

# The Pleistocene Gomphotheriidae (Proboscidea) from South America

José Luis Prado<sup>a,\*</sup>, Maria Teresa Alberdi<sup>b</sup>, Beatriz Azanza<sup>b,c</sup>, Begonia Sánchez<sup>b</sup>,  
Daniel Frassinetti<sup>d</sup>

<sup>a</sup> INCUAPA—Universidad Nacional del Centro de la provincia de Buenos Aires, Olavaria, Argentina

<sup>b</sup> Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

<sup>c</sup> Universidad de Zaragoza, Zaragoza, Spain

<sup>d</sup> Museo Nacional de Historia Natural, Santiago, Chile

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## Abstract

Gomphotheres arrived in South America during the “Great American Biotic Interchange” and occurred in South America from the early middle Pleistocene (Ensenadan Land-mammal Age) to the late Pleistocene (Lujanian Land-mammal Age). Only two genera are recognized: (1) *Cuvieronius*, which has only one species, *Cuvieronius hyodon*; and (2) *Stegomastodon*, which has two species, *Stegomastodon waringi* and *Stegomastodon platensis*. The small *Cuvieronius* utilized the Andean corridor and was almost exclusively a mixed-feeder. The large *Stegomastodon* dispersed through the East route and the coastal area. *Stegomastodon waringi* showed an adaptive trend from mixed-feeder to grazer, while *Stegomastodon platensis* showed a trend from mixed to browser feeding. *Cuvieronius* seems to have been adapted to temperate-cold climate conditions, while *Stegomastodon* appears to have predominated in lower latitudes, and was better adapted to warm or temperate climatic conditions.

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## 1. Introduction

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: (1) *Cuvieronius*, which has only one species, *Cuvieronius hyodon*; and (2) *Stegomastodon*, which has two species, *Stegomastodon waringi* and *Stegomastodon platensis* (Alberdi and Prado, 1995; Alberdi et al., 2002; Prado et al., 2002; Prado et al., 2003). Recently, Casamiquela et al. (1996) presented a simplified classification modified after Simpson and Paula Couto (1957). *Cuvieronius hyodon* is geographically restricted to the Andean Region of Ecuador, Peru, Bolivia, Chile and Northwest Argentina. *Stegomastodon waringi* has been recorded in Brazil (Alberdi et al., 2002)

and Ecuador (Santa Elena peninsula and Quebrada Pistud locality, near the Bolivian 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 (Prado et al., 2002; Fig. 1).

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 indicates that the small *Cuvieronius* utilized the Andes corridor, while the large *Stegomastodon* dispersed through an eastern route and some coastal areas (Fig. 1).

## 2. Taxonomic background

Cuvier (1806) grouped the South American mastodons into<sup>1</sup> “mastodonte des cordilleres” and “mastodonte humboldien”, according to their respective

\*Corresponding author.

E-mail addresses: [jprado@fioq.fio.unicen.edu.ar](mailto:jprado@fioq.fio.unicen.edu.ar) (J.L. Prado), [malberdi@mncn.csic.es](mailto:malberdi@mncn.csic.es) (M.T. Alberdi), [azanza@posta.unizar.es](mailto:azanza@posta.unizar.es) (B. Azanza), [bebo@mncn.csic.es](mailto:bebo@mncn.csic.es) (B. Sánchez), [frassinetti@mnhn.cl](mailto:frassinetti@mnhn.cl) (D. Frassinetti).

<sup>1</sup>The term “mastodon” had an archaic usage referring to gomphotheres, but should now be restricted as a common name for the genus *Mammot*.

