José Luis Prado [1], María Teresa Alberdi [2], Begoña Sánchez [2] & Beatriz Azanza [2]
[1] Universidad Nacional del Centro UNC, Olavarría
[2] Museo Nacional de Ciencias Naturales, Madrid

Diversity of the Pleistocene Gomphotheres (Gomphotheriidae, Proboscidea) from South America

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The gomphotheres were recorded in South America from the early Middle Pleistocene (Ensenadan Land-mammal Age) to the latest Pleistocene (Lujanian Land-mammal Age). They were descendants of the gomphothere stock that originated in North America and arrived to South America during the 'Great American Biotic Interchange'. Only two genera are recognised: *Cuvieronius* with only one species (*Cuvieronius hyodon*), and *Stegomastodon* with two species (S*tegomastodon waringi* and *Stegomastodon platensis*). Two corridors would have developed during the Pleistocene in South America. These two corridors have conditioned the paleobiogeographic history of most North American mammals in South America. In fact, different models can be postulated for different groups depending on their capacity to produce distinct adaptive types throughout the duration of their dispersion process. In the case of South American gomphotheres, the small *Cuvieronius* utilised the Andean corridor, whereas the larger *Stegomastodon* dispersed through the eastern route. *Cuvieronius hyodon* is geographically restricted to the Andean Region in Ecuador, Peru, Bolivia, Chile and Northwestern Argentina, it inhabited an arid landscape. *Cuvieronius* from Tarija indicated that they were almost exclusively mixed-feeders. This species seems to have been adapted to a temperate-cold climate, since in the inter-tropical zones it has been only found at the highest levels, while in Chile it expanded to the littoral zone, that surely offered similar living conditions, in terms of temperature as the Andes corridor. *Stegomastodon waringi* was recorded in the Santa Elena peninsula in Ecuador, and in Brazil. *S. waringi* from the Peninsula of Santa Elena, shows an adaptive trend of mixed-feeder to grazer. *Stegomastodon platensis* was recorded in the Middle to latest Pleistocene of Argentina, especially the Pampean Region, and also during Late Pleistocene in Uruguay and Paraguay. *S. platensis* from the Middle Pleistocene of Argentina shows mixed-feeder to browser feeder adaptations. *Stegomastodon* seems to have predominated in lower latitudes, where it would occupy savannahs or xerophytic pasture areas, and consequently it would be better adapted to warm or temperate climatic conditions. Their most austral distribution does not surpass the 37th parallel in the Buenos Aires province. The frequency of *Stegomastodon platensis* diminishes in the Pampean Region by the latest Pleistocene, when environmental conditions became colder and drier.

Correspondence: José Luis Prado, INCUAPA - Departamento de Arqueología, Universidad Nacional del Centro UNC, Del Valle 5737, 7400 Olavarría (Argentina); María Teresa Alberdi *, Begoña Sánchez and Beatriz Azanza, Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal, 2, 28006 Madrid (Spain); e-mail: malberdi@mncn.csic.es; Azanza also at Area de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, 50009 Zaragoza (Spain). [* to whom correspondence should be addressed]

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INTRODUCTION

The family Gomphotheriidae is considered a long-living ancestral stock that gave origin to a succession of other groups. Members of this group spread into Asia, Europe and North America from Late Eocene to Late Pleistocene and arrived to South America in early Middle Pleistocene times. Casamiquela *et al.* (1996) consider that gomphotheres arrived in South America during the Pliocene or Plio-Pleistocene boundary but there are no data to confirm this early arrival. The gomphotheres *sensu lato* existed in North America from the Middle Miocene to the end of the Pleistocene (Late Barstovian to the end of the Rancholabrean). Gomphothere diversity reached its peak during this span as well, with six genera known from the Late Clarendonian to the Early Hemphillian: *Gomphotherium*, *Rhynchotherium* (in Central America), *Amebelodon*, *Serbelodon*, *Platybelodon*, and *Torynobelodon*. Gomphotheres were greatly reduced in numbers during the late Hemphillian with only three genera: *Gomphotherium*, *Rhynchotherium*, and *Amebelodon*. Webb (1977, 1983) based this decline of the North American ungulate fauna during the Miocene on the continent-wide replacement of forests by more open forested savannahs that began in the Hemingfordian, and the subsequent transformation of this savannah into open grassland that began in the Late Clarendonian/Early Hemphillian. Since woodland savannahs can support a greater diversity of herbivores than either closed forest or open grassland, this situation had the effect of enlarging available herbivore niche space. During Blancan times, *Rhynchotherium* was more abundant, and *Stegomastodon* and *Cuvieronius* were recorded. *Stegomastodon* became extinct near the Middle Irvingtonian in North America and *Cuvieronius* at the end of the Rancholabrean (Kurtén & Anderson 1980).

The purpose of this paper is to present the taxonomic scenario of the Pleistocene gomphotheres from South America. Based on morphology and isotopic evidences we hypothesised about the paleoecology and niche differentiation of the three species of South American gomphotheres: *Cuvieronius hyodon*, *Stegomastodon platensis* and *Stegomastodon waringi*.

MATERIAL AND METHODS

We have studied the characteristics of the skull, jaw, and appendicular skeleton following Alberdi (1971), Mazo (1977), Tassy (1983, 1988), Boeuf (1992) and Shoshani (1996a). From them we have selected the more important characters and parameters to compare the fossil specimens from the more important localities of South America. Most of the material comes from the middle and late Pleistocene localities in Argentina, Bolivia, Ecuador and Chile. We have reviewed some remains from Museo Nacional de Historia Natural, La Paz (MNHN), Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires (MACN), Museo de la Escuela Politécnica Nacional de Quito (MEPN), Museo Nacional de Historia Natural, Santiago de Chile (MNHN), and we compared with the bibliographic data from Cabrera (1929), Hoffstetter (1952), Simpson & Paula Couto (1957), Alberdi & Prado (1995), Casamiquela (1972, 1976), and Casamiquela *et al.* (1996).

