



REPORT ON MANDIBULAR REMAINS OF *NOTIOMASTODON PLATENSIS* (MAMMALIA, PROBOSCIDEA) AND REVIEW OF ITS FOSSIL RECORD IN THE PALEOECOLOGICAL CONTEXT OF VALLE DEL CAUCA, COLOMBIA

JONATHAN S. PELEGRIN

Grupo de Investigación en Ecología y Conservación de la Biodiversidad (EcoBio), Equipo PaleoEco, Área de Biología, Facultad de Ciencias Básicas y Programa de Maestría en Educación Ambiental y Desarrollo Sostenible, Facultad de Educación, Universidad Santiago de Cali, Cali, Colombia.
jonathan.pelegrin00@usc.edu.co (corresponding autor)

SILVIA A. QUIJANO

Grupo de Investigación en Ecología y Conservación de la Biodiversidad (EcoBio), Programa de Microbiología, Facultad de Ciencias Básicas, Universidad Santiago de Cali, Cali, Colombia. *silvia.quijano00@usc.edu.co*

LEONARDO BELALCÁZAR

Grupo de Investigación en Ecología y Conservación de la Biodiversidad (EcoBio)-Equipo PaleoEco, Programa de Biología, Facultad de Ingeniería y Ciencias, Pontificia Universidad Javeriana, Cali, Colombia. *leonardolbs@javerianacali.edu.co*

ALBERTO BENAVIDES-HERRÁN

Departamento de Ciencias Naturales y Matemáticas, Facultad de Ingeniería y Ciencias, Pontificia Universidad Javeriana, Cali, Colombia. *alben@javerianacali.edu.co*

SEBASTIÁN ESCOBAR-FLÓREZ

Grupo de Investigación en Ecología y Conservación de la Biodiversidad (EcoBio)-Equipo PaleoEco, Laboratório de Mastozoologia, Departamento de Zoologia, Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal do Estado do Rio de Janeiro, Rio de Janeiro, Brazil. *sebastianescobar1594@gmail.com*

DIMILA MOTHÉ

Laboratório de Mastozoologia, Departamento de Zoologia, Universidade Federal do Estado do Rio de Janeiro. Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil. *dimila.mothe@gmail.com*

LEONARDO DOS SANTOS AVILLA

Laboratório de Mastozoologia, Departamento de Zoologia, Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal do Estado do Rio de Janeiro. Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.
leonardo.avilla@gmail.com

ABSTRACT – The Proboscidea were very prominent in South American ecosystems during the Pleistocene and part of the Holocene. Specifically, in Valle del Cauca (Colombia), fossils of these large mammals have been found, reflecting an abundant presence in the region. In this work, a mandibular fragment with a complete last molar (m3) is reported, found near the bed of the Cauca River, in the Juanchito municipality of Santiago de Cali. According to the morphological features of the specimen, it is proposed that the remains belong to the proboscidean *Notiomastodon platensis*. This study emphasizes the large geographical distribution of this proboscidean in South America, including the Valle del Cauca, and provides new information on its presence in Colombia. In a paleoecological context, this work supports a generalist condition based on the use of food resources associated with the tropical dry forest during the processes of glacial and interglacial fluctuation that this type of ecosystem experienced during the Pleistocene epoch and that led to various changes in habitat aridity, fragmentation, and heterogeneity.

Keywords: *Notiomastodon*, Quaternary, paleoecology, megafauna, South America.

RESUMO – Os proboscídeos foram muito proeminentes nos ecossistemas sul-americanos durante o Pleistoceno e parte do Holoceno. Especificamente, no Valle del Cauca (Colômbia), foram encontrados fósseis desses grandes mamíferos, refletindo uma presença abundante na região. No presente estudo, é registrado um fragmento de osso dentário com um molar 3 completo (m3) encontrado nas proximidades do leito do Rio Cauca na área de Juanchito, município de Santiago de Cali. De acordo com as suas características morfológicas, é proposto que o espécime pertença à espécie *Notiomastodon platensis*. Este estudo fornece evidências da grande distribuição geográfica desta espécie na América do Sul, incluindo o Valle del Cauca e contribui com informações importantes sobre a presença da espécie na Colômbia. Em um contexto paleoecológico, este trabalho permite sustentar uma condição generalista baseada no uso de recursos alimentares associados à floresta tropical seca durante os processos de flutuação glacial e interglacial que esse tipo de ecossistema experimentou durante o Pleistoceno e que levou a várias mudanças na aridez, fragmentação e heterogeneidade do habitat.

Palavras-chave: *Notiomastodon*, Quaternário, paleoecologia, megafauna, América do Sul.

INTRODUCTION

Among mammals, the order Proboscidea order is currently represented by three species, the two African elephants (*Loxodonta africana* and *L. cyclotis*) and the one from Asia (*Elephas maximus*). Since their origin in Africa during the Paleocene (60 Ma; Gheerbrant, 2009), the proboscideans reached an outstanding diversity, managing to inhabit diverse ecosystems at a global level during Paleogene and Neogene (Shoshani & Tassy, 2005; Fisher, 2018). The historical diversity of the group is estimated at over 175 species and subspecies (Shoshani & Tassy, 2005), and there is a continuous increase of taxa and new records, substantially developing the knowledge of the evolution of proboscideans (Mothé *et al.*, 2017a; Zhang & Wang, 2020; Cantalapiedra *et al.*, 2021).

The proboscideans arrived in North America during the early Miocene, specifically Mammutidae (true mastodons from genus *Mammut*) and Gomphotheriidae (gomphotheres, Fisher, 2018; Smith & De Santis, 2020). Finally, Elephantidae (mammoths, *Mammuthus* genus) reached North America during the early Pleistocene (Lucas *et al.*, 2017; van der Valk *et al.*, 2021). Later, during the Great American Biotic Interchange, only the brevirostrine gomphotheres came to colonize South America (Lucas, 2013; Cione *et al.*, 2015; Mothé *et al.*, 2017a; Pelegrin *et al.*, 2018), with the presence of the monospecific genera *Cuvieronius* and *Notiomastodon*. The former was widely distributed in the Americas, while the latter is endemic to South America (Mothé & Avilla, 2015; Mothé *et al.*, 2016). Particularly in South America, the oldest records with reliable datings are from the Argentine Marplatian, with approximately 2.5 Ma, although the vast majority of findings are from the middle–late Pleistocene (Lucas, 2013; Alberdi & Prado, 2016; Mothé *et al.*, 2017a).

Unlike other proboscideans, the gomphotheres from South America present characteristic features related to the configuration of cranial bones, showing a brachycephalic skull, rounded and slightly elongated in the upper part and developed tusks that could vary from straighter and more elongated to upcurved in their most distal region (Mothé & Avilla, 2015). The mandibular structure is short (brevirostrine condition), and the complex structure of the premolars and molars is of paramount taxonomic significance, traditionally being a source of diagnostic characteristics. The molars present serial transverse rows of blunt cusps (lophs/lophids),

which appear along the occlusal surface. Each loph/lophid is composed by a pair of rounded dome-shaped main cusps and smaller accessory cusps that cover the intermediate spaces between the cones or toward the midline of the molar. Likewise, the study of tooth wear patterns has been key in taxonomic differentiation, with the trefoil wear patterns being an outstanding feature (Alberdi *et al.*, 2002; Chávez-Aponte *et al.*, 2008; Mothé *et al.*, 2012a,b, 2017a,b; Mothé & Avilla, 2015).

