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Sixty years after 'The mastodonts of Brazil': The state of the art of South American proboscideans (Proboscidea, Gomphotheriidae)

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ABSTRACT

Studies on South American Gomphotheriidae started around 210 years ago and, 150 years later, the classic study "The mastodonts of Brazil" by Simpson and Paula Couto (1957) attempted to clarify the complex issues related to our understanding of these proboscideans. Here, we update state of knowledge regarding proboscideans in South America subsequent to the publication of Simpson and Paula Couto (1957). The taxonomy of South American proboscideans is now stable and two species are recognized, *Notiomastodon platensis* and *Cuvieronius hyodon*. The former had a wide distribution in South America (from lowlands to highlands and from east to west coasts), while the latter was restricted to Ecuador, Peru and Bolivia. Although records of *Notiomastodon* are abundant and occur in almost overlapping geographic distribution with *Cuvieronius*, they have never been recorded in the same locality. Here, we evaluated over 500 South American localities with proboscidean remains, although only cranial and dental specimens show recognizable diagnostic features. As both proboscideans in South America had a generalist-opportunist alimentary strategy, a competitive exclusion probably precluded their sympatry. Their origin is most probably related to independent migrations from Central America during the Great

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American Biotic Interchange. They are not sister-taxa – *Cuvieronius hyodon* is sister-taxon of *Rhynchotherium*, and this clade is closer to *Notiomastodon platensis* than to the other proboscideans, supporting the hypothesis of independent origins. *Notiomastodon platensis* has a continuous record from the Early Pleistocene to Early Holocene, when it became extinct, probably due to synergy of human impact and climatic changes during the Pleistocene/Holocene transition. In contrast, extinction of *Cuvieronius hyodon* happened much earlier, and it was not related to the terminal Pleistocene event that lead the extinction of selected megafauna in South America, including *Notiomastodon*.

1. Introduction

After the publication of the first record of a South American proboscidean 210 years ago (Cuvier, 1806), the taxonomic history of this group had several chapters, and most researchers consider the revision of Simpson and Paula Couto (1957) a watershed (Prado et al., 2005; Shoshani and Tassy, 2005; Ferretti, 2010). Why is this classic paper so important? It comprises the first effort in 150 years to review the taxonomy and to congregate information on proboscideans from many localities in South America; a contrast to previous traditional taxonomical studies that frequently proposed new names. The only exception is Cabrera (1929), a paper that was most certainly the basis of the study by Simpson and Paula Couto (1957). In the following six decades, due to more critical studies, the taxonomy of South American proboscideans further stabilized (Mothé et al., 2012; Mothé and Avilla, 2015). Inspired by Simpson and Paula Couto (1957), here we gathered a group of South American researchers to present the current state of the knowledge on taxonomy, phylogeny, geographic distribution, chronology and the feeding paleoecology of South American proboscideans.

2. Materials and methods

The information presented here includes a detailed survey of the literature of the last 210 years, since the first record of Proboscidea in South America (Cuvier, 1806). We also comment and make new inferences on taxonomy, geographic distribution, systematics and paleoecology based on more recently collected data. The specimens of proboscideans from all over South America were, for the first time, catalogued in a single database (Supplementary Materials – Table 1), reviewed and classified according to the current proposed taxonomic classification (Mothé and Avilla, 2015). Each South American locality with a record of Proboscidea was georeferenced with the help of the software Google Earth Pro™. The localities were plotted according to their geographic description in the literature or, when the coordinates were absent from the original publication, we estimated the most suitable geographic position according with Google Earth Pro™. The localities with diagnostic remains of *Cuvieronius hyodon* and *Notiomastodon platensis* were used to construct an updated distribution map of these proboscideans in South America (Supplementary Materials – Interactive Google Earth Map). Non-diagnostic specimens were also plotted in order to consolidate knowledge of geographic occurrences of South American proboscideans.

3. Results and discussion

3.1. The timeline of 210 years of taxonomic issues

The complex taxonomic history of South American proboscideans began more than two centuries ago with only two intermediate molars collected by Humboldt (Fig. 1), one found near the volcano Imbabura, Quito, Ecuador, and the other probably from Concepción, Chile (Cuvier, 1806). Both specimens were described and figured by Cuvier (1806), who failed to assign generic or specific names (binomial system of Linnaeus) in their descriptions and referred to them using the informal terms “mastodonte des cordillères” and “mastodonte humboldien”, respectively (Fig. 2).

Fischer (1814) proposed the first valid specific name, *Mastotherium hyodon*, for the specimen from Ecuador (“mastodonte des cordillères”), and Cuvier (1824) later formally named these materials as *Mastodon andium* (specimen from Ecuador) and *Mastodon humboldtii* (specimen from Chile). However, the name *Mastotherium hyodon* had priority over the name *M. andium* proposed by Cuvier (1824). Nevertheless, the isolated teeth described by *Cuvier* (1806, 1824) and Fischer (1814) are not diagnostic to any bunodont proboscidean at the specific level, based on recent diagnoses, and they could represent either of the South American taxa, including the same taxon (*Mastotherium hyodon* and/or *Mastodon humboldtii*; Ficcarelli et al., 1995; Ferretti, 2008; Lucas, 2008).

Lund (1839) mentioned some proboscidean remains from Lagoa Santa, Minas Gerais State in Brazil, but he gave no classification, description or illustration of the specimens (a *nomen nudum*), and Lesson (1842) listed only the name “*Mastodon brasiliensis* Lund”. Almost seven decades later, when describing the specimens mentioned by Lund (1839), Winge (1906) referred to them as “*Mastodon andium*”, although *Mastotherium hyodon* had priority over this name for almost a century (Fig. 2). Furthermore, Winge (1906) did not validate the name “*Mastodon brasiliensis*”. Only in Hoffstetter (1952), when he properly published a systematic description of “*Stegomastodon brasiliensis*”, was the name credited to Lund and became valid. However, it was antedated by several other names proposed before his study (see Cabrera, 1929; Simpson and Paula Couto, 1957; Ferretti, 2008; Lucas, 2008; and Fig. 2).

At the end of the 19th century and beginning of 20th century, Ameghino published several studies on South American proboscideans (1888; 1889; 1891; 1902), especially on materials from Argentina. In these studies, he named several species of the genus *Mastodon*, including *Mastodon bonaerensis*, *M. argentinus*, *M. platensis*, *M. superbus*, *M. maderianus*, *M. tarijensis* and *M. rectus*. Those species were distinguished by size, upper tusks features and complexity of molar morphology, although Ameghino mentioned the occurrence of individual variation (Cabrera, 1929). Holland (1920) described the species *Mastodon waringi* based on several specimens from Pedra Vermelha, Bahia State in Brazil, collected by Gerald Waring in 1912 (housed at the Carnegie Museum of Natural History, CM:VP:11033 series), but did not figure the specimens. Simpson and Paula Couto (1957) indicated that the specimens described by Holland (1920) as *M. waringi* did not distinguish this species clearly from others related to the genus *Mastodon* and all remains from Brazil known at that time could probably be recognized as a single species.

Two years later, Proaño (1922) published the species name *Masthodon chimborazi*, preceded by some partial publications in 1894 and 1903 (Hoffstetter, 1952; Ficcarelli et al., 1995; Ferretti, 2010). This species was based on a proboscidean skeleton from