# The Pleistocene Gomphotheres (Proboscidea) from South America: diversity, habitats and feeding ecology

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SUMMARY: Gomphotheres were recorded in South America from the early-middle Pleistocene (Ensenadan Land-mammal Age) to the late Pleistocene (Lujanian Land-mammal Age). They arrived in South America during the "Great American Biotic Interchange". Only two genera are recognised: *Cuvieronius*, which has only one species, *Cuvieronius hyodon*; and *Stegomastodon*, which has two species, *Stegomastodon waringi* and *Stegomastodon platensis*. The small *Cuvieronius* utilised the Andean corridor and it was almost exclusively mixed-feeder. The large *Stegomastodon* dispersed through the east route and the coastal area, where *Stegomastodon waringi* shows an adaptive trend from mixed-feeder to grazer, and *Stegomastodon platensis* shows a trend from mixed to browser feeding. *Cuvieronius* seems to have been adapted to a temperate-cold climate conditions, while *Stegomastodon* seems to have predominated in lower latitudes, and was better adapted to warm or temperate climatic conditions.

## 1. Introduction

The proboscidea gomphotheres (family Gomphotheriidae) are known in South America from the early Pleistocene (Ensenadan Land-mammal Age) to the late Pleistocene (Lujanian Land-mammal Age). They were descendants of the gomphothere stock that originated in North America and arrived in South America during the "Great American Biotic Interchange" (Webb 1991). Only two genera are recognized: *Cuvieronius*, which has only one species, *Cuvieronius hyodon*; and *Stegomastodon*, which has two species, *Stegomastodon waringi* and *Stegomastodon platensis* (Alberdi & Prado 1995; Alberdi *et al.* in press). Recently, Casamiquela *et al.* (1996) presented a simplified classification modified after Simpson & Paula Couto (1957), and Shoshani (1996) suggested including all South American gomphotheres into the subfamily Cuvieroniinae. In any case, the problem of nomenclature is a complex one. *Cuvieronius hyodon* is geographically restricted to the Andine Region of Ecuador, Peru, Bolivia, Chile and Northwest Argentina. *Stegomastodon waringi* has been recorded in Brazil and Ecuador (on the Santa Elena peninsula and in the Quebrada Pistud locality, near Bolivar province of Carchi). *Stegomastodon platensis* has been recorded in Argentina from the middle to the latest Pleistocene, principally in the Pampean Region, and also in Uruguay and Paraguay during the late Pleistocene.

During the Pleistocene, two corridors developed in South America. These two corridors shaped the paleobiogeographic history of most North American mammals in South America. The most viable model postulated for the gomphothere dispersal process seems to indicate

that the small *Cuvieronius* utilised the Andes corridor, whereas the large Stegomastodon dispersed through the East route and some coastal areas.

## 2. Feeding and Habitat

Generally, it is considered that the habitat of *Cuvieronius* would have been high grassland with cold to temperate climatic conditions, while *Stegomastodon* would have been adapted to more open grassland with warm to temperate climatic conditions. By means of isotopic analyses, Sánchez *et al.* (in press) have analysed the diet of different gomphothere species from Pleistocene deposits of South America, and have reconstructed the diet of *Cuvieronius hyodon, Stegomastodon waringi* and *Stegomastodon platensis.*

The carbon isotopic results for *Cuvieronius* and *Stegomastodon* from the middle Pleistocene indicate different feeding ecologies for these two genera. *Cuvieronius* from Tarija has isotopic values that are more homogeneous. These values agree with those previously described by MacFadden & Sockey (1997), and indicate that this genus was predominantly a mixed-feeder. On the other hand, *Stegomastodon platensis* from middle and late Pleistocene of Argentina exhibits more negative isotopic values, suggesting an adaptive trend from mixed-feeding to browser-feeding (Sánchez *et al.*, in press). In addition, isotopic composition in *S. waringi* from the late Pleistocene of Santa Elena Peninsula, Ecuador, suggests that this species was a mixed-feeder with grazer tendencies. This may be related to the altitudinal and latitudinal distribution of this species.