The gomphotheres of South America come from the Andean corridor (from Colombia at the North and Chile at the South), Tarija (Bolivia), and Pampean Region (Argentina), and several localities in Brazil (Fig. 1). The localities placed on the Andean corridor are characterised in many sites by rugged plateau terrain at 4000 m altitude. Most of the fossil remains were recovered from eolian deposits assigned to the Cangahua Formation in Ecuador. Sauer (1965) presented the most complete geological overview of this formation. Clapperton & Vera (1986) referred this formation to the last cold stage of the Pleistocene. The most significant fossil assemblages from the coastal area are those of La Carolina (Santa Elena Peninsula).

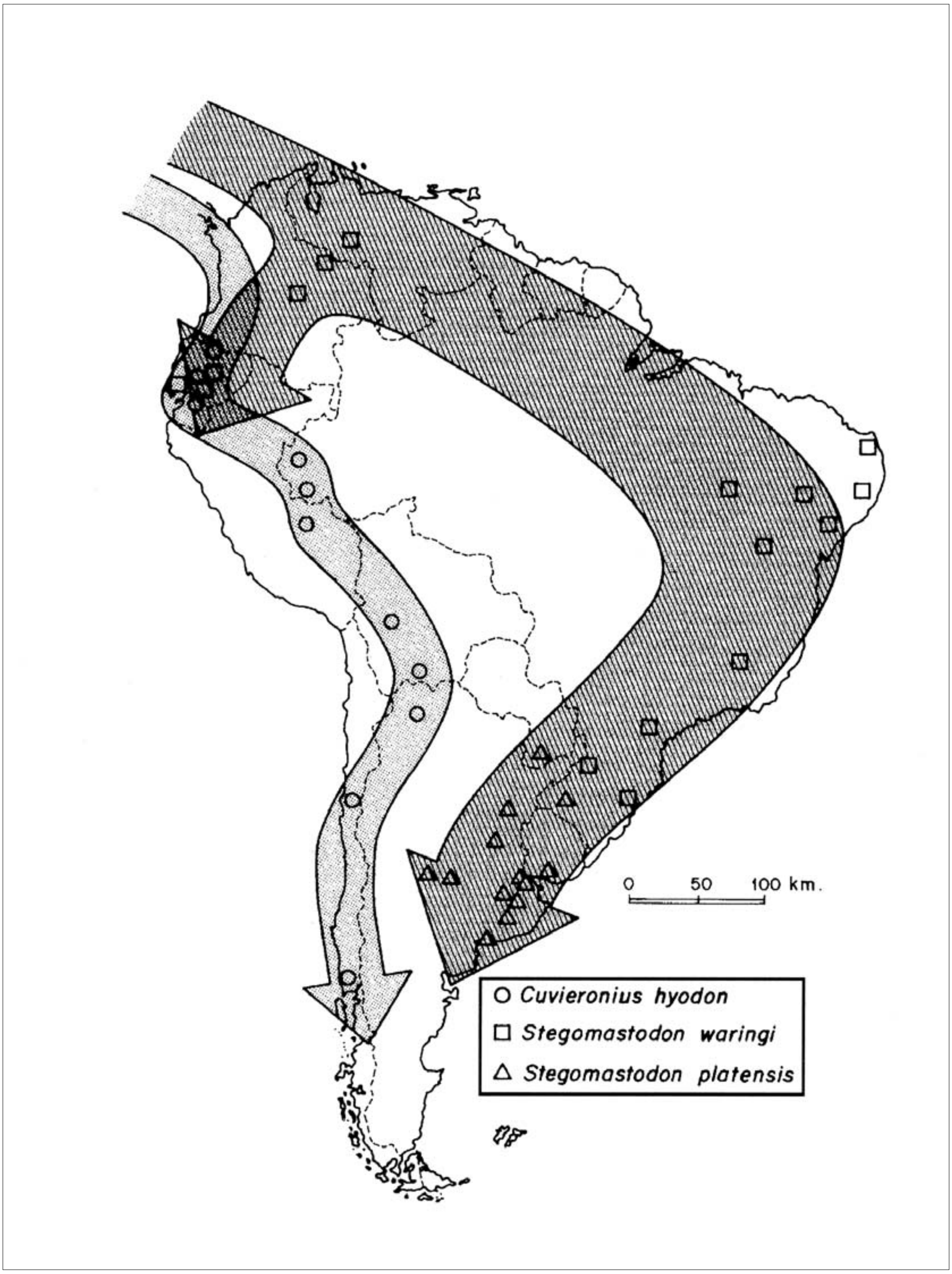


Figure 1 Possible geographic distribution routes of South American gomphotheres. The small *Cuvieronius* utilised the Andes corridor (arrow, clearer and narrower), and the large *Stegomastodon* dispersed through the Eastern route (arrow, darker and larger). Modified from Alberdi & Prado (1995).

