the posterior portion of the trefoil, consisting of two small rounded cusps. All four lophs have several small cusps anterior and posterior to the labial portion of the loph, just labial to the midline, that would have worn into small secondary or double trefoils. The valleys separating the major lophs are wide and deep, interrupted only by the primary trefoils just lingual to the midline. The M3 has two prominent cingula, one on the anterior margin of the tooth and another on the posterior margin. The anterior cingulum consists of at least eight small cusps in a horizontal row that form a low, beaded ridge at the base of the crown immediately anterior to loph 1. The posterior cingulum is composed of at least ten tiny cusps at the base of the crown that extend from the posterolabial corner of loph 5 around the posterior margin of the tooth to a position labial to the anterior edge of loph 5.

#### 4.1.4. Gomphotheres from El Hatillo and La Triniada, Panama

In addition to the fossils from the Pearl Islands, there are two other records of the gomphothere *Cuvieronius* from Panama. Gazin (1957, p. 346–347) mentioned several specimens from the El Hatillo site in the Azuero Peninsula (Fig. 1, site 2), including “... associated skeletal portions of a single individual of the mastodon *Cuvieronius*... including two badly worn last molars and sections of tusk.” He noted that this specimen was “...characterized by tusks

having enamel developed in a spiral form.” We examined several specimens of *Cuvieronius* from El Hatillo in the USNM collection, including a lower third molar (m3), a partial tusk, an ulna, and a tibia. The m3, cataloged under the number USNM 540665, is so heavily worn that very little of the occlusal morphology remains; however, this specimen clearly possesses five lophids which is similar to the m3 from south of Isla del Rey. Measurements of the m3 from El Hatillo are presented in Table 1. Lucas (2014) illustrated and described the m3 of *C. hyodon* from El Hatillo (USNM 540665). More informative is a partial upper tusk from El Hatillo that exhibits the spiraled enamel band characteristic of *Cuvieronius*. From the La Triniada site, also in the Azuero Peninsula (Fig. 1, site 1), Pearson (2005) referred a tooth fragment, complete tibia, several vertebrae, and a proximal rib to *Cuvieronius tropicus*.

**Table 1**

Dental measurements of third upper and lower molars (M3/m3) of *Cuvieronius hyodon* from the Pearl Islands, Panama, compared to measurements of teeth of *C. hyodon* from Mexico, New Mexico, Texas, and Florida. The teeth from Panama, Mexico, Texas, and Daytona Beach, Florida are Rancholabrean NALMA in age. The specimens from Leisey Shell Pit and Punta Gorda in Florida and Tortugas Mountain in New Mexico are early Irvingtonian NALMA. Museum acronyms are: MCNP (Museo de Ciencias Naturales, Panama); STRI/CTPA (Smithsonian Tropical Research Institute/Center for Tropical Paleontology and Archaeology, Panama); INAH-MRG (Instituto Nacional de Antropología e Historia-Museo Regional de Guadalajara, Jalisco, Mexico); MPG (Museo de Paleontología de Guadalajara, Jalisco, Mexico); NMMNH (New Mexico Museum of Natural History); NMSU (New Mexico State University, Biology Department); TMM (Texas Memorial Museum, University of Texas, Austin); UF (Florida Museum of Natural History, University of Florida); UF/DMAS (Daytona Museum of Arts and Sciences, specimens housed in the UF collection); USNM (U. S. National Museum of Natural History, Smithsonian Institution). All measurements are in mm.

Locality and tooth position	Total length	Maximum width
Pearl Islands, Panama		
USNM 421665		
right M3	182	84
MCNP 1		
right M3	197	84
MCNP 2		
right m2/m3 (partial)	–	91
STRI/CTPA 1		
right m3	201	88
El Hatillo, Panama		
USNM 540665		
m3 (heavily worn)	185	92
Lago Chapala, Jalisco, Mexico <sup>a</sup>		
INAH-MRG uncat.		
right M3	173	85
MPG uncat		
M3	201	91
INAH-MRG uncat.		
right m3	198	82
INAH-MRG uncat.		
right m3	202	82
MPG 5		
m3	199	94
MPG 712		
m3	193	87
MPG 726		
m3	179	82
Tortugas Mountain, New Mexico <sup>b</sup>		
NMMNH 27232		
right M3	211	106
NMSU 79.17.1		
right m3	183	83
Ingleside, Texas <sup>c</sup>		
TMM 30967-1219		
right m3	218	94
Sinton, Texas <sup>d</sup>		
USNM 11377		
right M3	202	105
left m3	225	101

(continued on next page)

Table 1 (continued)

Locality and tooth position	Total length	Maximum width
Leisey Shell Pit, Florida <sup>e</sup> UF 129033 left M3	181	91
Punta Gorda, Florida <sup>e</sup> UF 9741 right M3	178	87
UF 9742 left m3	192	85
UF 11230 right m3	187	87
Daytona Beach, Florida <sup>e</sup> UF/DMAS 571 right m3	192	83
UF/DMAS 694 right m3	194	85

<sup>a</sup> Measurements from Lucas (2008b).

<sup>b</sup> Measurements from Lucas et al. (2000).

<sup>c</sup> Measurements from Lundelius (1972).

<sup>d</sup> Measurements from Hay (1926).

<sup>e</sup> Measurements from Lucas (2008a).

#### 4.2. Comparisons of gomphothere teeth from the Pearl Islands with teeth of *Cuvieronius* from Mesoamerica, temperate North America, and South America

Morphological comparisons among the four gomphothere teeth from the Pearl Islands indicate that either one highly variable species or two different species are represented. The most revealing comparisons are between two right M3s from near Isla San José. These two teeth were collected in the same general area, but differ in several important morphological characters. Both teeth are almost totally unworn. One M3 (USNM 421665; Fig. 5) has 4½ lophids that are essentially horizontal to the long axis of the tooth with wide valleys between the lophids. A second M3 (MCNP 1; Fig. 3) has 5½ lophids that form an angle to the long axis of the tooth (the lingual portion of the lophid is located distinctly anterior to the labial portion) and the valleys between the lophids are narrow especially between the lingual cones. However, both of these M3s have a similar number of total cusps (major cusps plus accessory cusps; after Mothé and Avilla, 2015), 45 in the MCNP tooth, 48 in the USNM tooth. A lower m3 from the Pearl Islands (STRI/CTPA 1; Fig. 2) is similar to the MCNP M3, with 5½ angled lophids, but has a considerably larger number of total cusps (about 60) than either of the other complete third molars from the Pearl Islands.