The taxonomic study of South American proboscideans has been very controversial. Historically, various analyses from fossils have led to frequent synonymy in their classification (Alberdi *et al.*, 2004; Prado *et al.*, 2005; Lucas, 2009; Mothé *et al.*, 2014; Mothé *et al.*, 2016, 2017a; Buckley *et al.*, 2019). Among the widely described and studied species, *Cuvieronius hyodon* is a taxonomic consensus (Alberdi *et al.*, 2004; Prado *et al.*, 2005; Lucas, 2009; Ferretti, 2010; Lucas *et al.*, 2013; Mothé *et al.*, 2016, 2017a; Buckley *et al.*, 2019). It was distributed throughout the western Andean system of South America, presenting the oldest records for the lower–middle Pleistocene of Ecuador (Imbabura) and many fossilized individuals from Tarija, Bolivia (Mothé *et al.*, 2016) and Peru (Alberdi *et al.*, 2004; Mothé *et al.*, 2017a). The debate on the taxonomy of the other South American proboscideans is more controversial. The genus *Stegomastodon* was defined by Pohling (1912) from North American remains dated to the Pliocene/Early Pleistocene, and three species were identified (*S. primitivus*, *S. mirificus*, and *S. aftoniae*). In South America, Cabrera (1929) proposed the presence of this genus represented by the species *S. platensis* and *S. superbus*. In addition, Cabrera (1929) also described the species *Notiomastodon ornatus* that he considered more primitive than those mentioned above, with a more derived condition. Osborn (1936) proposed the genera *Cordillerion* and *Notiomastodon* as valid for South America, excluding the presence of *Stegomastodon*. Subsequent paleontological studies followed the taxonomic proposal of Cabrera (1929), and therefore, the use of *Stegomastodon* for some South American records (see Ferretti, 2010; Mothé *et al.*, 2012a,b, 2017a). It should be emphasized that despite the relative stability and consensus of *Stegomastodon* for several decades, some studies proposed differences between the specimens from North and South American *Stegomastodon* and, therefore, that both lineages should be distinguished (Osborn, 1936; Madden, 1984; Ferretti, 2008), thus rethinking

Notiomastodon and *Haplomastodon*, the latter being defined from remains found in Ecuador as *H. chimborazi* (Ferretti, 2010). Later works showed that there were no significant differences between these South American taxa, and they are considered synonyms (Mothé *et al.*, 2012a,b, 2017a,b; Lucas, 2013, Mothé & Avilla, 2015).

In this context, there is a need to know if *Stegomastodon* would have colonized South America giving rise to two species, *S. platensis* and *S. waringi*, as Alberdi & Prado (1995) initially suggested, or if, in contrast, there is a divergence between the North American (*Stegomastodon*) and South American (*Notiomastodon*) lineage. In this sense, the most recent studies by Mothé & Avilla (2015) and Mothé *et al.* (2012b, 2017a,b) have analyzed this conflict, showing significant evidence regarding cranial, mandibular, and dental features exclusive of *Stegomastodon* specimens from North America. This genus would have been distributed in North America (with the southernmost record in Mexico), whereas *Notiomastodon* is known as endemic to South America so far (Lucas & Alvarado, 2010; Mothé *et al.*, 2012b, 2017a), a proposal which gained support in the most recent studies in South American proboscideans (Mothé *et al.*, 2012a,b, 2017a,b; Fisher, 2018; Buckley *et al.*, 2019). Therefore, the presence of two species in South America is currently considered: *Cuvieronius hyodon* and *Notiomastodon platensis*.

The Colombian findings of proboscideans correspond to *Notiomastodon platensis*, being recorded in the departments of Cundinamarca, Boyacá, Santander, Atlántico, Bolívar, Huila, Antioquia, Cauca, Nariño, and Valle del Cauca (Hoffsteter, 1971; Correal-Urrego, 1993; Correal-Urrego *et al.*, 2005; Villarroel & Clavijo, 2005; Gómez, 2006; Rodríguez-Flórez *et al.*, 2009; Gutiérrez-Olano, 2010; Páramo-Fonseca & Escobar-Quemba, 2010; Pardo-Jaramillo, 2012; Mothé *et al.*, 2012a,b, 2017a; Valencia-Giraldo *et al.*, 2016; Suárez-Ibarra *et al.*, 2021). Diagnostic *Cuvieronius hyodon* remains are still unknown for Colombia, although its key position at northern South America might have been part of its migratory route between Panamá and Ecuador (see Lucas & Alvarado, 2010; Mothé & Avilla, 2015; Morgan *et al.*, 2016). Many of these proboscidean reports, nevertheless, show a high degree of fragmentation and stratigraphic uncertainty, requiring a more detailed study on diagnostic features for better taxonomic identification and more precise dating of some occurrences.

For the department of Valle del Cauca, there are various records of *Notiomastodon platensis*. The material reported from the municipality of Toro was found in the bed of the Cauca River and corresponds to various pieces, including molars, fragments of the jaw, femurs, and ribs, in association with human tools made with stone and other megafauna bones (Rodríguez-Flórez *et al.*, 2009). In the towns of Zarzal and La Victoria, remains of molars within the mandible were found, attributed to an adult specimen. In the construction zone of the current Alfonso Bonilla Aragón airport (Palmira), many ribs remain were found, later sent to the Universidad del Valle. In the municipality of Guacarí, fragmented tusks were found, associated with an archaeological excavation corresponding to the late Quimbaya (700–1300 BC); however,

they must be much older (Rodríguez, 2002, 2007). In Yumbo, a condylar fragment, a molar, and a humeral head were found. Of these remains, only the humeral head has been studied so far (Rodríguez-Flórez *et al.*, 2009). Finally, in Cali, various reports have been made and findings have taken place in the bed of the Cauca River as it passes through the city, mainly of molars, tusks, and jaws of juveniles and adults.

This paper reports a molar (m3) associated with a mandible fragment found in the area of Juanchito, east of Santiago de Cali. Its morphological characteristics are studied in detail in the context of what is known for the region's environmental conditions during the Pleistocene–Holocene (Berrío *et al.*, 2002; Berrío, 2004), to shed more light on the knowledge of the proboscideans from Colombia.

MATERIAL AND METHODS

Geographical location and geological context of the discovery

This fossil specimen was retrieved from the bed of the Cauca River near the town of Juanchito, on the right bank of the river in the border area between the municipalities of Santiago de Cali, Palmira, and Candelaria (3°26'36''N; 76°28'14''W, Figure 1). Sand and gravel are massively and disorderly extracted for construction purposes at the site by dredging the sedimentary material in the Cauca riverbed.

The precise location of the discovery is difficult to pin down as the specimen was found among construction sand purchased in a sandbox in the Juanchito sector in 2018. As the piece was removed from its site, the stratigraphic information was lost, but sand alluvium from the Holocene is likely to occur (López *et al.*, 2005; Soto, 2015; Corporación Autónoma Regional del Valle del Cauca/CVC, 2017).

The fossil was found in the area of the Cauca River identified as Valle Alto, between Timba, in the department of Cauca and La Virginia in Risaralda, where the river descends from 1,000 to 900 m above sea level (Soto, 2015; CVC, 2017). In this area, 29 sub-basins of rivers classified as torrential are recognized, which contributed drag material and sediments to the Cauca River through their floods (Soto, 2015; CVC, 2017).

As it flows through the inter-Andean depression, the Cauca River established an extensive, thick, and heterogeneous alluvial plain of intercalated layers of clayey silts, fine and coarse sands, gravels, and silts of very variable thickness (Instituto de Geología y Minas – INGEOMINAS – & Departamento Administrativo de Gestión Medio Ambiente – DAGMA, 2005). In addition to these deposits of heterogeneous materials that make up the Quaternary alluvial plain of the Cauca River identified on the local map as geological unit Qalc, we can add the materials transported by torrential tributaries that flow down from the western mountain range and which, upon reaching the plain, abruptly lose their dragging capacity, forming alluvial fans. This hydrological dynamic makes it possible to identify a zone of main alluvial plains fed by the divergence of the Cauca River on its northward course, the filling of the riverbed, its drained areas and old swamps with fine sediments, and the zone of