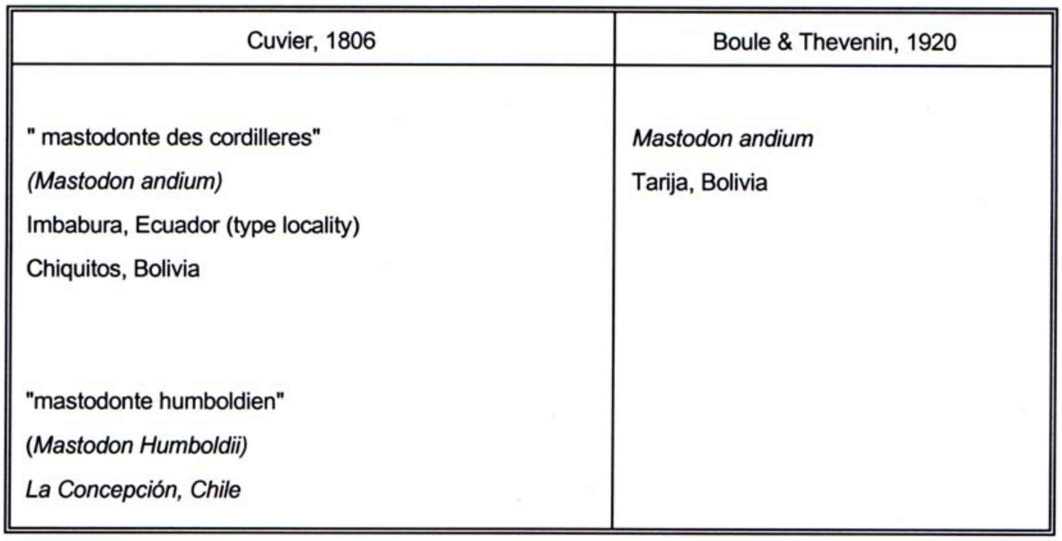
Hoffstetter (1952) suggests that all these fossils come from a single geological horizon referred to the Late Pleistocene. Most records from Bolivia are from Tarija. This site is located at an elevation of 1950 m at latitude 21°33'S and longitude 64°46'W in southern Bolivia. Oppenheim (1943) presented the most complete geological overview of the Tarija Formation, which is well known for its classic vertebrate faunas. This formation spans a time interval from about 1 to 0.7 MyBP or perhaps younger (MacFadden *et al.* 1983). Tarija fauna is classically assigned to the Ensenadan SALMA (South American Land Mammal Age). Geographically, Tarija is considered part of the sub-Andean physiographic zone. The deposits from the Pampean Region are considered by the palaeomagnetic stratigraphy and were deposited during the last 2.5 My. The stratigraphy of the Pampean loess typically consists of superposed 1-2 m thick beds separated by either erosional discontinuities or palaeosols. Most of the *Stegomastodon* remains came from the localities assigned to Ensenadan and Lujanian SALMA. The most important Chilean localities come from central-southern and central Chile. Monte Verde is located in the southern limit of continental Chile in the central Depression or Central Valley, at around 600 m altitude, between the Andean Cordillera and the Coastal Mountain Range. Monte Verde fossils are located in a depression filled by fluviatile, glacial, and moraine sediments covered by volcanic ash. The Tagua-Tagua locality is placed in the Laguna of Tagua-Tagua (latitude 34º30'S), in the Central Valley of Chile, approximately 120 km south of Santiago City. The basin lies at 200 m altitude on the eastern margin of the coastal cordillera, and it appears to have resulted from a large lahar or volcanic debris avalanche event in the late Quaternary. The majority of the Brazilian remains have no stratigraphic data, but it can be considered that many or most of the Brazilian finds are from rather late in the Pleistocene.

TAXONOMIC FRAMEWORK

Cuvier (1806) studied for the first time the remains found by Dombey in Perú and Humboldt in Colombia, Ecuador (Imbabura), Bolivia (Chiquitos) and Chile (La Concepción). Cuvier grouped these mastodons in relation to their provenance in "*mastodonte des cordillères*" and "*mastodonte humboldien*", respectively. In 1920, Boulé & Thevenin described the specimens collected in Bolivia as *Mastodon andium* (Table 1). Later, taxonomic controversy arose about in which families these gomphotheres must be placed (Table 2).

Cabrera (1929) included three families in the Elephantoidea: Gomphotheriidae, Mammutidae and Elephantidae, where bunodont, zygodont and stegodont mastodons and elephants were included respectively. All proboscideans from South America are bunodonts and brevirostrines and are placed in the Gomphotheriidae family. He created the subfamily Cuvieroniinae differentiated from the Anancinae only by the presence of an enamel band on the upper tusks. Hoffstetter (1952), as Cabrera, included all South American proboscideans in two subfamilies: the Cuvieroniinae that originated in North America and spread to South America and that included remains from Ecuador (Imbabura at N), Colombia, Bolivia and Chile; and the Anancinae that arose in Africa and spread into Europe and part of Asia, including all other genera from Ecuador, and Brazil and Argentina. Simpson & Paula Couto (1957) indicated that these subfamilies in discussion, Anancinae and Cuvieroniinae, have a pattern similar of that of modern elephants in the loss of their lower tusks, elongation of their molars, and deepening of their skulls. Consequently, they included all South American gomphotheres in one subfamily: Anancinae. This subfamily has priority following the rules of nomenclature (Simpson 1945; and ICZN 1985). Alberdi & Prado (1995) agree with Simpson & Paula Couto (1957) and included the South American gomphotheres in one subfamily: the

Table 1 Taxonomic history of the South America gomphotheres before 1920.