We compared the gomphothere teeth from the Pearl Islands with descriptions and illustrations of upper and lower third molars (M3/m3) of the Quaternary gomphothere *Cuvieronius* from both the tropical and temperate regions of North America, including specimens from the following localities: Río Tomayate in El Salvador (Cisneros, 2005); Lago Chapala in the state of Jalisco, west-central Mexico (Lucas, 2008b); the “Valley of Mexico” in central Mexico (Cope, 1884, 1893; Osborn, 1936); Tortugas Mountain in New Mexico (Lucas et al., 1999, 2000); Sinton and Ingleside in Texas (Hay, 1926; Lundelius, 1972); and Leisey Shell Pit, Punta Gorda, and Daytona Beach in Florida (Webb and Dudley, 1995; Lucas, 2008a). Measurements of the gomphothere teeth from the Pearl Islands and of the M3s/m3s of *Cuvieronius* from elsewhere in North America are presented in Table 1. We also made comparisons between the gomphothere teeth from the Pearl Islands and teeth of *Cuvieronius hyodon* from Tarija, Bolivia (Boule and Thevenin, 1920; Mothé and Avilla, 2015). The most common dental morphology of the M3s/m3s among North American specimens of *Cuvieronius* is to have 4½ lophids/lophids, single trefoiling, and rather simple enamel with limited development of small accessory cusps. An M3 from the Pearl Islands (USNM 421665) closely matches the typical dental

morphology of *Cuvieronius* (Fig. 5). Two other complete teeth from the Pearl Islands, an m3 and an M3 (Figs. 2 and 3), have 5½ lophids/lophids, incipient double trefoiling, and a somewhat more complex enamel pattern.

Cisneros (2005) illustrated six mandibles with m3s of *Cuvieronius* from Río Tomayate, El Salvador, although he did not provide measurements of these specimens. Cisneros described the m3s from Río Tomayate as having 4½ to 5 angular lophids, single trefoiling, and simple enamel. Several of the El Salvador specimens have a well-developed 5th lophid on m3, but none has 5½ lophids. Cisneros also noted that several isolated upper tusks from Río Tomayate exhibited a spiral enamel band. A sample of upper and lower third molars of *Cuvieronius* from Lago Chapala, Mexico, representing at least five individuals (Lucas, 2008b), overlap in morphology and size with the teeth from the Pearl Islands. Most of the specimens from Lago Chapala have 4½ lophids/lophids on M3/m3 (four complete lophids/lophids and one or two small posterior midline cusps/cuspids constituting a ½ lophid/lophid), single trefoiling, and a rather simple enamel pattern with limited plications. However, one of the illustrated m3s from Lago Chapala (Lucas, 2008b, fig. 3D) is similar to the m3 from the Pearl Islands in possessing 5½ lophids. In his description of the type specimen of *Cuvieronius* (= *Dibelodon*) *tropicus* from Mexico, a mandible with m2–m3, Cope (1884, p. 7) stated that “Reference to Von Meyer’s figure [1867] shows that the last inferior molar [m3] has five well-developed cross-crests and a heel.” Von Meyer’s illustration of the specimen Cope later designated the type of *C. tropicus* was reproduced by Osborn (1936, fig. 513). Even though most M3s/m3s of *Cuvieronius* from North America have 4½ or 5 lophids/lophids, the type specimen of *C. tropicus* has 5½ lophids (“five ... cross-crests and a heel”), in agreement with an M3 and an m3 from the Pearl Islands.

Samples of *Cuvieronius* teeth from Pleistocene sites in temperate North America, including New Mexico, Texas, and Florida, exhibit the same general dental morphology as described above for *Cuvieronius* from Mexico and Central America, including the teeth from the Pearl Islands. As with the Mesoamerican *Cuvieronius*, there is considerable dental variation in the temperate North American sample. Specimens of *Cuvieronius* from the early Pleistocene (early Irvingtonian) Tortugas Mountain Fauna in New Mexico include a palate with two M3s having 4 lophids and a single posterior midline cusp and a lower jaw from a different individual with an m3 that has four lophids and two well-developed cuspids on the posterior margin that could be interpreted as an incipient 5th lophid or half lophid, or as a posterior cingulum (Lucas et al., 1999, 2000). An associated maxilla and mandibles of *Cuvieronius* from the late Pleistocene (Rancholabrean) Sinton Local Fauna (LF) in southern Texas have 5½ lophids/lophids on the M3/m3 (Hay, 1926). An isolated m3 of *Cuvieronius* from the Rancholabrean Ingleside LF in southern Texas also has 5½ lophids (Lundelius, 1972). The *Cuvieronius* teeth from Texas closely resemble the M3 and m3 from the Pearl Islands with 5½ lophids/lophids. The Florida sample of *Cuvieronius* includes isolated M3s from the early Irvingtonian Leisey Shell Pit and Punta Gorda LFs and two mandibles with m3s from the Rancholabrean Daytona Beach LF. The M3s from Leisey and Punta Gorda have four lophids with a small midline cusp on the posterior midline and the two m3s from Daytona Beach have four lophids with a fifth (half) lophid posteriorly consisting of two small cusps. The M3s of *Cuvieronius* from Leisey and Punta Gorda are similar to the simpler of the two M3s from the Pearl Islands (USNM 421665).