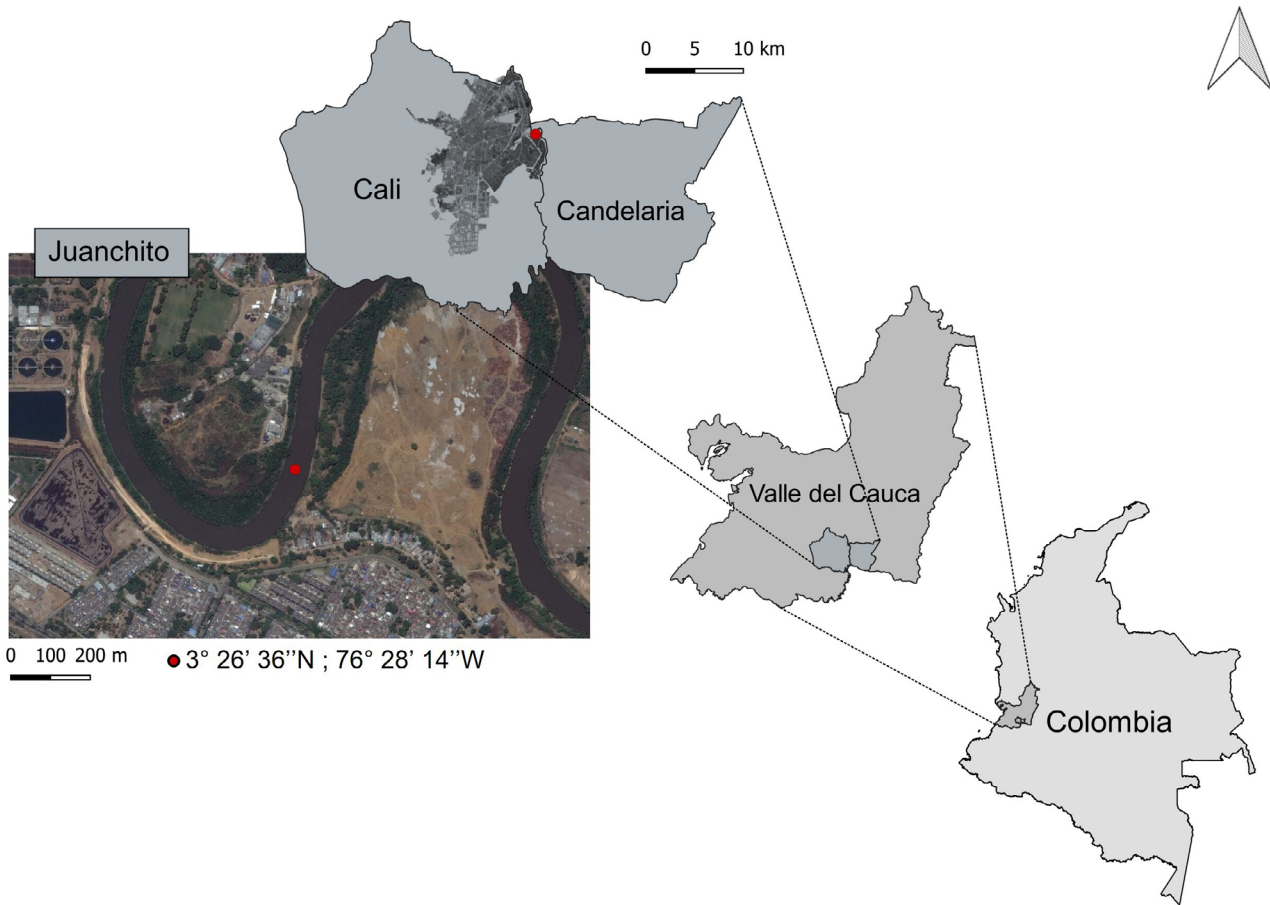


Figure 1. Meander of the Cauca River in the Juanchito district, Candelaria municipality, Valle del Cauca. In the sector, formal and informal sand dumps have been established that sell sedimented material from the Cauca riverbed.

the old riverbed with sandbanks in the abandoned meandering bends (INGEOMINAS & DAGMA, 2005). In addition to the geological and geomorphological studies carried out by INGEOMINAS & DAGMA (2005), which provide very good information about the alluvial deposit of the western bank of the Cauca River as it passes through Santiago de Cali, there is a second source of palaeoecological data that allows us to reconstruct the environmental history of the Holocene south of the Valle del Cauca from pollen, carbon, and ^{14}C in nuclei extracted in Quilichao and La Teta, carried out by Berrío *et al.* (2002) and Berrío (2004).

Biometry of the studied material

In relation to the morphometric measurements of the tooth, the criteria of Alberdi *et al.* (2002), Corona-M & Alberdi (2006), and Chávez-Aponte *et al.* (2008) were considered, including the proposal of the following measurements: maximum length of the anteroposterior axis (**mL**) and maximum width of the lingual-labial axis (**mW**). Cones or rounded cusps were identified in the anteroposterior axis according to their grouping as L1–L4. Likewise, the main internal or lingual (IC) and external or labial (EC) cones or cusps, which are grouped in pairs, the cones close to the midline or mesocones (**mc**), the central cones (**cc**), the mesial cingulum (**cm**) and the characterization of the talonid (**T**), as

well as the last lophid or cone (narrowest distal region), are also morphologically described. As for the lophids, the length and width of the segments corresponding to each one (L1–L4) were measured, as well as in the talonid (Figure 2). Finally, the fossil was donated to the Environmental Sciences Laboratory of the Ecology and Biodiversity Conservation research group at the Universidad de Santiago de Cali (**USC**). Once it was studied, the fossil was stored in the Reference Collection of Zoological Practices- Universidad del Valle (CPZ-UV 7367), located at Santiago de Cali.

SYSTEMATIC PALEONTOLOGY

Order PROBOSCIDEA (Illiger, 1811)
 Superfamily ELEPHANTOIDEA (Gray, 1821)
 Family GOMPHOTHERIIDAE (Hay, 1922)

Notiomastodon (Cabrera, 1929)

Notiomastodon platensis (Ameghino, 1888)
 (Figure 3)

Material. CPZ-UV 7367, fragment of the left mandibular ramus.

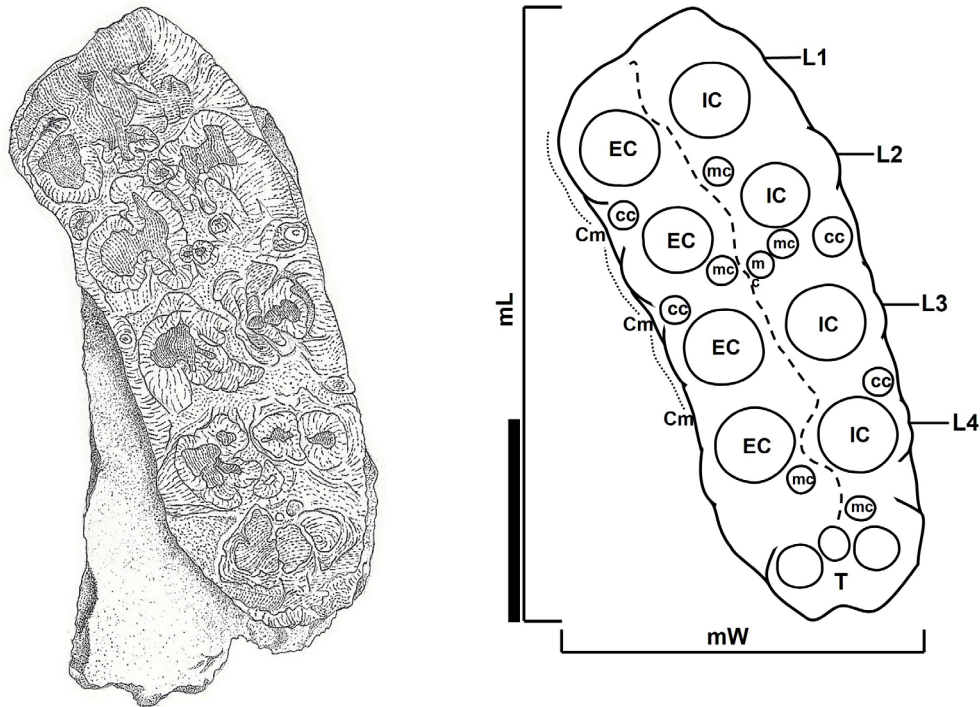


Figure 2. Schematic drawing of the specimen CPZ-UV 7367, which shows the occlusal surface and details for measures (see text for abbreviations). Illustration by Leonardo Belalcázar. Scale bar = 10 cm.