Cuvier, 1806	Boule & Thevenin, 1920
" mastodonte des cordilleres" *(Mastodon andium)* Imbabura, Ecuador (type locality) Chiquitos, Bolivia "mastodonte humboldien" *(Mastodon Humboldii)* *La Concepción, Chile*	*Mastodon andium* Tarija, Bolivia

Anancinae, given that the differences among them are few and slight. Recently, Shoshani & Tassy (1996: Appendix B), suggested a classification of the Proboscidea based on combined results by Tassy (in the same book) and Shoshani, where they included the South American gomphotheres in the Gomphotheriidae Hay, 1922 and the Cuvieroniinae Cabrera, 1929, and not in the Anancinae subfamily. The result is the following: Tassy (1996: Cp. 6) in his cladogram indicates two gomphothere groups: the first for the Old World trilophodont gomphotheres, and the second for the New World trilophodont gomphotheres that included all South American forms. He considers the New World gomphotheres to be more closely related to tetralophodont gomphotheres than to trilophodont gomphotheres from Eurasia due to the presence of lower tusks with a rounder cross-section. He also suggested the possible relationship between *Sinomastodon* of China and brevirostrines from South America as indicated by Tobien *et al*. (1986, 1988). In the same book, Shoshani (1996b: Cp. 16) included all South American gomphotheres in the subfamily Cuvieroniinae through the cladistic analysis without explanation about their relationship with subfamily Anancinae. The only explanation is in footnote 19, page 172, where he writes: "19. This possible 'shuffling' of genera within Cuvieroniinae was predicted by Simpson & Paula-Couto (1957)". But these authors consider that all South American gomphotheres must be included in only one subfamily and "(…) the earliest name formed according to the Rules and available for a subfamily uniting these genera is Anancinae" (Simpson & Paula-Couto 1957: 181).

We found no significant differences between Anancinae and Cuvieroniinae. The subfamily Anancinae is characterised by a brachycephalic skull with tendency to elephantoid skull, and a brevirostrine jaw with curved symphysis. The upper tusks varied from more or less elongated and straight to curved in the distal part. There is no enamel band in the adult specimens. Bunodont molars, with angular disposition of the pretrite and posttrite cusps, are brachydonts or subhypsodonts, with single or slight complicate trefoils in the occlusal surface. M2 are trilophodont with a developed talon sometimes.

Table 1 Taxonomic history of the South America gomphotheres after 1920.

Cabrera 1929	Hoffstetter, 1952	Simpson & Paula Couto, 1957	Alberdi & Prado, 1995	Casamiquela, Shoshani and Dillehay, 1996	In this Paper
Suborder Elephantoidea Family Gomphotheriidae Subfamily Cuvieroniinae *Cuvieronius hyodon* *Notiomastodon ornatus* Subfamily Anancianae *Stegomastodon platensis* *Stegomastodon superbus* Subfamily Mammutidae Subfamily Elephantidae	Family Gomphotheriidae Subfamily Cuvieroniinae Genus *Cuvieronius* Species *C. hyodon* Subfamily Anancinae Genus *Haplomastodon* Subgenus *Haplomastodon* Species *H. (H.) chimborazi* Subgenus *Aleamastodon* Species *H. (A.) guayasensis* Genus *Stegomastodon* Subgenus indet. Subgenus *Notiomastodon* Species *N. ornatus* Subgenus *Stegomastodon* Species *S.(S.) platensis* Species *S.(S.) superbus* Species A Species B Species C	Family Gomphotheriidae Subfamily Anancinae Genus *Cuvieronius* Species *C. hyodon* Genus *Haplomastodon* *(=Aleamastodon)* Species *H. waringi.* *(=H. chimborazi;* *=H. guayasensis;* *=S. brasiliensis)* Genus *Stegomastodon* Species *S. platensis* Species *S. superbus* Genus *Notiomastodon* Species *N. ornatus*	Family Gomphotheriidae Subfamily Anancinae Genus *Cuvieronius* Species *C. hyodon* Genus *Stegomastodon* Species *S. waringi* Species *S. platensis*	Family Gomphotheriidae Genus *Cuvieronius* Species *C. hyodon* Genus *Stegomastodon* Species *S. platensis* Species *S. superbus* Genus *Notiomastodon* Species *N. ornatus* Genus *Haplomastodon* Species *H. waringi*	Family Gomphotheriidae Subfamily Anancinae Genus *Cuvieronius* Species *C. hyodon* Genus *Stegomastodon* Species *S. waring* Species *S. platensis*

M3 vary from tetralophodont to heptalophodont. We observed that these features are the generalised pattern for all South American gomphotheres. The subfamily Cuvieroniinae is only differentiated by the enamel band in adult upper tusks. We will try to establish an overview where we evaluate if the differences among the forms are simply individual variations or represent some differences that can occur at genus or species level or if they reach the subfamily level.

Family Gomphotheriidae CABRERA, 1929
Genus *Cuvieronius* OSBORN, 1923

Synonymy: *Mastodon* (part) Auct., *nec* CUVIER, 1817: 233 (= *Cuvieronius* OSBORN, 1923: 1; = *Cordillerion* OSBORN, 1926: 15; = *Teleobunomastodon* REVILLIOD, 1931: 21). *Haplomastodon* (part) HOFFSTETTER, 1950; = *Haplomastodon* (*Haplomastodon*) HOFFSTETTER, 1952: 192. *Cuvieronius* from Tagua-Tagua (Casamiquela *et al*. 1967, 1996; Casamiquela 1972; Montané 1967, 1968). *Cuvieronius* from Monte Verde (Dillehay 1989, 1997; Casamiquela *et al*. 1996).

Type species: *Cuvieronius hyodon* (FISCHER, 1814: 341).

Stratigraphic distribution: The genus is known from late Pliocene-late Pleistocene localities in the United States (Tedford *et al*. 1987). The most ancient in South America corresponds to the lower-middle Pleistocene (Ensenadan SALMA) and the most recent to the late Pleistocene (Lujanian SALMA), Lujanian - Holocene boundary.