We also made comparisons of the gomphothere teeth from the Pearl Islands with a large sample of *Cuvieronius* teeth from the early to middle Pleistocene (Ensenadan SALMA) fauna from Tarija, Bolivia, based on illustrations and descriptions of the Bolivian sample in Boule and Thevenin (1920) and Mothé and Avilla (2015),

as well as specimens from Tarija in the UF/FLMNH collection. Mothé and Avilla (2015) illustrated two lower m3s of *C. hyodon* from Tarija, one with a simple enamel pattern and one with a complex enamel pattern. These two teeth encompass much of the dental variation observed in *Cuvieronius* teeth from the Pearl Islands, elsewhere in Central America, Mexico, and temperate North America. The Tarija teeth have 4½ to 5 lophids and range from a very simple enamel pattern with little development of accessory cusps to a more complex pattern with numerous accessory cusps.

Mothé and Avilla (2015) proposed a method for evaluating the enamel complexity of the third molars (M3/m3) of South American gomphotheres by counting the total number of cusps, including both major cusps and accessory cusps. They determined that the third molars of South American *Cuvieronius* have between 33 and 60 total cusps, with most specimens ranging from 40 to 53. Two complete upper third molars (M3s) of gomphotheres from the Pearl Islands are within the average range of total cusps for *Cuvieronius* third molars from South America, with 45 cusps in MCNP 1 and 48 in UNSM 421665. The other complete third molar from the Pearl Islands, a lower m3 (STRI/CTPA 1), has considerably more complex enamel, with about 60 total cusps (ranging from 58 to 65 cusps, depending on whether or not the tiniest accessory cusps are counted). The m3 from the Pearl Islands agrees more closely with the total cusp count for *Notiomastodon* third molars from South America, which have between 35 and 82 total cusps, with most specimens ranging from 46 to 58. However, Mothé and Avilla (2015) noted there is considerable overlap in total cusp count between *Cuvieronius* and *Notiomastodon* and, with the exception of extremely complex teeth of *Notiomastodon*, the number of cusps on the last molars is not valid to differentiate these two genera.

Lambert and Shoshani (1998) observed that North American samples of *Cuvieronius* exhibit a remarkable range of variation in cheek tooth morphology, including four and a fraction to five and a fraction lophids, single to double trefoiling, and ptychodont enamel (numerous small accessory cusps, often with highly striated enamel) to simple aptychodont enamel. Much of the range of dental variation in the *Cuvieronius* teeth from Central America, Mexico, New Mexico, Texas, and Florida, as well as Tarija, Bolivia, can be duplicated in the small sample of teeth from the Pearl Islands. Overall, there is substantial variation in dental features both within and between North American samples of *Cuvieronius*. Measurements in Table 1 indicate that the *Cuvieronius* teeth from the Pearl Islands fall within the observed size range for the majority of *Cuvieronius* third molars from North America. There are several notably large M3s/m3s in the North American sample, including specimens from the early Irvingtonian Tortugas Mountain Fauna in New Mexico and the Rancho Labrean Ingleside and Sinton LFs in Texas (Table 1). Despite the considerable range of variation in dental morphology observed in the Pearl Islands teeth, we tentatively refer all of these specimens to *Cuvieronius hyodon*, the common late Pleistocene gomphothere species from Central America. See taxonomic discussion below for our usage of *C. hyodon* rather than *C. tropicus* for North American *Cuvieronius*.

#### 4.3. Age of *Cuvieronius* from the Pearl Islands

We did not attempt to obtain a radiocarbon date on the teeth from the Pearl Islands because all of the specimens have been submersed in saltwater for a long period of time, probably since the end of the Pleistocene, if not earlier. According to Ron Hatfield from Beta Analytic (in litt. October 8, 2013), "Tooth proteins can be leached away if submersed in water for long periods of time. Given the very long time that these samples were submerged it's likely that any tooth proteins have been removed." No other mammal fossils have been found in association with the *Cuvieronius* teeth

from the Pearl Islands that might provide additional information on their biochronology. The identification of the teeth as *Cuvieronius* restricts their age to between the early Irvingtonian and late Rancho Labrean (~1.6 Ma–10 ka). As discussed below, most records of *Cuvieronius* from Central America are late Pleistocene in age, with the exception of two early Pleistocene faunas from El Salvador (Webb and Perrigo, 1984; Cisneros, 2005).

The most useful information on the age of the *Cuvieronius* teeth from the Pearl Islands comes from their provenance. All four of the teeth were found in a marine environment, and the two specimens with the most complete data were recovered in shrimp nets from a depth of approximately 50 fathoms (= 300 feet = ~90 m). All four of the teeth are in excellent condition, although lacking roots, suggesting that they were not transported a long distance and were probably buried for a considerable period of time and not subjected to movement by tides or currents. Two of the teeth have attached specimens of modern epiphytic marine invertebrates (see Figs. 3B, C, 4B), indicating that the specimens rested on the sea floor for at least a short period of time, although not long enough to have suffered much damage. If the teeth were not transported a long distance from where they were recovered on the sea floor in the Gulf of Panama, then the depth at which they were found (~90 m) should give a good indication of sea level at the time the fossils were deposited, considering that the continental shelf must have been dry land for the gomphotheres to have survived there.

Precise data pertaining to Pleistocene sea levels are only available for about the past 130 ka, covering the last glacial–interglacial cycle or Marine Isotope Stages (MIS) 1–5 (Lambeck et al., 2002). According to several proxies of sea level change, including uplifted coral reefs with uranium-series dates, estimated ice volumes, and oxygen (<sup>18</sup>O/<sup>16</sup>O) isotopes from marine microfossils, at only one time in the last 130 ka, during the Last Glacial Maximum (LGM) between about 30 and 15 ka (MIS 2), were sea levels as low as 90 m below current mean sea level (msl) (Lambeck et al., 2002). Sea level reached its lowest level (~120 m below msl) near the end of the LGM about 19 ka; however, sea level remained approximately 90 m below msl until about 15 ka (Lambeck et al., 2002). We strongly suspect that the Pearl Islands gomphothere teeth date to the LGM or the latest Pleistocene (late Rancho Labrean NALMA), probably between 30 and 15 ka, based on the recovery of two of the teeth from depths of approximately 90 m on the continental shelf in the Gulf of Panama.