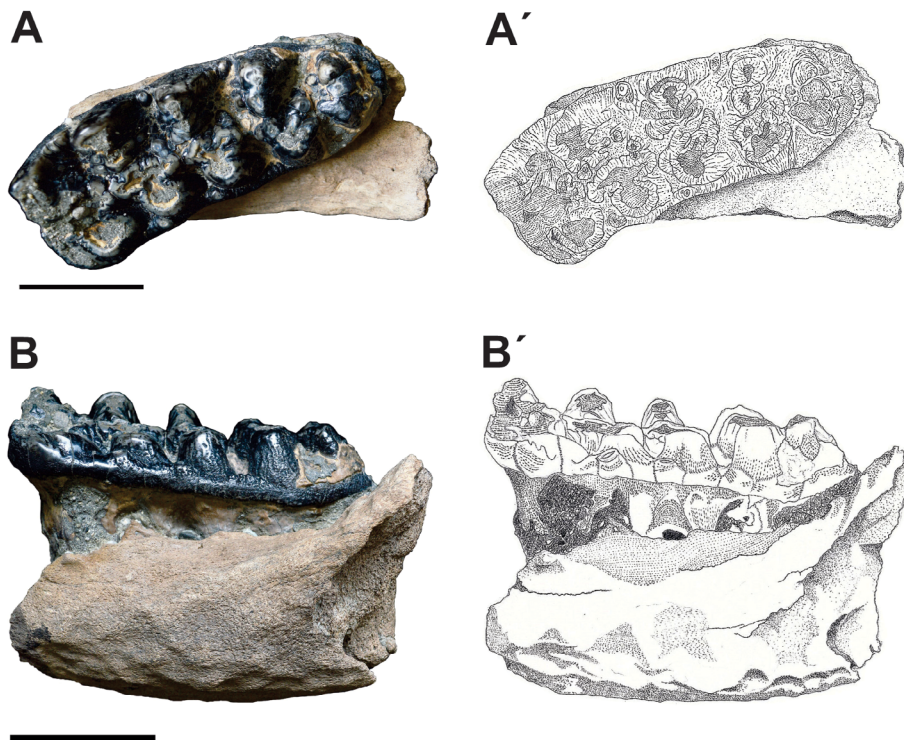


Figure 3. Photograph and illustration of CPZ-UV 7367, in occlusal (A, A') and left lingual (B, B') views. Scale bars = 10 cm.

Description. The fossil specimen corresponds to a fragment of the left mandibular ramus, with an average height of 11 cm, with a last molar (m3) in use. The labial side of the mandibular fragment is smooth and relatively well preserved

with a convex surface, while its lingual side shows more wear, having a concave surface, a protruding dental root and the canal of the mandibular duct can be seen, which is 1.5 cm in diameter, and about 16.5 cm are preserved. Toward the distal

region, the beginning of the left mandibular ramus and part of the retromolar fossa is preserved (Figure 3). However, in both the anterior and posterior regions, an irregular fracture is evident, exposing the fossilized spongy tissue. In the specimen, some incrustations of sediment can be observed, which consist mainly of siliceous sands and small pebbles of variable composition. The molar is a bunodont tooth, the upper region of the dental root presents the same color as the bone, while, in the crown, the surface of the enamel is very glossy and becomes dark gray to almost black. In the occlusal wear, a light gray to almost white coloration and a trefoil pattern is evident, and part of the yellowish-white dentin can be observed. In addition, a 30° angle is observed on the occlusal surface towards the labial surface, which would be the result of wear due to chewing activity (Figure 3).

Cones or rounded cusps have been identified in the anteroposterior axis based on their grouping as L1–L4. They are also morphologically described as main IC and EC cones that are grouped in pairs with the cones close to the midline or midshaft or mesocones (mc), the central cones (cc), the mesial cingulum (cm), and the characterization of the talonid (T), as well as the last lophid (narrower distal region). Measurements are presented in Table 1.

Table 1. Dimensions (in mm) of the *Notiomastodon platensis* molar (CPZ-UV 7367) from Juanchito, Santiago de Cali. **Abbreviations:** L, length; W, width; NA, not applicable.

Measurement	with cingulum	without cingulum
Max. L.	219.7	NA
Max. W.	88.5	NA
L. L1	46.6	NA
W. L1	87.7	81.8
L. L2	43.0	NA
W. L2	87.4	78.4
L. L3	49.0	NA
W. L3	83.0	79.0
L. L4	37.3	NA
W. L4	80.8	77.0
L. Talonid	52.8	NA
W. Talonid	60.0	51.1

DISCUSSION

From a descriptive point of view, the dental morphology reported for m3 CPZ-UV 7367, with a maximum length of 219.7 mm and a maximum width of 88.5 mm, falls within the ranges of morphological variability reported in other studies for the South American species (Table 2), which is evidence of a great intraspecific variability of m3 size. In addition, the dental morphology studied in the specimen is consistent with dental material reported for other locations in South America and Colombia specifically, providing additional information on the dental variability of South American proboscideans. Some morphometric analyses show that the *Cuvieronius hyodon* and *Notiomastodon platensis* molars

are quite similar, although *Notiomastodon* tends to have larger teeth (Recabarren *et al.*, 2014). Therefore, aspects associated with dental complexity, cranial anatomy, and tusks become relevant among the characteristics that differentiate them. In this regard, Mothé & Avilla (2015) evince a greater complexity in the dental structure with respect to the number of cusps in *Notiomastodon* (from 35 to 82) with respect to that reported for *Cuvieronius* (from 33 to 60), with both forms showing significant differences in this aspect. Specifically, the described specimen shows 70 cusps.

It should be noted that, despite the wide variability reported and the measurements obtained, the taxonomic assignment of the remains reported to the species *Notiomastodon platensis* is fundamentally based on the comparison with the material included in the literature. However, despite the wide intraspecific variation evidenced here and in previous studies, the specific assignment proposed here is also based on various ecological and distribution analyses that have been carried out for the South American forms, including those reported in Colombia (Mothé *et al.*, 2017a). During many years, several reports for Colombia assigned specimens to *Stegomastodon*. However, due to the most recent revisions and advances in taxonomy of South American gomphotheres (Mothé *et al.*, 2012a, 2017a), the forms previously classified as *Stegomastodon* are attributed to *Notiomastodon*, and that makes the former exclusive to North America. According to the above, the Juanchito proboscidean report contributes to expanding the records of *Notiomastodon platensis* for the Valle del Cauca. The various reports for the department of Valle del Cauca (Table 3, Figure 4) show that this species was an important inhabitant of the ecosystems of the Cauca River valley during the Pleistocene–Holocene and adds to the growing evidence that describes significant ecosystem complexity during these times (Escobar-Flórez, 2017). In addition, it is interesting to note that the remains reported so far are grouped into two areas of great geographical proximity, which may suggest the importance of increasing the sampling effort or analyzing the taphonomic conditions and the dynamics of the Cauca River in the different areas where reports have been made. In this way, these points show a wide distribution of *Notiomastodon* in the Valle del Cauca along the alluvial plain formed by the river.