Geographic distribution: *Cuvieronius* occurs in Mexico as far north as NW Oaxaca (Ferrusquía-Villafranca 1978), and probably it is present during the Pliocene in Valsequillo (Miller & Carranza-Castañeda 1984). The genus is also known in Central America from Guatemala but with doubts (Woodburne 1969; Lucas *et al*. 1997). In Nicaragua it is cited again, with doubts by Espinoza (1976), Reshetov (1982), and Lucas *et al.* (1997). In El Salvador it is noted by Webb & Perrigo (1984) and it is very common during the Pleistocene in Costa Rica (Lucas *et al.* 1997) on the Cordilleras. In El Salvador it is observed during the Late Pleistocene, and also in Panama (Gazin 1957). The most important record for this genus in South America comes from the Andean Cordillera. In Colombia specimens are cited in Tibitó and Mosquera, close to Bogotá at 3.800m altitude (Hoffstetter 1952; Simpson & Paula-Couto 1957; Correal Urrego 1981). In Ecuador specimens are recorded at Imbabura volcano, Rio Chiche and Andean localities (Hoffstetter 1952). There are also remains in Ulloma and Tarija in Bolivia (Boule & Thevenin 1920; Hoffstetter 1952; Simpson & Paula-Couto 1957; Alberdi & Prado, 1995). In Chile remains are cited in Tagua-Tagua, La Ligua and Chillán in the Central Chile and Monte Verde, Southern Chile (Casamiquela 1972; Dillehay 1984, 1989, 1997; Alberdi & Prado 1995). See Figure 1.

Diagnosis: The skull is comparatively low and elongate. They are brevirostrine, bunolophodont, trilophodont mastodons with single trefoils or with posttrite cusps poorly developed (M2 trilophodont). Pretrite and posttrite cusps opposite of slightly alternating, on posterior lophs of M3 (with 4 1/2 to 5 lophs having a certain angular inclination). Tusks twisted in a long, cross-section sub-circular, open spiral and with a spiral band of enamel persisting in the adults, and tusks alveolus more or less divergent.

Discussion: It is important to note that all authors agree in recognise the presence of the genus *Cuvieronius* in South America with only one species: *C. hyodon.*

Cuvieronius hyodon (FISCHER, 1814)

Synonymy: *Mastotherium hyodon* FISCHER, 1814: 341. *Mastotherium Humboldtii* FISCHER, 1814: 341. *Mastodon rhomboides* RAFINESQUE, 1814: 182. *Mastodon Andium* CUVIER, 1824: 527. *Mastodon argentinus* AMEGHINO, 1888: 7. *Mastodon chilensis* PHILIPPI, 1893: 88. *Mastodon bolivianus* PHILIPPI, 1893: 89. *Mastodon tarijensis* AMEGHINO, 1902: 2. *Cuvieronius hyodon* (FISCHER, 1814), in Cabrera (1929: 82-90). *Cuvieronius hyodon* (FISCHER, 1814), in Hoffstetter, 1952: 186. Species A from Rio Chiche, in Hoffstetter, 1952: 223-224. *Cuvieronius tarijensis* FICCARELLI *et al.* 1995: 754.

Type: M^2 figured by Cuvier (1806: pl. II, fig.1), from Imbabura (Northern Ecuador).

Stratigraphic distribution: The more ancient remains known in South America come from the early Middle Pleistocene in the Andean region from Imbabura. The most recent come from the Late Pleistocene from Tibitó in Colombia, and Tagua-Tagua and Monte Verde in Chile (Fig. 1).

Geographic distribution: *Cuvieronius hyodon* entered in South America extending from Colombia in the North to Monte Verde, Chile in the South. The most important data come from Colombia (Tibitó and Mosquera localities), Ecuador (Imbabura volcano, Rio Chiche), Bolivia (Ulloma and Tarija), and Perú (Cabrera 1929, Boule & Thevenin 1920, Hoffstetter 1952, Simpson & Paula-Couto 1957, Correal Urrego 1981, Alberdi & Prado 1995, Ficcarelli *et al.* 1995). The record in Chile comes from Tagua-Tagua, La Ligua and Chillán in Central Chile and Monte Verde in Southern Chile (Casamiquela 1972, 1976; Casamiquela & Dillehay 1989; Dillehay 1989, 1997; Casamiquela *et al.* 1996). Burmeister (1867) and Siroli (1954) cited some localities in NW Argentina, but we found no reliable data about them.

Diagnosis: The same as for the genus.

Discussion: We accept the assignment to this species of material from most of the localities

cited above, as Ulloma and Tarija in Bolivia, Imbabura in the North of Ecuador and the Andean Ecuadorian localities, Tagua-Tagua and Monte Verde in Chile. Ficcarelli *et al.* (1995: 747) identified the gomphothere of Tarija as *Cuvieronius tarijensis* nov. sp. We do not understand why they revalidated this specific name created by Ameghino (1902) for the Tarija site, without any explanation about it. Hoffstetter (1952) considered it as nomem nudum which opinion met general consensus among the specialists.
The genus *Haplomastodon* has not been well described. Their separation from *Cuvieronius* and *Stegomastodon* is not clear and sometimes arduous. The only characteristic feature is the presence of a transverse foramen in the atlas (Hoffstetter 1950, 1952). Simpson & Paula Couto (1957) indicated that this character is variable. The differential characters between these genera are not very clear because of their great variability related to age or to the allometric state.

Genus *Stegomastodon* POHLIG, 1912

Synonyms: *Notiomastodon* CABRERA, 1929: 90-96, figs. 2 and 4; = *Stegomastodon* (*Haplomastodon*) HOFFSTETTER, 1950: 22, figs. 2 and 3; = *Haplomastodon* (*Aleamastodon*) HOFFSTETTER, 1952: 208). *Haplomastodon* sensu Ficcarelli *et al.* 1993: 233, 1995: 753. Species actually placed in this genus have also been referred to *Mastodon*, *Gomphotherium*, *Anancus*, *Cuvieronius* and probably to other genera (see Cabrera 1929, Osborn 1936).