## 5. Discussion

### 5.1. Taxonomy and systematics of *Cuvieronius*

The species-level taxonomy of *Cuvieronius* in both North America and South America is complex and confusing. Several comprehensive works on North American Pleistocene Proboscidea have identified *Cuvieronius* only to the generic level (e.g., Kurtén and Anderson, 1980; Lambert and Shoshani, 1998). Arroyo-Cabrales et al. (2007) noted that three different species names have been applied to this genus in Mesoamerica, *C. hyodon*, *C. oligobunus*, and *C. tropicus*. Webb and Dudley (1995) used the oldest available name for a North American species of *Cuvieronius*, *C. tropicus* (Cope, 1884), for specimens from the early Pleistocene Leisey Shell Pit and Punta Gorda faunas in Florida. *C. tropicus* was originally named for a lower jaw from the state of Michoacan in the Valley of Mexico, central Mexico, presumably of late Pleistocene age (Cope, 1884). Cope (1893) later named a second species, *C. oligobunus*, based on a pair of lower jaws from the late Pleistocene Tequixquiac fauna, also from the Valley of Mexico in central Mexico. Webb and Dudley (1995) synonymized *C. oligobunus* with *C. tropicus*. Most recent authors (e.g., Ferretti, 2008; Mothé et al.,

2013) recognize a single species of *Cuvieronius* from South America, *C. hyodon* (Fischer, 1814), the oldest available name for a South American species in this genus.

Until recently, the trend has been to recognize two species of *Cuvieronius*, *C. tropicus* from North America and *C. hyodon* from South America. However, the range of dental variation in samples of *C. tropicus* and *C. hyodon* appears to overlap substantially (Lucas, 2008a; Lucas and Alvarado, 2010). In comparisons of *Cuvieronius* teeth from Florida, Mexico, Central America, and South America, Lucas (2008a) could find no consistent differences in the dentition, size, or other characters to separate North American *Cuvieronius*, previously referred to *C. tropicus*, and South American populations of *Cuvieronius* referred to *C. hyodon*. The similarity between these two species led Lucas (2008a, 2013) and Lucas and Alvarado (2010) to refer all *Cuvieronius* from temperate North America and Mesoamerica to *C. hyodon* (Fischer, 1814), which has priority over *C. tropicus* (Cope, 1884).

Pending a detailed taxonomic review of all New World *Cuvieronius*, we recognize a single pan-American species in this genus, *C. hyodon*. A similar situation occurs in late Pleistocene populations of the giant ground sloth *Eremotherium*, which had been split into North American (*E. mirabile*) and South American (*E. laurillardii*) species, until Cartelle and de Iuliis (1995) combined them as the pan-American species *E. laurillardii*. *Cuvieronius* and *Eremotherium* are often associated in Central American Pleistocene faunas, including Panama where these two genera co-occur in the El Hatillo and El Trinidaita sites (Gazin, 1957; Pearson, 2005; Lucas, 2014). Cisneros (2005) noted the abundance of *Cuvieronius* in the Irvingtonian Río Tomayate fauna in El Salvador, where at least six individuals occur, together with a skeleton of *Eremotherium*. *Cuvieronius* and *Eremotherium* are two of the most common large mammals in the Rancholabrean Daytona Beach fauna along the Atlantic coast of Florida (Morgan and Hulbert, 1995).

*Cuvieronius* and another gomphothere genus, *Rhynchotherium*, appear to be closely related based on the presence of the derived character of the helicoidal (spiral) curvature of the upper tusks, including the enamel band (Lambert and Shoshani, 1998; Lucas and Morgan, 2008). These two genera can be easily distinguished from the morphology of the mandibles. *Cuvieronius* has a short (brevirostrine) mandibular symphysis and lacks lower tusks, whereas *Rhynchotherium* has a longer symphysis that is downturned at a 45° angle or greater and bears a pair of small lower tusks that are rounded to elliptical in cross-section and often have a lateral enamel band. Webb and Perrigo (1984) recommended that the presence (*Rhynchotherium*) or absence (*Cuvieronius*) of lower tusks be used as the defining character separating these two genera. In addition, *Rhynchotherium* has third molars with only 4 or at most 4½ lophs/lophids and rather simple enamel, whereas *Cuvieronius* tends to have more complicated teeth with third molars having 4½ to 5½ lophs/lophids and enamel with some development of accessory cusps. Several late Miocene (Hemphillian NALMA) gomphothere species from Mexico and Central America previously referred to *Rhynchotherium*, *R. blicki* (including *Aybelodon hondurensis*) and *R. tlascalae* (Webb and Perrigo, 1984), are now considered to be advanced species of *Gomphotherium* (Tobien, 1973; Lucas and Morgan, 2008).

## 5.2. Biochronology of *Cuvieronius*

Despite references to the contrary (e.g., Kurtén and Anderson, 1980; Webb and Dudley, 1995), there is no credible evidence for the occurrence of *Cuvieronius* in North America prior to the beginning of the Irvingtonian (about 1.6 Ma). Among specimens that possess the symphyseal region of the lower jaws revealing the presence or absence of lower tusks, *Rhynchotherium* occurs only in