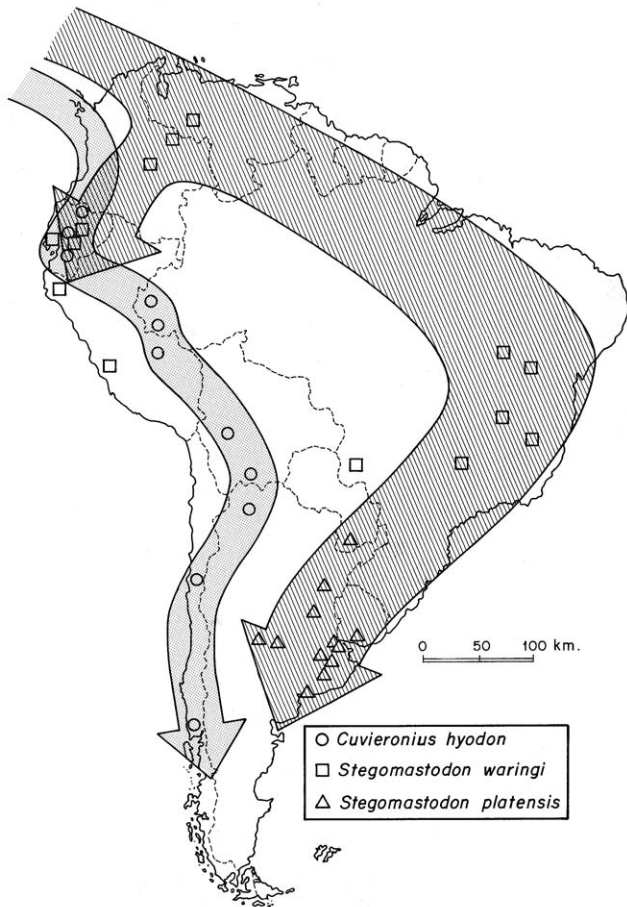


Fig. 1. Geographic distribution of Gomphotheriidae from South America and possible migratory routes. ○: *Cuvieronius hyodon*; □: *Stegomastodon waringi*; △: *Stegomastodon platensis*.

provenances. Boule and Thevenin (1920) regarded all specimens from Bolivia to be *Mastodon andium*. Cabrera (1929, p. 74) believed that “mastodons” and elephants should be grouped together and included them in the superfamily Elephantoidae: Gomphotheriidae Hay, 1922, Mammutidae Hay, 1922, and Elephantidae Gray, 1821. Cabrera placed all South American proboscideans into the family Gomphotheriidae and created the subfamily Cuvieroninae, distinguishing it from the Anancinae subfamily based on the presence of an enamel band on the upper tusks. Hoffstetter (1952), like Cabrera, assigned all South American proboscideans into two subfamilies—Cuvieroninae and Anancinae. The Cuvieroninae originated in North America, and spread to South America. In South America, its remains can be found in Colombia, Bolivia, Chile, and in Imbaburra, northern Ecuador. The Anancinae emerged in Africa and spread into Europe and parts of Asia. This subfamily includes all other South American genera from Ecuador, and all genera from Brazil and Argentina. Simpson and Paula Couto (1957) pointed out that both Anancinae and Cuvieroninae share similar features with the modern elephant. These

features include comparable skull shape, loss of the lower tusks, and similar molar elongation patterns. Consequently, they assigned all South American gomphotheres into one subfamily, Anancinae, which has priority following the rules of zoological nomenclature (Simpson, 1945; ICZN, 2000), and Cuvieroninae became a junior synonym (Simpson and Paula Couto, 1957, p. 133). Following those authors and based on the homogeneous morphology of South American gomphotheres, Alberdi and Prado (1995) and Prado et al. (1999) assigned them to the subfamily Anancinae. In contrast, Tassy and Shoshani (1996, Appendix B) proposed a new proboscidean classification and placed the South American gomphotheres in the subfamily Cuvieroninae (Cabrera (1929) (family Gomphotheriidae Hay, 1922). Tassy (1996) proposed a phylogeny of the Proboscidea order that includes two gomphotheres groups (both paraphyletic): one for Old World gomphotheres, and another for New World gomphotheres. He included all South American forms in the New World gomphotheres, without assigning them to a specific family or subfamily. On the other hand, Shoshani (1996) included these groups into the subfamily Cuvieroninae without justification. In the same book, Tassy (1996) further suggested a possible relationship between *Sinomastodon* of China and the brevirostrines from South America—a relationship that had already been proposed by Tobien et al. (1986, 1988). But Chen (1999) questioned the relationship between *Sinomastodon* and the buno-brevirostrine-trilophodont gomphotheres from the upper Cenozoic of North America, basing his doubts on discrepancies in dental morphology. Lambert (1996) and Dudley (1996) maintained that the genus *Anancus* never arrived to North America.

Like Simpson and Paula Couto (1957), we believe there is not sufficient supporting evidence to place South American gomphotheres into two distinct subfamilies. Also, we do not consider it accurate to include all South American species in the subfamily Cuvieroninae, because Cabrera (1929) defined this subfamily based only on *Cuvieronius* tusks. In any case, the nomenclature is unclear. Therefore, until we finish a new cladistic study, we tentatively include both genera (*Stegomastodon* and *Cuvieronius*) in the family Gomphotheriidae (Prado et al., 2001) and refrain from placing them in subfamilies.