Type species: *Stegomastodon mirificus* LEIDY, 1858: 10.

Stratigraphic distribution: The genus was recorded in the Late Pliocene and the Early Pleistocene in central and western regions of North America. In South America it is present in the Middle - Late Pleistocene of Brazil, Argentina, Paraguay and Uruguay, and the late Pleistocene of Ecuador, Colombia and Venezuela.

Geographic distribution: The most significant record of *Stegomastodon* in South America comes from the Taima-Taima site in Venezuela (Bryan *et al.* 1978, Bryan 1986, Casamiquela *et al.* 1996), and Santa Elena peninsula in Ecuador (Hoffstetter 1952). Also, it was widely dispersed through the Eastern route into the tropical region of South America (Proaño 1922, Hoffstetter 1952). It arrived as far as Argentina, the most austral distribution, especially the Pampean Region and in Uruguay, and possibly in Paraguay (Cabrera 1929; Simpson & Paula Couto 1957; Mones & Francis 1973). Simpson & Paula Couto (1955, 1957) indicated their presence in Brazil as well as in tropical and warm zones (Figure 1).

Diagnosis: Gomphotheres with short and high elephantoid skull, less depressed than *Cuvieronius*. Brevirostrine, jaw with bunolophodont and trilophodont teeth (M2). Less bunodont or choerodont than the most primitive Old World Anancinae but more than *Cuvieronius*. Moderate alternance of posterior lophs of M3 (have a certain angular inclination, pretrite and posttrite cusps opposite, and lophs 5 - 5 1/2 principally). With double trefoils but relatively simple pattern. Tusks simply curved to nearly straight, without enamel, only in some juvenile individuals.

Stegomastodon waringi (HOLLAND, 1920)

Synonymy: *Mastodon brasiliensis* LUND, 1842; in Lesson (1842: 157), is considered a *nomen nudum*. *Mastodon andium* WINGE, 1906: 48, *nec* CUVIER, 1806: 413. *Mastodon waringi* HOLLAND, 1920: 229. *Mastodon chimborazi* PROAÑO, 1922. *Bunolophodon Ayora* SPILLMANN, 1928: 70. *Bunolophodon postremus* SPILLMANN, 1931: 73. *Notiomastodon vidali* CASTELLANOS, 1948: 139. *Haplomastodon* (*Aleamastodon*) *guayasensis* HOFFSTETTER, 1952: 208. Species B from La Carolina, in Hoffstetter, 1952: 224.

Haplomastodon (*Haplomastodon*) *chimborazi* (Proaño, 1922), in Hoffstetter 1952: 192. *Stegomastodon brasiliensis* Hoffstetter 1952: 222. *Haplomastodon waringi* (Holland, 1920), in Simpson & Paula Couto 1957: 171. *Haplomastodon chimborazi* (Proaño, 1922), in Ficcarelli *et al.* 1995: 753. *Haplomastodon waringi* (Holland, 1920), in Casamiquela *et al.* 1996: 316.

Type: CM-11033 described by Holland (1920: 229) as a partial lower jaw and other fragments from Pedra Vermelha, Bahia, Brazil. Simpson & Paula Couto (1957:172) notified that in the Carnegie Museum collections there are only three molar fragments, the tip of a tusk, a fragment of tusk dentine, and part of the distal end of a tibia, under number CM-11033.

Stratigraphic distribution: *Stegomastodon waringi* is characteristic from the Middle to Late Pleistocene (Ensenadan and Lujanian SALMAs).

Geographic distribution: *Stegomastodon waringi* is known from Lagoa Santa (southern Brazil) and Santa Elena Peninsula in Ecuador. In Brazil they were found on the so-called 'East route' or 'plain corridor' (Webb 1978, 1985). Possibly, it also exists in the Taima-Taima locality in Venezuela (Fig. 1).

Diagnosis: The skull is somewhat less elephantoid than in the type species but somewhat less depressed than in *Cuvieronius*. The occlusal surfaces have a relatively simple trefoil pattern. The pretrite and posttrite cups with stronger mean tendency towards alternation that in *Cuvieronius*. Tusks simply curved to nearly straight or very slightly spiral, with enamel band in some juvenile individuals; and usually simply upcurved and without enamel in adults.

Discussion: We understand that the species *waringi* is closer to *Stegomastodon* than to *Haplomastodon* because, as we explained above, *Haplomastodon* is poorly defined. We consider that the skull and other remains from Barranca Pistud, near Bolivar province of Carchi, Northern Ecuador, described by Ficcarelli *et al.* (1995:753) as *Haplomastodon chimborazi*, must be included in *Stegomastodon waringi*. The differences noted by these authors (p. 754), are in our opinion not consistent with this taxonomic separation because they correspond to an allometric variability. In general we consider that there are few differences among the gomphotheres species from South America. We think that the smallest differences between *Stegomastodon* species are more related to differences in the environmental conditions than to genetic conditions.

Stegomastodon platensis (Ameghino, 1888)

Synonymy: *Elephas Humboldtii* Blainville, 1845: 249, nec Cuvier, 1824: 527. *Mastodon platensis* Ameghino, 1888: 7. *Mastodon superbus* Ameghino, 1888: 7; also in Casamiquela *et al.* 1996: 316. *Mastodon bonaerensis* Moreno, 1888: 17-18 (*nomen nudum*). *Mastodon rectu*s Ameghino, 1889: 643. *Mastodon maderianus* Ameghino, 1891: 243. *Notiomastodon ornatus* Cabrera, 1929: 91; also in Casamiquela *et al.* 1996: 316. See Cabrera (1929) and Simpson & Paula Couto (1957) to complete the synonymies.