late Hemphillian and Blancan faunas, becoming extinct in the latest Blancan at about 2.2 Ma (Lucas and Morgan, 2008), whereas *Cuvieronius* is restricted to early Irvingtonian and younger faunas, becoming extinct at the end of the Rancholabrean with the remainder of the Pleistocene megafauna. Specimens previously referred to *Cuvieronius* from Blancan faunas consist of isolated teeth or mandibles that lack the symphysis, and thus their identification cannot be confirmed. The non-overlapping biochronologic ranges of *Rhynchotherium* and *Cuvieronius* suggest an ancestor–descendant relationship between the two genera. *Cuvieronius* apparently evolved from *Rhynchotherium* in the late Blancan, with the anterior shortening of the mandibles and loss of the lower tusks. There is currently no evidence for this evolutionary transition in late Blancan faunas from temperate North America. All late Blancan specimens of this lineage that preserve the symphysis are referable to *Rhynchotherium*. Although Webb and Dudley (1995, p. 648) mentioned that “An early plesiomorphous (or transitional) form of *Cuvieronius* occurs in the late Blancan of Florida, e.g., at Macaspalt Pit in Sarasota Co., Florida...” an examination of the mandibles from the late Blancan Macaspalt Shell Pit, upon which their observation was based, confirms the identification of this specimen as *Rhynchotherium* not *Cuvieronius*. The lack of evidence for *Cuvieronius* in temperate North American Blancan faunas suggests that the evolution of this genus may have occurred in Mesoamerica where late Blancan faunas are scarce (Mexico) or absent (Central America). During the early Pleistocene, *Cuvieronius* dispersed across the Panamanian Isthmus and entered South America as a participant in the GABI (Lucas, 2013).

*Cuvieronius* occurs in early through late Pleistocene faunas (Irvingtonian and Rancholabrean NALMAs) in North America, including Central America, and early through late Pleistocene faunas (Ensenadan and Lujanian South American land mammal ages—SALMAs) in South America. The oldest confirmed specimens of *Cuvieronius hyodon* are early Pleistocene (early Irvingtonian, ~1.6–1.0 Ma) records from North America, including the Leisey Shell Pit and Punta Gorda faunas from Florida (Webb and Dudley, 1995; Lucas, 2008a), the Tortugas Mountain fauna from New Mexico (Lucas et al., 1999; Morgan and Lucas, 2003), and the Baranco del Sisimico and Río Tomayate faunas from El Salvador (Webb and Perrigo, 1984; Cisneros, 2005). Other Irvingtonian records of *Cuvieronius* from New Mexico, Texas, Florida, and North Carolina consist of less diagnostic fossils that probably are not identifiable to the species level (Hibbard and Dalquest, 1966; Morgan and Hulbert, 1995; Sanders, 2002; Morgan and Lucas, 2003). Records of *Cuvieronius* from late Pleistocene (Rancholabrean) sites in temperate North America are not as widespread as in the Irvingtonian, with the most complete Rancholabrean specimens from Daytona Beach on the Atlantic Coast of Florida (Morgan and Hulbert, 1995) and Sinton and Ingleside on the Gulf Coast of southern Texas (Hay, 1926; Lundelius, 1972). Most records of *Cuvieronius* from Central America and Mexico appear to be late Pleistocene, although the age of many Mesoamerican proboscidean sites is problematic (Arroyo-Cabrales et al., 2007; Lucas and Alvarado, 2010).

The earliest well-dated specimens of *Cuvieronius hyodon* in South America are from Tarija, Bolivia (Ferretti, 2008; Mothé et al., 2013). Recent studies of the geochronology and biostratigraphy of the Tarija Fauna confirm an age range of 0.99 to 0.76 Ma, corresponding to a late early to middle Pleistocene age and referral to the Ensenadan SALMA (MacFadden, 2013; MacFadden et al., 2013).

## 5.3. Biogeography of *Cuvieronius*

*Cuvieronius* is the most common proboscidean in late Pleistocene deposits in tropical regions of North America, including southern Mexico and Central America from Guatemala south to

Panama (Arroyo-Cabrales et al., 2007; Lucas and Alvarado, 2010). *Cuvieronius* also is known from two early Pleistocene faunas in Mesoamerica, Barranca del Sisimico and Río Tomayate in El Salvador (Webb and Perrigo, 1984; Cisneros, 2005). *Cuvieronius* is uncommon in the temperate portion of North America, with a rather restricted geographic distribution in the southern United States and northern Mexico. The northernmost occurrences of *Cuvieronius* in the Irvingtonian are from New Mexico, Texas, Florida, and North Carolina (Webb and Dudley, 1995; Lucas et al., 1999, 2000; Sanders, 2002; Lucas, 2008a). Records of *Cuvieronius* from two early Irvingtonian faunas from the Rio Grande valley in southern New Mexico at about 1200 m are among the highest elevation records of this genus in North America (Lucas et al., 1999, 2000). *Cuvieronius* disappears from the American Southwest in the early Irvingtonian about a million years ago (Lucas et al., 1999), presumably related to the increasingly cooler and drier climate. The northern distribution of *Cuvieronius* during the Rancholabrean was restricted to the Gulf and Atlantic coastal plains of the southeastern United States, with records from Texas, Florida, and South Carolina (Hay, 1926; Lundelius, 1972; Sanders, 2002; Baskin and Thomas, 2007; Lucas, 2008a).

General patterns of Pleistocene proboscidean abundance and distribution in tropical North America reveal some interesting trends. Among the three genera of late Pleistocene proboscideans known from Mexico and Central America (*Cuvieronius*, *Mammuthus*, and *Mammuthus*), the mastodon *Mammuthus* is the rarest with 15 records from northern and central Mexico and a single record from Honduras (Arroyo-Cabrales et al., 2007; Lucas and Alvarado, 2010). The mammoth *Mammuthus* is the most abundant proboscidean in northern and central Mexico, but was uncommon in southern Mexico (Arroyo-Cabrales et al., 2007). Mammoths are even rarer in Central America where there are fewer than ten records, with the southernmost occurrence in northwestern Costa Rica (Lucas et al., 1997; Lucas and Alvarado, 2010). *Cuvieronius* was rare in the northern half of Mexico, but was the most common proboscidean in late Pleistocene faunas in southern Mexico and Central America (Arroyo-Cabrales et al., 2007; Lucas and Alvarado, 2010). In southern Central America south of 10° North latitude, including central and eastern Costa Rica and Panama, *Cuvieronius* is the only known Pleistocene proboscidean (Gazin, 1957; Pearson, 2005; Lucas and Alvarado, 2010; Lucas, 2014).