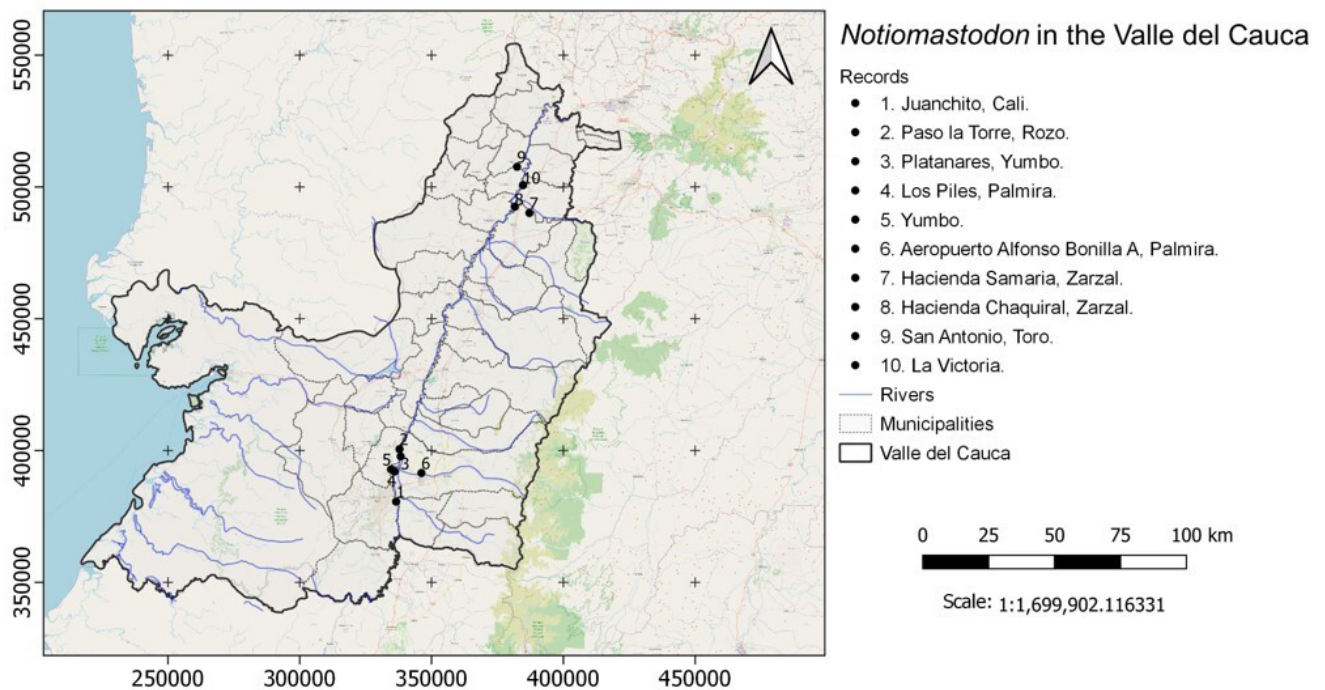
According to the palaeoecological evidence of the region (Berrío *et al.*, 2002, 2012; Berrío, 2004) at 13,150 BP, dry forest environments were transforming into open environments dominated by grasslands, reaching aridity peaks 7,500–4,300 years ago. Paleoecological studies have established that 13,150 years ago (¹⁴C yr BP), there was an active late glacial drainage in the region and a dry forest that gradually transformed into open pastures, which is considered an indicator of dry climate conditions. The regional dryness reached its maximum severity 7,500 and 4,300 years ago, which affected the dry forest ecosystem of southern Valle del Cauca and the riverbed itself (Berrío *et al.*, 2002; Berrío, 2004). This explains the terraces and the system of intercalated layers of clay sediments and sand horizons in its passage

Table 2. Range of morphological variability of *Notiomastodon* associated with total lengths and widths measured in m3 for South America.

Morphometric measurement report of m ³	Max length range (mm)	Max. width range (mm)	n specimens	Country of the specimens
Villarroel <i>et al.</i> (1996)	197–208	74–76	3	Colombia
Alberdi <i>et al.</i> (2002)	155–210	73–92	9	Brazil
Alberdi <i>et al.</i> (2004)	188–236	81–99.5	4	Peru
Gutiérrez <i>et al.</i> (2005)	not available	95–97	1	Uruguay
Alberdi <i>et al.</i> (2008)	185–260	72–95.5	15	Argentina
Chávez-Aponte <i>et al.</i> (2008)	180–211	78–99.7	5	Venezuela
Ferreti (2010)	189–250	78–92	9	Ecuador
Labarca-Encina & Alberdi (2011)	c 205–248	c 75–95	10	Chile
Recabarren <i>et al.</i> (2014)	not available	c 83–103	7	Chile

Table 3. Fossil reports of *Notiomastodon* made in various locations of the Department of Valle del Cauca.

Age	Location	Reported anatomical elements	Reference
Holocene	Juanchito, Cali	m3 associated with mandibular ramus fragment	This study
Holocene	Paso la Torre, Rozo	various elements	Escobar-Flórez (2017)
Holocene	Platanares, Yumbo	various elements	Escobar-Flórez (2017)
Holocene	Los Piles, Palmira	juvenile molar	Escobar-Flórez (2017); De Andrade (2020)
Holocene	Yumbo	femoral head	Rodríguez-Flórez <i>et al.</i> (2009)
Pleistocene	Alfonso Bonilla A Airport, Palmira	rib fragments	Gutiérrez-Olano (2010)
Pleistocene	Hacienda Samaria, Zarzal	remains without detail	Correal-Urrego (1981)
Pleistocene	Hacienda Chaquiral, Zarzal	jaw fragment with molars	Rodríguez-Flórez <i>et al.</i> (2009)
Pleistocene	San Antonio, Toro	various molars, ribs, f. Femur with head, f. mandibular, associated with lithic projectile	Correal-Urrego <i>et al.</i> (2005); Gutiérrez-Olano (2010)
Pleistocene	La Victoria	Molar fragment	Rodríguez-Flórez <i>et al.</i> (2009)

**Figure 4.** Geographical location of the findings reported in Valle del Cauca for *Notiomastodon*.

through the geographical valley of the Cauca River and, in particular, through the Juanchito sector.

This paleoecological scenario suggests that environmental conditions with a high tendency towards aridity gave rise to mixed environments with forest fragments and open areas of grasses in the geographic valley. According to isotopic analyses carried out for *Notiomastodon* in other regions of South America with respect to feeding habits, it has been estimated that these animals would have presented a mixed and relatively flexible diet, consisting mainly of a mixture of C3 and C4 plant components (Domingo *et al.*, 2012, 2020; Mothé *et al.*, 2017). Therefore, *Notiomastodon* would have been especially distributed in areas within a warm–temperate climatic range, preferably occupying environments in an ecological spectrum from partially open, dry tropical forests, wooded savannas, and xerophilous grasslands, having a mixed herbivorous diet (Rodríguez-Flórez *et al.*, 2009; Dantas *et al.*, 2013; Gutiérrez-Olano, 2010; Domingo *et al.*, 2012, 2020). This mosaic of environments and variations is consistent with the palaeoecological estimations made in the context of the geographical valley of the Cauca River for the Pleistocene–Holocene (Berrío *et al.*, 2002) (Figure 5).

Besides, van der Hammen & Correal-Urrego (2001) dated by ^{14}C some localities with *Notiomastodon platensis* suggesting the presence of this species in Colombian ecosystems for an interval of about 15,000 years. This hypothesis suggests

a scenario of coexistence between these mammals and the first Paleo-American inhabitants, a factor that may be relevant in understanding the causes that contributed to the extinction of the Pleistocene megafauna and specifically of *Notiomastodon* in the territory of Valle del Cauca and Colombia. Evidence suggests that the first inhabitants of South America would have made active use of the resources from proboscideans, especially *Notiomastodon* (Mothé *et al.*, 2020). For the Valle del Cauca, in the municipality of Toro, in particular, the remains reported have marks, probably of human activity, and many tools made with hard tissues, which could suggest some type of exploitation of these animals by the first human inhabitants of the region (Rodríguez-Flórez *et al.*, 2009). Finally, from the evolutionary point of view, the suggested generalist condition of *Notiomastodon* in terms of the eurybiomic occupation due its wide range of geographic distribution (Dantas *et al.*, 2013; Mothé *et al.*, 2017a,b) reflects an outstanding adaptive capacity, as well as a wide spectrum of food resources utilization (Domingo *et al.*, 2012, 2020). Therefore, the species would have a greater chance of survival in the event of climatic and environmental changes (Vrba, 1992; Moreno Bofarull *et al.*, 2008). This scenario could suggest that the extinction process of South American proboscideans may have been also triggered by the pressure exerted by first American inhabitants reinforcing transformations associated with environmental and climatic