We observed that all South American gomphotheres present a generalised pattern. The characteristic features are a brachycephalic skull with a tendency towards an elephantoid skull, and a brevirostrine jaw with a slightly curved symphysis. The upper tusks are elongate, and vary from straight or slightly curved to very twisted. An enamel band on the upper tusks may or may not be present. In South American gomphotheres, only *Cuvieronius hyodon* adults conserve a true enamel band. The pretrite and posttrite cusps, at times, are not transversely linear on the loph(id)s and angle slightly forward

angle as they approach the mid-line on the bunodont molars. These molars are brachyodont or subhypo-dont, with single or slightly complex trefoils on the occlusal surface. M2 is trilophodont and occasionally has a developed talon. M3 varies from tetralophodont to heptalophodont.

In this work, we give an overview in order to evaluate the gomphothere forms present in South America and the possible differences among them at the genus or species level, and if possible, at the subfamily level.

### 3. Systematic paleontology

#### 3.1. Family Gomphotheriidae Cabrera, 1929

##### 3.1.1. Genus *Cuvieronius* (Osborn, 1923)

*Synonyms:*

*Mastodon* (part) Auct., nec (Cuvier, 1817, p. 233).

*Cuvieronius* (Osborn, 1923, p. 1).

*Cordillerion* (Osborn, 1926, p. 15).

*Teleobunomastodon* (Revilliod, 1931, p. 21).

*Haplomastodon* (part) (Hoffstetter, 1950).

*Cuvieronius* from Taguatagua: Casamiquela (1972), Casamiquela et al. (1996), Montané (1968).

*Cuvieronius* from Monte Verde: Dillehay (1989, 1997), Casamiquela et al. (1996).

Type species: *Mastotherium hyodon* (Fischer, 1814, p. 341).

*Stratigraphic distribution:* The genus is known from late Pliocene to late Pleistocene localities in North America (Tedford et al., 1987). In El Salvador it is known during the late Pleistocene, and also in Panama (Gazin, 1957). The most ancient record in South America corresponds to the lower Pleistocene (Ensenadan Land Mammal Age) and the most recent to the late Pleistocene (Lujanian Land Mammal Age).

*Geographic distribution:* *Cuvieronius* occurs in Mexico as far north as northwestern Oaxaca (Ferrusquía-Villafranca, 1978), and is probably present during the Pliocene in Valsequillo (Miller and Carranza-Castañeda, 1984). The genus is also claimed, although not without some doubt, from Guatemala (Woodburne, 1969; Lucas et al., 1997). Espinoza (1976), Reshetov (1982), and Lucas et al. (1997) cite its possible presence in Nicaragua. In El Salvador it is noted by Webb and Perrigo (1984) and is very common in the Pleistocene of Costa Rica (Lucas et al., 1997) on the Cordilleras, and in the Pleistocene of South America.

*Diagnosis:* The same as the type species, the only species of the genus.

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

*Cuvieronius hyodon* (Fischer, 1814):

*Synonyms:*

*Mastotherium hyodon* (Fischer, 1814, p. 341).

*Mastotherium Humboldtii* (Fischer, 1814, p. 341).

*Mastodon rhomboides* (Rafinesque, 1814, p. 182).

*Mastodon Andium* (Cuvier, 1824, p. 527).

*Mastodon argentinus* (Ameghino, 1888, p. 7).

*Mastodon chilensis* (Phillipi, 1893, p. 88).

*Mastodon bolivianus* (Phillipi, 1893, p. 89).

*Mastodon tarijensis* (Ameghino, 1902, p. 2).

*Cuvieronius hyodon* (Fischer, 1814), in Cabrera (1929, pp. 82–90).

*Cuvieronius hyodon* (Fischer, 1814), in Hoffstetter (1952, p. 186).

Species A from Rio Chiche, in Hoffstetter (1952, pp. 223–224).

*Cuvieronius tarijensis* (Ficcarelli et al., 1995, p. 754) for the material from Tarija. They determine this to be a “new species”, without giving further explanation. Ameghino (1902) had already assigned the material from Tarija to *M. tarijensis*. Hoffstetter (1952) considered it as nomen nudum.