Overall abundance patterns in North America during the late Pleistocene reveal that *Mammuthus* is the most common proboscidean in the more heavily forested eastern half of the continent, *Mammuthus* is most abundant in the western grasslands, and *Cuvieronius* is the dominant proboscidean of the savannas and tropical forests of southern Mexico and Central America. Mesoamerican records of *Cuvieronius* are found in both lowland and upland sites, but are more common in the lowlands, including the specimens reported here from the Panamanian continental shelf in the vicinity of the Pearl Islands. Despite their differing biogeographic patterns, these three genera do not have mutually exclusive distributions. *Mammuthus* and *Mammuthus* are found together in many late Pleistocene sites in temperate North America and *Cuvieronius* and *Mammuthus* are often associated in sites in the southern United States and Mexico. Arroyo-Cabrales et al. (2007) stated that *Cuvieronius* and *Mammuthus* have an ecologically parapatric distribution in Mexico. Although a rare association, *Cuvieronius* and *Mammuthus* are known to co-occur in several Rancholabrean sites in temperate North America, including Daytona Beach in Florida where these two genera are found with *Mammuthus* (Morgan and Hulbert, 1995). *Cuvieronius*, *Mammuthus*, and *Mammuthus* are also associated in the Rancholabrean Ingleside and Nueces River faunas on the Gulf Coastal Plain of southern Texas (Lundelius, 1972; Baskin and Thomas, 2007).

North American proboscidean distributional patterns were somewhat different during the early Pleistocene. *Cuvieronius* is more common than *Mammuthus* in Florida early Irvingtonian faunas, where *Cuvieronius* often occurs in association with *Mammuthus*, including Leisey Shell Pit and Punta Gorda (Morgan and Hulbert, 1995; Webb and Dudley, 1995). Rancholabrean records of *Mammuthus* in the southeastern United States far outnumber *Cuvieronius*, perhaps suggesting a change to more temperate forests after the Irvingtonian. The abundance and distribution of proboscideans in Mesoamerica during the Irvingtonian is poorly known because of the paucity of faunas of this age, although the largest reported sample of *Cuvieronius* from North America occurs in the early Irvingtonian Río Tomayate LF in El Salvador, a fauna that lacks other taxa of proboscideans (Cisneros, 2005).

Among the three families of proboscideans known from the Pleistocene of North America (Elephantidae, Gomphotheriidae, Mammotidae), only the Gomphotheriidae occurs in South America. There have been numerous studies of the taxonomy, biogeography, and paleoecology of South American gomphotheres over the past decade (e.g., Sánchez-Chillón et al., 2004; Prado et al., 2005; Ferretti, 2008; Mothé et al., 2012, 2013; Lucas, 2013; Mothé and Avilla, 2015). The taxonomy of Pleistocene gomphotheres in South America is complicated because as many as four genera have been recognized, including *Cuvieronius*. Several recent taxonomic reviews of South American Pleistocene gomphotheres have reduced the number of valid species to two (Mothé et al., 2012, 2013; Lucas, 2013), *Cuvieronius hyodon* and *Notiomastodon platensis*. *Notiomastodon* can be separated from *Cuvieronius* by "...the absence of spiraled torsion and spiral enamel band in upper tusks ... and molar teeth more complex and with larger number of cones" (Mothé et al., 2012, p. 6). South American gomphotheres previously referred to the genera *Haplomastodon* and *Stegomastodon* are included under *Notiomastodon*, following Mothé et al. (2012, 2013) and Lucas (2013). *Haplomastodon* is a synonym of *Notiomastodon*, whereas *Stegomastodon* is restricted to Blancan and early Irvingtonian faunas from North America (Morgan and Lucas, 2011; Lucas, 2013; Mothé and Avilla, 2015).

With the exception of a few records from Ecuador and Peru, the Pleistocene distribution of *Cuvieronius* and *Notiomastodon* in South America is non-overlapping. *Cuvieronius* is mostly restricted to upland sites in the Andes of western South America, including Ecuador, Peru, and Bolivia, although this genus is known from a few lowland localities in Ecuador (Mothé and Avilla, 2015). The adaptation of *Cuvieronius* to the South American uplands is supported not only by its geographic distribution, but also by isotopic studies (Sánchez-Chillón et al., 2004; Mothé et al., 2013). *Notiomastodon* is found primarily in lowland sites, but does occur in several Andean localities in Colombia, Ecuador, and Peru (Mothé and Avilla, 2015). *Notiomastodon* is widely distributed throughout much of South America where *Cuvieronius* has not been found, including Chile, Argentina, Uruguay, Paraguay, Brazil, Colombia, and Venezuela. *Notiomastodon* is not known from Surinam and the Guyanas, and there are very few records from the northern Amazon basin (Mothé and Avilla, 2015).

The paleoecology of *Cuvieronius* in North America and South America appears to be somewhat contradictory. *Cuvieronius* in South America is primarily restricted to the highlands in the Andean region, with a few lowland records from Ecuador and Peru (Mothé and Avilla, 2015). In contrast, *Cuvieronius* in Central America is found primarily in lowland sites, including the specimens from the Pearl Islands that were collected on the continental shelf below modern sea level. Late Pleistocene proboscideans from similar lowland tropical faunas in northern South America are mostly *Notiomastodon*, including several localities in northwestern Colombia less than 400 km southeast of the Pearl Islands (Mothé

et al., 2013; Mothé and Avilla, 2015). The closest site in South America where *Cuvieronius* has been identified is in northern Ecuador, about 1000 km south of the Pearl Islands (Mothé and Avilla, 2015). There do not appear to be any obvious geographic barriers between Panama and Colombia in the late Pleistocene that would have limited the dispersal of *Cuvieronius* south from Central America into northern South America or *Notiomastodon* north from Colombia and Venezuela into Panama. During low sea level stands of the Pleistocene, narrow coastal corridors would appear to have functioned as natural dispersal routes along the Pacific coast between Panama and Colombia and the Caribbean coast between Panama and Colombia and Venezuela.