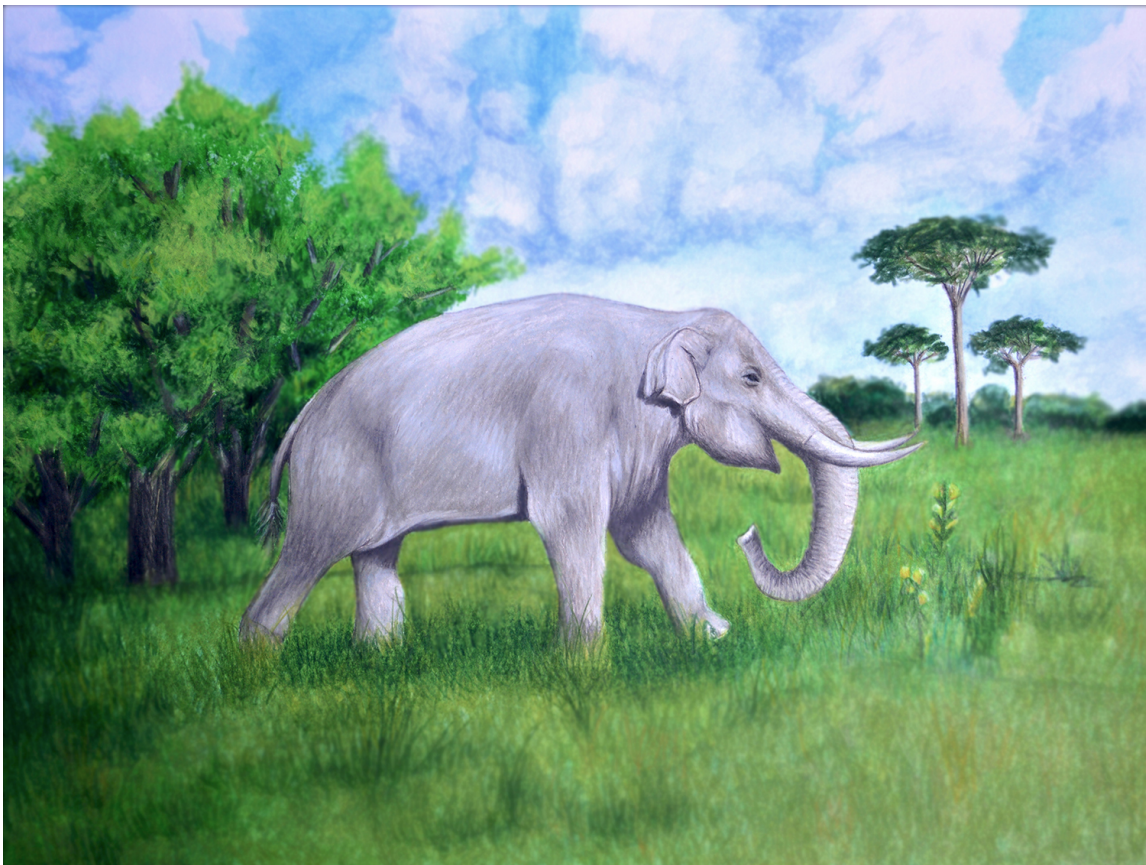


Figure 5. Paleoreconstruction of *Notiomastodon* in the environmental context of the Valle de Cauca for the Pleistocene–Holocene. Illustration by Jacobo Sabogal (after Pelegrin & Sabogal, 2019).

variations affecting biomes as main driver in megafaunal lineages extinction (Barnosky *et al.*, 2004; Gutiérrez-Olano, 2010; Lima-Ribeiro *et al.*, 2013; Mothé *et al.*, 2020; Prates & Perez, 2021; Araújo *et al.*, 2021; Cantalapiedra *et al.*, 2021).

ACKNOWLEDGMENTS

We would like to thank the USC research group in Ecology and Conservation of Biodiversity (EcoBio) and its research team in Paleobiology, Ecology, and Biodiversity Evolution (PaleoEco) for the continuous discussions. This research was funded by the General Research Directorate (DGI) of Universidad Santiago de Cali (Call 01-2021) (JSP and SAQ). The authors thank Crimson Interactive Pvt. Ltd. (Enago) – <https://www.enago.com/es/> for their assistance in manuscript translation and editing. We would like to extend special thanks to scientific illustrator J. Sabogal for the illustrations in the document that provide visual support and to the reviewers who undoubtedly contributed to the substantial improvement of the final manuscript. This work was also funded by the National Council for Scientific and Technological Development (PDJ 153536/2016-0 - DM; 248772/2013-9 - LSA) and Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro (202.375/2018 and 202.376/2018 – DM); (204036-E_25/2014 - Jovem Cientista do Nosso Estado - LSA).

REFERENCES

- Alberdi, M.T.; Cerdeño, E. & Prado, J.L. 2008. *Stegomastodon platensis* (Proboscidea, Gomphotheriidae) en el Pleistoceno de Santiago del Estero, Argentina. *Ameghiniana*, **45**:257–271.
- Alberdi, M.T. & Prado, J.L. 1995. Los mastodontes de América del Sur. In: M.T. Alberdi; G. Leone & E.P. Tonni (eds.) *Evolución biológica y climática de la Región Pampeana durante los últimos 5 millones de años. Un ensayo de correlación con el Mediterráneo occidental*, Monografías del Museo Nacional de Ciencias Naturales, CSIC, p. 277–292.
- Alberdi, M.T. & Prado, J.L. 2016. Fossil Gomphotheriidae from Argentina. In: F.L. Agnolin; G.L. Lio; F. Brisson Egli; N.R. Chimento & F.E. Novas (eds.) *Historia Evolutiva y Paleobiogeográfica de los Vertebrados de América del Sur*. Contributions from MACN 6, *Museo Argentino de Ciencias Naturales* “Bernardino Rivadavia,” Buenos Aires, Argentina, 275–283.
- Alberdi, M.T.; Prado, J.L. & Cartelle, C. 2002. El registro de *Stegomastodon* (Mammalia, Gomphotheriidae) en el Pleistoceno superior de Brasil. *Revista Española de Paleontología*, **17**:217–235.
- Alberdi, M.T.; Prado, J.L. & Salas, R. 2004. The Pleistocene Gomphotheriidae (Proboscidea) from Peru. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **231**:423–452. doi:10.1127/njgpa/231/2004/423
- Araújo, T.; Machado, H.; Mothé, D. & dos Santos Avilla, L. 2021. Species distribution modeling reveals the ecological niche of extinct megafauna from South America. *Quaternary Research*, **104**:151–158. doi:10.1017/qua.2021.24
- Barnosky, A.D.; Koch, P.L.; Feranec, R.S.; Wing, S.L. & Shabel, A.B. 2004. Assessing the causes of late Pleistocene extinctions on the continents. *Science*, **306**:70–75. doi:10.1126/science.1101476
- Berrio, J.C. 2004. Comparación paleoambiental del Bosque Seco en los Valles de los ríos Cauca y Patía, Suroccidente Colombiano. In: J.O. Rangel-Ch *et al.* *Memorias Octavo Congreso Latinoamericano y Segundo Colombiano de Botánica*, Instituto de Ciencias Naturales, Universidad Nacional de Colombia.
- Berrio, J.C.; Hooghiemstra, H.; Marchant, R. & Rangel, O. 2002. Late glacial and Holocene history of the dry forest area in the South Colombian Cauca valley. *Journal of Quaternary Science*, **17**:667–682. doi:10.1002/jqs.701
- Berrio, J.C.; Wouters, H.; Hooghiemstra, H.; Carr, A.S. & Boom, A. 2012. Using paleoecological data to define main vegetation dynamics along the savanna–forest ecotone in Colombia: Implications for accurate assessment of human impacts. In: R.W. Myster (ed.) *Ecotones between forest and grassland*, Springer Science+Business Media, p. 209–225.
- Buckley, M.; Recabarren, O.P.; Lawless, C.; García, N. & Pino, M. 2019. A molecular phylogeny of the extinct South American gomphothere through collagen sequence analysis. *Quaternary Science Reviews*, **224**:105882. doi:10.1016/j.quascirev.2019.105882
- Cabrera, Á. 1929. Una revisión de los Mastodontes Argentinos. *Revista del Museo de la Plata*, **32**:61–147.
- Cantalapiedra, J.L.; Sanisidro, Ó.; Zhang, H.; Alberdi, M.T.; Prado, J.L.; Blanco, F. & Saarinen, J. 2021. The rise and fall of proboscidean ecological diversity. *Nature Ecology & Evolution*, **5**:1266–1272. doi:10.1038/s41559-021-01498-w
- Chávez-Aponte, E.O.; Alfonso-Hernández, I. & Carrillo-Briceno, J.D. 2008. Morfología dentaria de los gonfoterios de la localidad de Muaco, estado Falcón, Venezuela. *Interciencia*, **33**:771–775.
- Cione, A.L.; Gasparini, G.M.; Soibelzon, E.; Soibelzon, L.H. & Tonni, E.P. 2015. *The great American biotic interchange: a South American perspective*. Netherlands, Springer, 97 p.
- Colombian Institute of Geology and Mines (INGEOMINAS) & Administrative Department of Environmental Management (DAGMA). 2005. *Proyecto Microzonificación Sísmica de Cali, Mapa de Unidades Geológicas MZSC-G1*. Informe técnico. 50 p.
- Corona-M, E. & Alberdi, M.T. 2006. Two new records of Gomphotheriidae (Mammalia: Proboscidea) in Southern México and some biogeographic implications. *Journal of Paleontology*, **80**:357–366. doi:10.1666/0022-3360(2006)080[0357:TNROGMJ]2.0.CO;2
- Corporación Autónoma Regional del Valle del Cauca (CVC). 2017. *Evaluación regional del agua, Valle del Cauca – 2017*:209–210.
- Correal-Urrego, G.C. 1981. *Evidencias culturales y megafauna pleistocénica en Colombia*. Bogotá, Fundación de Investigaciones Arqueológicas nacionales del Banco de la República.
- Correal-Urrego, G.C. 1993. Nuevas evidencias culturales pleistocénicas y megafauna en Colombia. *Boletín de Arqueología*, **1**:3–13.
- Correal-Urrego, G.C.; Olano, J.G.; Calderón, K.J. & Cardozo, C.V. 2005. Evidencias arqueológicas y megafauna extinta en un salado del Tardiglacial Superior. *Boletín de arqueología*, **20**:3–58.
- Dantas, M.A.T.; Xavier, M.C.T.; de Melo França, L.; Cozzuol, M.A.; de Souza Ribeiro, A.; Figueiredo, A.M.G.; Kinoshita, A. & Baffa, O. 2013. A review of the time scale and potential geographic distribution of *Notiomastodon platensis* (Ameghino, 1888) in the late Pleistocene of South America. *Quaternary International*, **317**:73–79. doi:10.1016/j.quaint.2013.06.031