*Type:* M<sup>2</sup> figured by Cuvier (1806, pl. II, Fig. 1) comes from Imbabura (Northern Ecuador).

*Stratigraphic distribution:* The most ancient record known in South America comes from the early–middle Pleistocene in the Andean region and the most recent from the late Pleistocene.

*Geographic distribution:* The most important record for this genus in South America is geographically restricted to the Andean Region, from Colombia to the north to Monte Verde in southern Chile. In Colombia it is cited in Tibitó and Mosquera, close to Bogotá at 3800 m altitude (Hoffstetter, 1952; Simpson and Paula-Couto, 1957; Correal Urrego, 1981). It is recorded in Ecuador in the Imbabura volcano and Rio Chiche (Hoffstetter, 1952). Remains have also been found in Ulloma and Tarija, Bolivia (Boule and Thevenin, 1920; Hoffstetter, 1952; Simpson and Paula-Couto, 1957; Alberdi and Prado, 1995). In Chile it appears in Tagua-Tagua, La Ligua and Chillán in Central Chile, and Monte Verde in Southern Chile (Casamiquela, 1972, 1976; Casamiquela and Dillehay, 1989; Dillehay, 1984, 1989, 1997; Alberdi and Prado, 1995; Casamiquela et al., 1996; Frassinetti and Alberdi, 2000). Burmeister (1867) and Siroli (1954) cited some localities in northwestern Argentina, but data regarding these localities is unreliable (Fig. 1).

*Diagnosis:* The skull is low and elongate. Brevirostrine mandible with divergent tusk alveoli (Fig. 2). The intermediate teeth (D3, D4, M1 and M2) are bunolophodont and trilophodont, and M3 has four to four and half or five angular lophes. Single trefoils on the wear surface with poorly developed posttrite cusps. Opposing pretrite and posttrite cusps that alternate slightly on posterior lophes of M3 (Fig. 2). Tusks twist along their entire length and a spiraled band of enamel is present in adults. Tusk cross-section is sub-circular.



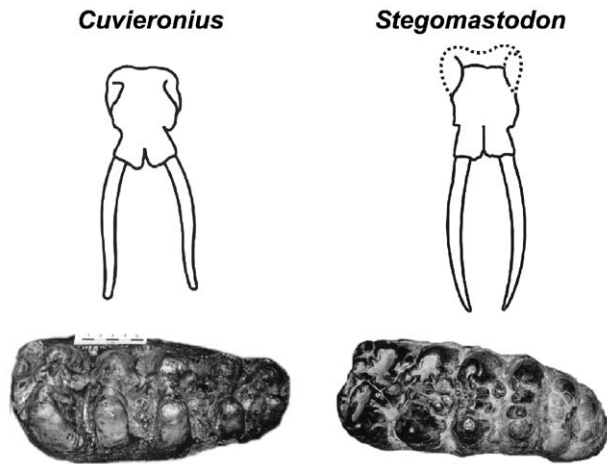


Fig. 2. Important cranial features distinguishing *Cuvieronius* from *Stegomastodon*. Above the skull profile. Below occlusal surface of the M3 tooth.

**Discussion:** It is widely accepted that the material cited above from Ulloma and Tarija in Bolivia, and Taguatagua and Monte Verde in Chile should be assigned to the species *C. hyodon*. The name “*tarijensis*”, which Ameghino (1902) used to describe a group of South American fauna, and which both Cabrera (1929) as well as Hoffstetter (1952) later considered to be *nomen nudum*, was revalidated by Ficarelli et al. (1995). These latter authors changed the classification of the Tarija remains from *C. hyodon* to *Cuvieronius tarijensis*, without explaining the nomenclatorial criteria on which they based this assignment. Initially most authors identified the Imbabura remain in northern Ecuador as the type *C. hydon*. Recently, however, some authors have begun to question the validity of this type assignment, as the M2 in *Cuvieronius* and *Stegomastodon* are very similar.

### 3.1.2. Genus *Stegomastodon* (Pohlig, 1912)

#### Synonyms:

*Mastodon* (Lesson, 1842, p. 157).

*Mastodon* (Winge, 1906, p. 48).

*Bunolophodon* (Spillmann, 1928, p. 67).

*Notiomastodon* (Cabrera, 1929, p. 90–96, Fig. 2 y 4).