The apparent discrepancy between the biogeography and paleoecology of *Cuvieronius* in North America compared South America may result from the difficulty in identifying isolated teeth of gomphotheres. A gomphothere m3 from the Pearl Islands is similar to the North American Pliocene and early Pleistocene (Blancan and early Irvingtonian) genus *Stegomastodon*, based on the presence of 5½ lophs/lophids, incipient double trefoiling, and numerous accessory cusps. The early Blancan species *S. primitivus* has similar dental characters to the Pearl Islands gomphothere m3, whereas the late Blancan and early Irvingtonian species *S. mirificus* has 6½ or more lophs/lophids on the M3/m3, double trefoiling, and highly complicated enamel (Morgan and Lucas, 2011). Despite the general dental similarities, it is unlikely that the Pearl Islands m3 represents *Stegomastodon* because there is no evidence of Blancan and early Irvingtonian vertebrate faunas in Panama. Moreover, the Pliocene and early Pleistocene was a period of generally high worldwide sea levels, whereas the teeth from the Pearl Islands must date to a glacial interval based on their occurrence on the continental shelf below modern sea level.

Prior to recent taxonomic revisions (Mothé et al., 2012; Lucas, 2013), South American gomphotheres now referred to *Notiomastodon platensis* were often placed in the genus *Stegomastodon*. This identification was based on the overall similarity between *Notiomastodon* (including *Haplomastodon*) and *Stegomastodon*, including complicated teeth, absence of lower tusks, and gently curved to nearly straight upper tusks lacking torsion and an enamel band. Most proboscidean workers now consider *Stegomastodon* to be a strictly North American genus, and regard its similarity to *Notiomastodon* as an example of morphological convergence (Mothé et al., 2012; Lucas, 2013). However, the general similarity of *Notiomastodon* to *Stegomastodon*, and the superficial resemblance of at least one of the gomphothere teeth from the Pearl Islands to *Stegomastodon*, leads to the suggestion that both *Cuvieronius* and *Notiomastodon* might be present in the sample of gomphothere teeth from the Pearl Islands.

Detailed comparisons of gomphothere specimens from Central America with *Notiomastodon* from northern South America and *Cuvieronius* from southern South America, as well as the discovery of more diagnostic specimens in Central America, preferably including jaws and skulls, will be required before the identification of tropical American gomphotheres can be fully resolved. For purposes of the present study, we follow current taxonomic doctrine and recognize the gomphothere teeth from the Pearl Islands as *Cuvieronius hyodon*, with the caveat that further study may require a name change for at least one of the specimens.

#### 5.4. Proboscidean fossils from the continental shelf

The discovery of four gomphothere teeth from the continental shelf in the Gulf of Panama has prompted a more comprehensive review of Quaternary fossils of large terrestrial mammals from the continental shelf. Quaternary proboscidean teeth are well known from the continental shelf off the Atlantic Coast of the northeastern

United States (Whitmore et al., 1967) and in the North Sea (van Kolfschoten and Laban, 1995; Mol et al., 2006), but are not well documented from tropical regions. Whitmore et al. (1967) recorded teeth of mammoths (*Mammuthus*) or mastodons (*Mammot*) from more than 40 sites at depths of 20–120 m along the continental shelf of the western North Atlantic Ocean, from the latitude of Massachusetts south to North Carolina. Large numbers of Pleistocene fossils representing a wide variety of terrestrial mammals have been dredged by fisherman from the Southern Bight of the North Sea between England and the Netherlands (van Kolfschoten and Laban, 1995; Mol et al., 2006). Among the most abundant of the North Sea Pleistocene fossils are isolated teeth of the woolly mammoth *Mammuthus primigenius*. Other reports of proboscidean teeth from the continental shelf include records from Japan, southern California, and Brazil (Whitmore et al., 1967; Lopes and Buchmann, 2011).

Several factors help to explain the abundance of proboscidean teeth in fossil samples dredged from the continental shelf by fisherman. Proboscidean teeth are large and sturdy, so would be more likely to have survived on the sea floor for more than 10,000 years. Teeth of the American mastodon (*Mammot americanum*) are more common on the northeastern U. S. continental shelf than are mammoth teeth (*Mammuthus columbi* and *M. primigenius*), at least in part because mastodon teeth are stronger, being composed of a continuous layer of thick enamel. Mammoth teeth consist of plates of dentine surrounded by rather thin enamel and held together by softer cement, causing the teeth to break apart between the plates (Whitmore et al., 1967). The teeth of *Cuvieronius* are similar to teeth of *Mammot*, with a continuous layer of thick enamel. Whitmore et al. (1967) mentioned only a few other species of large Pleistocene mammals caught in nets by fisherman off the northeastern coast of the United States, including the woodland musk ox *Bootherium* and the large cervid *Cervalces*. A diverse sample of large Pleistocene mammals, the so-called “Mammoth Fauna,” is known from the shallow waters of the North Sea, including woolly mammoth, woolly rhino, horse, Irish elk, muskox, bison, cave bear, and cave lion, among others (van Kolfschoten and Laban, 1995; Mol et al., 2006).

There are several examples of Quaternary vertebrate fossils found on the continental shelf in subtropical regions closer to Panama. Fossils of *Mammot americanum*, giant ground sloth *Eremotherium laurillardii*, *Bison*, and giant land tortoise *Hesperotestudo crassiscutata* have been caught in shrimp nets at depths of about 10 m in Nassau Sound, a small embayment of the Atlantic Ocean at the mouth of the Nassau River in northeastern Florida at about 30° North latitude (FLMNH vertebrate paleontology collection). Almost all of these fossils have attached specimens of modern marine invertebrates. Fossils of the pampathere *Holmesina*, the cheetah-like cat *Miracinonyx*, the horse *Equus*, and a proboscidean were collected by a scuba diver from a depth of about 20 m in the Gulf of Mexico about 25 km west of St. Petersburg, Florida at about 28° North latitude (Morgan and Seymour, 1997; FLMNH vertebrate paleontology collection). Several of these specimens also had attached marine invertebrates, including coral. Tunnell (1991) reported a mammoth tooth collected by a commercial shrimp trawler from a depth of 55 m on the continental shelf off Port Isabel along the Gulf Coast of Texas at about 26° North latitude.