- De Andrade, L.C.; Oliveira, É.V.; Mothé, D. & Maniesi, V. 2020. New record of an immature *Notiomastodon cf. platensis* (Mammalia, Proboscidea) from Pernambuco State, Northeastern Brazil. *Revista Brasileira de Paleontologia*, **23**:73–77. doi:10.4072/rbp.2020.1.05
- Domingo, L.; Prado, J.L. & Alberdi, M.T. 2012. The effect of paleoecology and paleobiogeography on stable isotopes of Quaternary mammals from South America. *Quaternary Science Reviews*, **55**:103–113. doi:10.1016/j.quascirev.2012.08.017
- Domingo, L.; Tomassini, R.L.; Montalvo, C.I.; Sanz-Pérez, D. & Alberdi, M.T. 2020. The Great American Biotic Interchange revisited: a new perspective from the stable isotope record of Argentine Pampas fossil mammals. *Scientific reports*, **10**:1–10. doi:10.1038/s41598-020-58575-6
- Escobar-Flórez, J.S. 2017. *Análisis del desgaste dental en relación con la dieta de bóvidos fósiles del Valle del Cauca (Mammalia: Artiodactyla: Bovidae: Bison)*. Programa de Biología, Universidad ICESI, Thesis, 34 p.
- Ferretti, M.P. 2008. Enamel structure of *Cuvieronius hyodon* (Proboscidea, Gomphotheriidae) with a discussion on enamel evolution in elephantoids. *Journal of Mammalian Evolution*, **15**:37–58.
- Ferretti, M.P. 2010. Anatomy of *Haplo mastodon chimborazi* (Mammalia, Proboscidea) from the late Pleistocene of Ecuador and its bearing on the phylogeny and systematics of South American gomphotheres. *Geodiversitas*, **32**:663–722. doi:10.5252/g2010n4a3
- Fisher, D.C. 2018. Paleobiology of pleistocene proboscideans. *Annual Review of Earth Planetary Sciences*, **46**:229–260. doi:10.1146/annurev-earth-060115-012437
- Gheerbrant, E. 2009. Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. *Proceedings of the National Academy of Sciences*, **106**:10717–10721. doi:10.1073/pnas.0900251106
- Gómez, M. 2006. *Revisión del registro fósil y distribución de los mastodontes (Proboscidea Gomphotheriidae) del Cuaternario en Colombia*. Programa de Biología, Universidad de Antioquia, Thesis, 84 p.
- Gutiérrez, M.; Alberdi, M.T. & Prado, J.L. 2005. Late Pleistocene *Stegomastodon* (Mammalia, Proboscidea) from Uruguay. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **11**:641–662.
- Gutiérrez-Olano, J. 2010. Érase una vez en Colombia: la megafauna suramericana durante el proceso de poblamiento del cono sur. *Revista de Arqueología del área intermedia*, **1**:11–82.
- Hoffstetter, R. 1971. Los vertebrados Cenozoicos de Colombia: Yacimientos, Faunas, Problemas Planteados. *Geología Colombiana*, **8**:37–63.
- Labarca-Encina, R. & Alberdi, M.T. 2011. An updated taxonomic view on the family Gomphotheriidae (Proboscidea) in the final Pleistocene of south-central Chile. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, **262**:43–57. doi:10.1127/0077-7749/2011/0184
- Lima-Ribeiro, M.S.; Nogués-Bravo, D.; Terribile, L.C.; Batra, P. & Diniz-Filho, J.A.F. 2013. Climate and humans set the place and time of Proboscidean extinction in late Quaternary of South America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **392**:546–556. doi:10.1016/j.palaeo.2013.10.008
- López, M.C.; Audemard, F.A. & Velásquez, A. 2005. Evidencias geomorfológicas y estratigráficas de compresión Holocena en el Valle del Cauca. In: *Memorias X Congreso Colombiano de Geología*, p. 150.
- Lucas, S.G. 2009. Case 3480 *Mastodon waringi* Holland, 1920 (currently *Haplo mastodon waringi*; Mammalia, Proboscidea): proposed conservation of usage by designation of a neotype. *The Bulletin of Zoological Nomenclature*, **66**:164–167. doi:10.21805/bzn.v66i2.a6
- Lucas, S.G. & Alvarado, G.E. 2010. Fossil Proboscidea from the upper Cenozoic of Central America: taxonomy, evolutionary and paleobiogeographic significance. *Revista Geológica de América Central*, **1**:9–42.
- Lucas, S.G.; Morgan, G.S.; Love, D.W. & Connell, S.D. 2017. The first North American mammoths: taxonomy and chronology of early Irvingtonian (early Pleistocene) *Mammuthus* from New Mexico. *Quaternary International*, **443**:2–13. doi:10.1016/j.quaint.2016.12.017
- Lucas, S.G.; Yuan, W. & Min, L. 2013. The palaeobiogeography of South American gomphotheres. *Journal of Palaeogeography*, **2**:19–40. doi:10.3724/SP.J.1261.2013.00015
- Madden, C.T. 1984. The Proboscidea of South America. In: Annual Meeting of the Geological Society of America, 1984. Reno, *Abstracts with Program*, vol. 12, p. 474.
- Moreno Bofarull, A.; Arias, A.; Hernández Fernández, M.; Ortiz-Jaureguizar, E. & Morales, J. 2008. Influence of continental history on the ecological specialization and macroevolutionary processes in the mammalian assemblage of South America: differences between small and large mammals. *BMC Evolutionary Biology*, **8**:1–18. doi:10.1186/1471-2148-8-97
- Morgan, G.S.; MacFadden, B.J. & Martínez, M. 2016. Quaternary gomphotheres (Mammalia: Proboscidea: Gomphotheriidae) from the continental shelf, Pearl Islands, Panama. *Quaternary International*, **392**:335–348. doi:10.1016/j.quaint.2015.11.003
- Mothé, D. & Avilla, L.S. 2015. Mythbusting evolutionary issues on South American Gomphotheriidae (Mammalia: Proboscidea). *Quaternary Science Reviews*, **110**:23–35. doi:10.1016/j.quascirev.2014.12.013
- Mothé, D.; Avilla, L.S.; Araújo-Júnior, H.I.; Rotti, A.; Prous, A. & Azevedo, S.A.K. 2020. An artifact embedded in an extinct proboscidean sheds new light on human-megafaunal interactions in the Quaternary of South America. *Quaternary Science Reviews*, **229**:106125. doi:10.1016/j.quascirev.2019.106125
- Mothé, D.; Avilla, L.S. & Cozzuol M.A. 2012a. The South American gomphotheres (Mammalia, Proboscidea, Gomphotheriidae): taxonomy, phylogeny, and biogeography. *Journal of Mammal Evolution*, **20**:23–32. doi:10.1007/s10914-012-9192-3
- Mothé, D.; Avilla, L.S.; Cozzuol, M.A. & Winck, G.R. 2012b. Taxonomic revision of the quaternary gomphotheres (Mammalia: Proboscidea: Gomphotheriidae) from the South America lowlands. *Quaternary International*, **276**:2–7. doi:10.1016/j.quaint.2011.05.018
- Mothé, D.; Avilla, L.S. & Kellner, A. 2014. Once upon a time, the Gomphotheriidae (Proboscidea, Mammalia) ruled South America. Abstract Book of the VIth International Conference on Mammoths and their Relatives. *Scientific Annals, School of Geology*, Special Volume 102:133–134.
- Mothé, D.; Ferretti, M.P. & Avilla, L.S. 2016. The dance of tusks: rediscovery of lower incisors in the Pan-American proboscidean *Cuvieronius hyodon* revises incisor evolution in Elephantimorpha. *PLoS ONE*, **11**:e0147009. doi:10.1371/journal.pone.0147009
- Mothé, D. *et al.* 2017a. Sixty years after ‘The mastodonts of Brazil’: The state of the art of South American proboscideans (Proboscidea, Gomphotheriidae). *Quaternary international*, **443**:52–64. doi:10.1016/j.quaint.2016.08.028