*Stegomastodon* (*Haplomastodon*) (Hoffstetter, 1950, p. 22, Fig. 2 y 3).

*Haplomastodon* (*Aleamastodon*) (Hoffstetter, 1952, (en parte), p. 208).

*Haplomastodon* (Hoffstetter, 1952; Simpson and Paula Couto 1957, p. 166).

*Haplomastodon* (Ficarelli et al., 1993, p. 233).

For more details see Cabrera (1929), Osborn (1936), among others.

**Type species:** *Stegomastodon mirificus* (Leidy, 1858, p. 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 was present in Brazil, Argentina, Paraguay, and Uruguay during the middle and late Pleistocene; and in Ecuador, Colombia, and Venezuela during the late Pleistocene.

**Geographic distribution:** The first records of *Stegomastodon* in South America come from the Taima-Taima site in Venezuela (Bryan et al., 1978; Bryan, 1986; Casamiquela et al., 1996). It was also found in Ecuador on the Santa Elena Peninsula and in Quebrada Pistud in Ecuador (Hoffstetter, 1952; Ficarelli et al., 1993, 1995). Furthermore, records demonstrate that it was widely dispersed along the East Route in the tropical region of South America, mainly in Brazil (Pains, Minas Gerais; Toca dos Ossos, Bahia; and Bonito, Mato Grosso) (Alberdi et al., 2002). *Stegomastodon* extended as far south as Argentina, and was particularly abundant in the Pampean region, as well as in Uruguay and possibly Paraguay (Cabrera, 1929; Simpson and Paula Couto, 1957; Mones and Francis, 1973; Prado et al., 2002). Simpson and Paula Couto (1955, 1957) indicated the presence of *Stegomastodon* in temperate southwestern Brazil, and suggested that it may have existed throughout most of South America except in the Andean region south of Ecuador (Fig. 1).

**Diagnosis:** Skulls short and high; less depressed than those of *Cuvieronius*. Brevirostrine jaw with bunolophodont and trilophodont intermediate teeth (D3, D4, M1, M2). Tusk alveoli are straight (Fig. 2). Teeth are more bunodont and choerodont than in *Cuvieronius* but less so than in most primitive Old World Anancinae. Moderate alternation on posterior lophs of M3; transversely slightly angled pretrite and posttrite cusps, and five to five and half lophs. Double trefoils vary in form and pattern from complicated to relatively simple (Fig. 2). Tusks are simply curved to nearly straight, without enamel. Enamel is present only in some juvenile individuals.

*Stegomastodon waringi* (Holland, 1920)

#### Synonyms:

*Mastodon brasiliensis* Luna (Lesson, 1842, p. 157) *nomen nudum*.

*Mastodon andium* Cuvier (Winge, 1906, p. 48, nec Cuvier, 1806, p. 413).

*Mastodon humboldti* (Cuvier, 1806; Boule and Thevenin, 1920, p. 68).

*Mastodon waringi* (Holland, 1920, p. 229).

*Mastodon chimborazi* (Proaño, 1922, p. 13).

*Bunolophodon ayora* (Spillmann, 1928, p. 67).

*Bunolophodon postremus* (Spillmann, 1931, p. 73).

*Notiomastodon vidali* (Castellanos, 1948, p. 139).

*Haplomastodon* (*Aleamastodon*) *guayasensis* (Hoffstetter, 1952, p. 208).

Especies B de La Carolina (Hoffstetter, 1952, p. 224).

*Stegomastodon brasiliensis* (Hoffstetter, 1952, p. 222).

*Haplomastodon waringi* (Holland, 1920; Simpson and Paula Couto, 1957, p. 171).

*Haplomastodon chimborazi* (Proaño, 1922; Ficarelli et al., 1995, pp. 753–754).

*Haplomastodon waringi* (Holland, 1920; Casamiquela et al., 1996, p. 316).

**Holotype:** Corresponds to an incomplete mandible and bone fragment (CM-11033) from Pedra Vermelha, Bahía, Brasil described by Holland (1920, p. 229). Simpson and Paula Couto (1957:172) further comment that there were three broken molars, two tusk fragments, and the distal part of a tibia—all with the number CM-11033.