There appears to be no biological explanation why *Mammuthus* (Elephantidae) and *Mammut* (Mammutidae), recorded in Florida and Honduras during the Pleistocene, and which might have been expected to cross the Panamanian land bridge, did not reach South America (Koch *et al.* 1998). The reasons may be found in the diet and habitat preferences of these genera. Mastodons (*Mammut*) have relatively low-crowned molars with cusps arrayed in widely spaced lophs. This dental morphology led to the recognition of mastodons as browsers (Webb *et al.* 1992). Mammoths (*Mammuthus*) have high-crowned molars with closely spaced enamel lophs coated with cement, which identifies them as grazers (Davis *et al.* 1985). Isotopic analyses confirm this hypothesis (MacFadden & Cerling 1996). By contrast, the gomphotheres from West Palm Beach, Florida, USA, and from South America have a $\delta^{13}C$ values which are intermediate between browsers and grazers (Koch *et al.* 1998; Sánchez et al. in press). Both *Mammut* and *Mammuthus* were more specialised feeders than *Cuvieronius*, which was a mixed-feeder, and *Stegomastodon* which was a mixed-feeder with tendencies toward browser-feeding or grazer-feeding (see above). These observations do not match the predictions of Vrba's (1992) model, who indicated that forms that would have tended to disperse from north to south would have been more adapted to open environments, and consequently would have been predominantly grazers.

## 3. Gomphothere Extinction in South America

There are many causes for Pleistocene mammal extinction, which make it difficult to consider and evaluate all of the complex phenomena that produced the disappearance of an important part of the Pleistocene fauna. Two types of theories have been offered for this extinction: the direct impact of man through hunting activities and climate and ecological changes.

Martin (1984) proposed that the extinction of large mammals from America and Australia are related to various, sudden human impacts. The overkill hypothesis is supported by the synchrony of extinction with the arrival of large numbers of humans in these continents. It seems that human activities, such as hunting pressure or habitat disturbance, affected the Pleistocene population of gomphotheres (Politis *et al.* 1995). The archaeological record from South America shows that gomphotheres were common in Paleo-Indian sites (Montané, 1968; Bryan *et al.* 1978; Correal Urrego 1981;

Dillehay & Collins 1988). Prado *et al.* (2001) show that large mammal extinctions were correlated with climate change, a process that began prior to the arrival of humans in the Pampean Region.

Climatic and ecological changes produced rapid change in plant communities. The nutritional stress induced by these changes is identified as the main cause of extinction by Graham & Lundelius (1984) and King & Saunders (1984). This models implies that gomphotheres died off because they were specialised feeders, adapted to a kind of plant that disappeared during the Holocene times. With this in mind, Guthrie (1984) hypothesised that plant diversity was greater and the growing season was longer in the Pleistocene than in the Holocene.

## 4. Final Remarks

The South American gomphotheres must be included in only one subfamily. We recognise two genera, *Cuvieronius* and *Stegomastodon*; and three species, C*uvieronius hyodon*, *Stegomastodon waringi*, and *Stegomastodon platensis*.

*Cuvieronius* genus arrived in South America during the Great American Biotic Interchange, and was recorded from the early Pleistocene to the late Pleistocene utilising the Andes corridor for its dispersal. The genus *Stegomastodon* appeared later, during the middle Pleistocene and dispersed through the East route and some coastal areas.

*Cuvieronius* was a mixed feeder, and *Stegomastodon* was a mixed-feeder with tendencies toward browser-feeding or grazer-feeding. These differences in diet preferences could explain why only the bunodont forms reached South America when both types, lophodont and bunodont, lived together in North America prior to the emergence of the Isthmus of Panama.

*Cuvieronius* hyodon would have inhabited high grasslands with cold to temperate climatic conditions, and *Stegomastodon* would have been adapted to more open grasslands with warm to temperate conditions.

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