Type: MLP-8-63, an isolated tusk, from the Pampean Region. Signalled by Ameghino (1888: 7), and figured in Ameghino (1889).

Stratigraphic distribution: *Stegomastodon platensis* is characteristically from the middle Late Pleistocene (Ensenadan and Lujanian SALMAs) from the Pampean Region.

Geographic distribution: *Stegomastodon platensis* was the more austral gomphothere, typical of the Pampean Region, specially from Buenos Aires, Córdoba, Santa Fé and Entre Ríos provinces (Argentina). It was also found in Uruguay (Mones & Francis 1973) and possibly in Paraguay (Cabrera 1929; Simpson & Paula Couto 1957). See Fig. 1.

Diagnosis: The skull is similar to the type species, short and high, elephantoid. The teeth are tetralophodont or pentalophodont upper and lower M3; and the occlusal pattern with secondary conules or conelets that give it a morphology that varies from simple to complex. The tusks are long and relatively thin, without enamel band, curved in males and straight in females.

Discussion: Ameghino (1888) created four species from the Pampean remains. Cabrera (1929) argued that three of these are synonyms and retained *Stegomastodon superbus*. However, following the International Code of Zoological Nomenclature (ICZN 1985), the priority lies with *S. platensis*. The *S. platensis* in both papers are referred firstly, and have a wide geographical and stratigraphical distribution. *Stegomastodon platensis* (AMEGHINO, 1888) show the characters of *Stegomastodon* in skull and jaw. We have observed that thickness and curvature of tusks is a very variable character and related to sexual dimorphism, not only in the South American forms but also in other parts of the world (Tobien 1973; Mazo 1977; Boeuf 1992). We also include in this genus and species the specimen from the late Pleistocene of Playa del Barco (a tusk number 5451-MACN, Montehermoso, Buenos Aires) referred by Cabrera (1929) to *Notiomastodon ornatus*. He created this genus and species based on a different stratigraphical provenance (the provenance is unclear), and the absence of an enamel band. In this sense, the discussion in Simpson & Paula Couto (1957: 177) is very interesting.

FEEDING AND HABITATS

Generally, it is considered that the *Cuvieronius* habitat could be high grassland with cold to temperate climatic conditions, and *Stegomastodon* would seem to be adapted to more open grassland with warm to temperate conditions. Sánchez *et al.* (in press) analysed the diet from different species of gomphotheres from Pleistocene deposits of South America through isotopic analysis and reconstructed the diets of *Cuvieronius hyodon*, *Stegomastodon platensis*, and *Stegomastodon waringi*. The carbon isotopic results for *Cuvieronius* and *Stegomastodon* from the Middle Pleistocene indicate significant ecological patterns. On the one hand, *Cuvieronius* from Tarija have more homogeneous values, in agreement with those previously analysed for MacFadden & Sockey (1997), and indicating that they were almost exclusively mixed-feeders. On the other hand, *Stegomastodon* from Argentina have more negative values showing a trend from mixed to browser feeders. The statistical test confirms significant differences between the two gomphothere groups from the Middle Pleistocene. *Stegomastodon waringi* from the Peninsula of Santa Elena, Ecuador shows an adaptational trend of mixed-feeder to grazer, clearly defined by the altitudinal and latitudinal distribution. *Stegomastodon platensis* from the Late Pleistocene of Argentina seem to be the contrary, indicating a trend from mixed to browser feeding (Sánchez *et al.* in press). The ecological pattern of the latter is in agreement with the results obtained from the modern elephant, *Loxodonta africana*, from Amboseli Park (Bocherens *et al.* 1996). From an ecological point of view, we can conclude that there is a feeder evolution since the Middle to the Late Pleistocene *Stegomastodon* group from Buenos Aires that implies a change of the diet from C3 to mixed plants, and from this last to exclusively mixed-feeders.

MAMMOTHS, GOMPHOTHERES AND THE GREAT AMERICAN BIOTIC INTERCHANGE (GABI)

Around 2.5 My ago, tectonic activities along the Pacific margin caused the American continents to be sutured. One habitat corridor opened, facilitating the dispersion of terrestrial plants and animals into and out of South America, triggering an event known as the GABI (Webb 1976, 1991). This land bridge functioned as an ecologically selective dispersal corridor (Webb 1978; Simpson 1980). Biogeographic data indicate an alternation among three major types of Plio-Pleistocene habitat corridors on the Panamanian land bridge: mesic tropical forest, mesic savanna, and xeric scrub savanna (Webb 1978). During the humid interglacial phase, the tropics were dominated by rain forests, and the principal biotic movement was from Amazonia to Central America and southern Mexico. During the more arid glacial phase, savannah habitats extended broadly right through tropical latitudes (Webb 1991). Simpson & Paula Couto (1957) proposed that all known gomphotheres from South America derived from an independent radiation in Central America. The early *Cuvieronius* and *Stegomastodon* apparently entered South America at the Early or Middle Pleistocene during the glacial phase.

No common biological feature appears to explain why *Mammuthus* (Elephantidae) and *Mammut* (Mammutidae), that were recorded in Florida and Honduras during the Pleistocene and which might be expected to have crossed the Panamanian land bridge, did not reach South America. The reasons for this were perhaps individualistic. As cited before, the Late Pleistocene mammoth and mastodon had distinct diets and perhaps different habitat preference. Mastodons had relatively low-crowned molars with cusps arrayed in widely spaced lophs and high relief on the occlusal surface prior to heavy wear. This dental morphology led to recognise mastodons as browsers (Webb *et al.* 1992). Mammoths had high-crowned molars with closely spaced enamel lophs coated with cement. This morphology led to the classification of mammoths as grazers (Davis *et al.* 1985). Isotopic analyses confirm this hypothesis (MacFadden & Cerling 1996). The gomphotheres from West Palm Beach, Florida and from South America had a δ^{13} C values intermediate between browsers and grazers. In sum, both extinct mammoths and mastodon species were more specialised feeders than modern elephants and extinct *Cuvieronius* that was a mixed-feeder. These different preferences among the mastodons, mammoths and gomphotheres could explain why only the bunodont forms arrived to South America when all types lived together in North America during the Pleistocene.