Fossils of large Pleistocene mammals have been caught by fisherman in bottom trawlers from depths between 20 and 50 m on the Atlantic continental shelf about 20–40 km offshore from the State of Rio Grande do Sul in southern Brazil, between 31° and 33° South latitude (Lopes and Buchmann, 2011). The Brazilian fossils include the tooth of a gomphothere and a partial skull, humerus, and femur of the toxodont *Toxodon*, all of which had attached specimens of modern marine invertebrates. The gomphothere

tooth, a lower m3 of *Notiomastodon platensis* (referred to *Stegomastodon waringi* by Lopes and Buchmann, 2011, but see taxonomic discussion above), is of particular interest because of its similarity to the occurrence of the gomphothere teeth from the Pearl Islands. This tooth has 5½ lophids that are angled from anterior to posterior and complicated enamel (Lopes and Buchmann, 2011), and bears a strong resemblance to a lower m3 (STRI/CTPA 1) from the Pearl Islands here referred to *Cuvieronius hyodon*. We are not aware of any published records of terrestrial vertebrate fossils from the continental shelf along the Pacific Coast between southern California and the Pearl Islands or in the Gulf of Mexico or the Caribbean Sea south of Florida and Texas.

## 6. Conclusions

Four proboscidean teeth from the continental shelf near the Pearl Islands in the Gulf of Panama, about 50–80 km offshore from the southern coast of Panama, are identified as the Pleistocene gomphothere *Cuvieronius hyodon*. Three complete third molars from the Pearl Islands, two M3s and one m3, exhibit a range of dental morphology: from 4½ to 5½ lophids/lophids that are either horizontal or set at an angle to the long axis of the tooth and rather simple enamel with single trefoils and limited development of small accessory cusps to more complex enamel with incipient double trefoils and numerous accessory cusps. Despite a rather significant range of dental variation, teeth of *Cuvieronius* from the southern United States, Mexico, and Central America, as well as the Pearl Islands, are referred to the pan-American species *C. hyodon*, which is also known from the Andean region of South America.

*Cuvieronius* can be differentiated from the closely related by *Rhynchotherium* by the shortened mandibular symphysis, lack of lower tusks, and more complicated enamel on the cheek teeth, particularly the M3s/m3s. *Cuvieronius* and *Rhynchotherium* are closely related based on the shared-derived character of spiraled upper tusks. The biochronology of these two genera in North America suggests an ancestor–descendant relationship: *Rhynchotherium* is known only from late Hemphillian and Blancan faunas; *Cuvieronius* is restricted to Irvingtonian and RanchoLabrean faunas. The absence of *Cuvieronius* in temperate North American late Blancan faunas suggests this genus may have evolved from *Rhynchotherium* in Central America. *Cuvieronius* reached South America in the early Pleistocene where it is first recorded from the Tarija fauna in Bolivia. *Cuvieronius* is the only Pleistocene gomphothere in Central America. In South America, this genus is primarily restricted to highland sites in Ecuador, Peru, and Bolivia. *Notiomastodon* is the common gomphothere in lowland Pleistocene faunas in South America, including sites in Colombia and Venezuela that are within 400 km of the Pearl Islands. Similarities between teeth of *Notiomastodon* and at least one of the gomphothere teeth from the Pearl Islands, and the lack of geographic barriers between Panama and northern South America during the late Pleistocene, suggest that the taxonomy of lowland gomphotheres in the northern Neotropics needs further study.

Two teeth of *Cuvieronius hyodon* from the Pearl Islands were recovered in nets by shrimp fisherman from depths of about 90 m, indicating that these fossils date to the Last Glacial Maximum between 30 and 15 ka, when sea level was as much as 120 m lower than present and the Gulf of Panama was dry land. Large areas of the continental shelf worldwide were subaerially exposed for significant periods of time since continental glaciation commenced at the beginning of the Pleistocene about 2.6 Ma, and should provide an excellent source of Pleistocene fossils of proboscideans and other large land mammals. Nonetheless, Pleistocene fossils from the continental shelf are only rarely reported, and are particularly uncommon from tropical regions such as Panama. Only in the North

Sea between the Netherlands and England (van Kolfschoten and Laban, 1995; Mol et al., 2006), and to a lesser extent the western North Atlantic off the northeastern coast of the United States (Whitmore et al., 1967), has there been a systematic attempt to document the Pleistocene mammal fauna recovered from the continental shelf. Elsewhere, information on late Pleistocene vertebrate fossils from the continental shelf has been obtained primarily from fishermen who occasionally notify paleontologists at museums or universities about fossils recovered from their nets. Interviewing fisherman in Panama who net shrimp or fish in the shallow waters of the Gulf of Panama would probably reveal the existence of more Quaternary fossils than the four gomphothere teeth reported here.

## Acknowledgments

David Bohaska assisted in our research on specimens in the U. S. National Museum of Natural History (USNM) from El Hatillo, Panama collected by Lewis Gazin. Dimila Mothé from the Laboratório de Mastozoologia (UNIRIO) in Rio de Janeiro, Brazil and Marco Ferretti, University of Firenze, Italy, provided helpful information on South American gomphotheres. Richard Cooke, Carlos Jaramillo, George Angehr, and Aaron Wood helped with our studies of a gomphothere tooth in the collection of STRI/CTPA. This study is part of the PCP (Panama Canal Project) PIRE (Partnerships in International Research and Education) project and was supported by US National Science Foundation grant 0966884 (OISE, EAR, DRL) University of Florida Contributions to Paleobiology 815.

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