- Mothé, D.; Aguanta, W.F.; Belatto, S.L. & Avilla, L. 2017b. First record of *Notiomastodon platensis* (Mammalia, Proboscidea) from Bolivia. *Revista Brasileira de Paleontologia*, **20**:149–152. doi:10.4072/rbp.2017.1.12
- Osborn, H.F. 1936. *Proboscidea*. New York, American Museum of Natural History, 802 p.
- Páramo-Fonseca, M.E. & Escobar-Quemba, I.C. 2010. Restos mandibulares de mastodonte encontrados en cercanías de Cartagena, Colombia. *Geología Colombiana*, **35**:50–57.
- Pardo-Jaramillo, M. 2012. Reporte del hallazgo de un cráneo de *Stegomastodon waringi* (Holland, 1920) juvenil (Mammalia, Proboscidea) en zona rural del municipio de Turbaná, Bolívar, Colombia. *Revista de la Academia Colombiana de Ciencias*, **36**:203–210.
- Pelegrin, J.S.; Gamboa, S.; Menéndez, I. & Hernández Fernández, M. 2018. El Gran Intercambio Biótico Americano: una revisión paleoambiental de evidencias aportadas por mamíferos y aves neotropicales. *Ecosistemas*, **27**:5–17. doi:10.7818/ECOS.1455
- Pelegrin, J.S. & Sabogal, J. 2019. Un retrato al pasado: el proceso de reconstrucción paleoartística del mastodonte del Valle del Cauca *Notiomastodon platensis* (Gomphotheriidae). *Focos*, **1**:37–46.
- Pohlig, H. 1912. Sur une vieille mandibule de *Tetracaulodon ohioiticum* Blum., avec defense in situ. *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie*, **26**:187–193.
- Prado, J.L.; Alberdi, M.T.; Azanza, B.; Sánchez, B. & Frassinetti, D. 2005. The Pleistocene Gomphotheriidae (Proboscidea) from South America. *Quaternary International*, **126**:21–30. doi:10.1016/j.quaint.2004.04.012
- Prates, L. & Perez, S.I. 2021. Late Pleistocene South American megafaunal extinctions associated with rise of Fishtail points and human population. *Nature Communications*, **12**:1–11. doi:10.1038/s41467-021-22506-4
- Recabarren, O.P.; Pino, M. & Alberdi, M.T. 2014. La Familia Gomphotheriidae en América del Sur: Evidencia de molares al norte de la Patagonia chilena. *Estudios Geológicos*, **70**:e001.
- Rodríguez, C.A. 2002. *El Valle del Cauca Prehispánico*. Santiago de Cali, Universidad del Valle, Department of History, p. 26–27.
- Rodríguez, C.A. 2007. *Alto y Medio Cauca Prehispánico*. Colección Colombia Antigua, Vol. 1, Syllaba Press Int.
- Rodríguez-Flórez, C.D.; Rodríguez-Flórez, E.L. & Rodríguez, C.A. 2009. Revisión de la fauna Pleistocénica (Gomphotheriidae) en Colombia y reporte de un caso para el Valle del Cauca. *Boletín Científico Museo de Historia Natural*, **13**:78–85.
- Shoshani, J. & Tassy, P. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behavior. *Quaternary International*, **126**:5–20. doi:10.1016/j.quaint.2004.04.011
- Smith, G.J. & De Santis, L.R. 2020. Extinction of North American *Cuvieronius* (Mammalia: Proboscidea: Gomphotheriidae) driven by dietary resource competition with sympatric mammoths and mastodons. *Paleobiology*, **46**:41–57. doi:10.1017/pab.2020.7
- Suárez-Ibarra, J.Y.; Cardoso, G.; Asevedo, L.; de Melo França, L.; Dantas, M.A.T.; Cruz-Guevara, L.E.; Rojas-Mantilla, A.F. & Ribeiro, A.M. 2021. Quaternary proboscidean (Mammalia) remains of the UIS Geological Museum, Colombia. *Revista Brasileira de Paleontologia*, **24**:70–75. doi:10.4072/rbp.2021.1.06
- Valencia-Giraldo, Y.P.; Escobar-Arenas, L.C.; Mendoza-Ramírez, J.; Delgado-Sierra, D. & Cárdenas-Rozo, A.L. 2016. Revisión de las localidades fosilíferas del departamento de Antioquia, Colombia. *Boletín de Ciencias de la Tierra*, **1**:46–54. doi:10.15446/rbct.n40.53748
- van der Hammen, T. & Correal-Urrego, G. 2001. Mastodontes en un humedal pleistocénico en el valle del Magdalena (Colombia) con evidencias de la presencia del hombre en el pleniglacial. *Boletín de Arqueología*, **16**:4–36.
- van der Valk, T. et al. 2021. Million-year-old DNA sheds light on the genomic history of mammoths. *Nature*, **591**:265–269. doi:10.1038/s41586-021-03224-9
- Villarroel, A.C.; Bieva, J. & Cadena, A. 1996. La fauna de mamíferos fósiles del Pleistoceno de Jútua, Municipio de Soatá (Boyacá, Colombia). *Geología Colombiana*, **21**:81–87. doi:10.15446/gc
- Villarroel, A.C. & Clavijo, J. 2005. Los mamíferos fósiles y las edades de las sedimentitas continentales del Neógeno de la Costa Caribe Colombiana. *Revista de la Academia Colombiana de Ciencias*, **29**:345–356.
- Vrba, E.S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy*, **73**:1–28. doi:10.2307/1381862
- Zhang, X. & Wang, S. 2020. First report of *Eozygodon* (Mammutidae, Proboscidea) in Eurasia. *Historical Biology*, **33**:1661–1670. doi:10.1080/08912963.2020.1723579

Received in 29 April, 2021; accepted in 19 January, 2022.