GOMPHOTHERE EXTINCTION IN SOUTH AMERICA

Causes for the Pleistocene extinction are many, making it difficult to consider and evaluate all of the complex phenomena that produced the disappearance of an important part of the Pleistocene fauna. Thus, to test the theories, analysis of certain factors are favoured over others. Two types of theories have been offered for this extinction. Some authors attribute the extinction to the direct impact of man through hunting activities. This hypothesis has been mainly held by Martin (1984) who proposed that the extinction of large mammals from North America, South America and Australia are related to sudden and several human impacts on these continents. It seems that human activities, through hunting pressure or disturbing the habitat, affected the Pleistocene population of gomphotheres (Politis *et al.* 1995). Human activities that would have disturbed the environment in such a way as to greatly affect gomphotheres include human-made fires on grasslands. The overkill hypothesis is supported by the synchrony of extinction with the arrival of large numbers of humans in these continents. In contrast, the data from South America do not support the overkill hypothesis because several data of coexistence with hunter-gatherer bands were recorded. The archaeological record from South America shows that gomphotheres are frequent in Paleo-Indian Sites. Evidence that gomphotheres were a human food resource come from Monte Verde in the southern Chile (Dillehay & Collins 1988), Tagua-Tagua in Central Chile (Montané 1968), Tibitó in the Bogotá Sabana of Colombia (Correal Urrego 1981), and Taima-Taima in the Coro Peninsula of

Venezuela (Bryan *et al.* 1978). These sites are dated between c. 13,000 to 11,000 yBP. Gomphotheres are also present in the Pampean Region during this time but no association with humans has been recorded yet.

On the other hand, climatic and ecological changes, particularly to nutritional stress induced by rapid change in plant communities, are identified as the main cause of extinction (Graham & Lundelius 1984; King & Saunders 1984). These models imply that gomphothere taxa were feeder specialists, adapted to a kind of plant that disappeared during the Holocene. The hypothesis proposed by Guthrie (1984) was based on the assertions that plant diversity was higher and that the growing season was longer in the Pleistocene than in the Holocene. With changes in seasons and diversity during the Holocene, these herbivores could not obtain the diverse mixture of plants needed for survival. This model implies a different type of specificity, namely that extinct megafauna were obligate mixed-feeders.

African and Asian elephants live in a diverse habitat. They are opportunists, capable of living on nearly any dietary mixture (Bocherens *et al.* 1996, Koch *et al.* 1995). If gomphotheres showed a similar level of opportunism, they seem unlikely victims of nutritional stress due to floral change. The South American gomphotheres from the Early to Middle Pleistocene exhibit similar feeding adaptation as modern elephants. Only populations from the late Pleistocene show more focused feeding, but in general all exhibit greater variability in the consumption of C_3 versus C_4 plants. These observations match the predictions of the Guthrie hypothesis and do not support the Graham & Lundelius model.

However, recent data from mastodons and mammoths from Florida (Koch *et al.* 1998) show different patterns. Data suggest that *Mammut* and *Mammuthus* partitioned resources and perhaps habitat. Mammut shows values that indicates a diet rich in C_3 plants, and Mammuthus have higher and more variable values, indicating a diet variably enriched in C_4 grass. These data seem to support the Graham & Lundelius model.

CONCLUDING REMARKS

The South American gomphotheres are included in the family Gomphotheriidae. We recognise two genera: *Cuvieronius* and *Stegomastodon*, and three species: *Cuvieronius hyodon*, *Stegomastodon waringi* and *S. platensis*. The genus *Cuvieronius* arrived to South America during the Great American Biotic Interchange, and it has been recorded from the Early Pleistocene to the Late Pleistocene. The genus *Stegomastodon* appeared later during the Middle Pleistocene.

Two corridors would have developed during the Pleistocene in South America. These two corridors have shaped the paleobiogeographic history of most North American mammals in South America. The model postulated most viable for gomphotheres dispersion process seems to indicate that the small *Cuvieronius* utilised the Andes corridor, whereas the large *Stegomastodon* dispersed through the Eastern route. *Cuvieronius* and *Stegomastodon* are bunodont mastodons. In general, the bunodont forms lived in open and drier areas, like woodland savannahs. The several preferences between the different kinds of proboscideans could explain why only the bunodont forms arrived to South America when both types, lophodont and bunodont, lived together in North America, previous to formation of the Panama isthmus connection.

Cuvieronius hyodon habitat could be high grassland with cold to temperate climatic conditions, since in the inter-tropical zones it has been only found at the highest levels, while in Chile it expanded to the littoral zone, that surely offered similar living conditions, in terms of temperature as the Andes corridor. This species would feed mainly on hard grasses, leaves, and seeds from bushy species.

Stegomastodon would seem to be adapted to more open grassland with warm to temperate conditions, because their most austral distribution does not surpass the 37th parallel in the Buenos Aires province (Tonni 1987). The frequency of *Stegomastodon platensis* diminishes in the Pampean Region by the latest Pleistocene, when environmental conditions became colder and drier. In lower latitudes, where *Stegomastodon* is more frequent, it would occupy savannahs or xerophytic pastures (Alberdi & Prado 1995).

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