**Stratigraphic distribution:** Middle to Upper Pleistocene.

**Geographic distribution:** It is recorded in Ecuador (Santa Elena peninsula and Quebrada Pistud), possibly in Taima–Taima (Venezuela), and in Brazil (Pains, Lagoa Santa area in Minas Gerais, Toca dos Ossos in Bahia, Bonito in Mato Grosso do Sul, and possibly in Rio Grande do Sul (Alberdi et al., 2002) Fig. 1.

**Diagnosis:** Skulls are short and high, elephantoid type; less elephantoid than the type species and less depressed than *Cuvieronius*. Double trefoils (on both pretrite and posttrite sides) pattern varies from simple to relatively complex due to the presence of secondary conules or conelets. Double trefoils pattern are less complicated in *S. platensis*. Tusks are relatively straight, without enamel band.

**Discussion:** In agreement with Simpson and Paula Couto (1957), we feel that the genus *Haplomastodon* cannot be clearly differentiated from *Stegomastodon*. The presence of transverse foramina in the atlas is variable (Simpson and Paula Couto, 1957). The distinguishing characters between these genera vary greatly with respect to the animal's age and are therefore not very clear. Consequently, we synonymize the species *H. waringi* in the genus *Stegomastodon*.

*Stegomastodon platensis* (Ameghino, 1888)

**Synonyms:**

*Elephas Humboldtii* (Blainville, 1845, p. 249, nec Cuvier, 1824, p. 527).

*Mastodon platensis* (Ameghino, 1888, p. 7).

*Mastodon superbus* (Ameghino, 1888, p. 7; also in Casamiquela et al., 1996, p. 316).

*Mastodon bonaerensis* (Moreno, 1888, pp. 17,18) nomen nudum.

*Mastodon rectus* (Ameghino, 1889, p. 643).

*Mastodon maderianus* (Ameghino, 1891, p. 243).

*Notiomastodon ornatus* (Cabrera, 1929, p. 91; also in Casamiquela et al., 1996, p. 316).

See Cabrera (1929), and Simpson and Paula Couto (1957) to complete the synonymies.

**Type:** MLP-8-63, an isolated adult tusk from San Nicolás de los Arroyos, (Buenos Aires province). Indicated by Ameghino (1888, p. 7) and illustrated in Ameghino (1889).

**Stratigraphic distribution:** *Stegomastodon platensis* is characteristic of the middle–late Pleistocene.

**Geographic distribution:** *S. platensis* is the southernmost gomphothere, typical of the Pampean region of Argentina, and especially prevalent in the Buenos Aires, Córdoba, Santa Fe, and Entre Ríos provinces. It has also been found in Uruguay (Mones and Francis, 1973) and possibly in Paraguay (Cabrera, 1929; Simpson and Paula Couto, 1957) (Fig. 1).

**Diagnosis:** Skull is short and high, similar to that of the type species. Upper and lower M3 are tetralophodont or pentalophodont; occlusal morphology varies from simple to complex due to the presence of secondary conules or conelets. Tusks are long and relatively thin, without an enamel band, and are curved in males and straight in females.

**Discussion:** Ameghino (1888, 1889, 1891) created four species out of the Pampean gomphothere remains. Cabrera (1929) argued that three of these were synonymous and that priority corresponded to *S. platensis* (following the ICZN rules). He retained *S. superbus* as a separate species, based on his observations that it did not come from the same geological time period. Simpson and Paula Couto (1957) expressed doubts concerning the correctness of Cabrera's determination. The skull and jaw of both species show the generic characters of *Stegomastodon*. We observed that in the South American forms, as well as in other species, thickness and curvature of the tusks are extremely variable characters that can be related to sexual dimorphism (Tobien, 1973; Mazo, 1977; Boeuf, 1992).

#### 4. Dispersal and extinction of gomphotheres in South America

There is general agreement that the habitat of *Cuvieronius* in South America was high grassland with cold to temperate climatic conditions, while *Stegomastodon* was adapted to more open grassland with warm to temperate climatic conditions. 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 and Shockey (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., 2003, 2004). 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 (Sánchez et al., 2003, 2004). This may be

Table 1  
Descriptive statistics of oxygen and carbon isotopes from South America gomphotheres

Groups	<i>n</i>	Mean $\delta^{13}\text{C}$ (‰)PDB	SD (‰)	Range (‰)	Mean $\delta^{18}\text{O}$ (‰)V-SMOW	SD (‰)	Range (‰)
<i>Cuvieronius</i>	30	−9.08	2.64	−13.9 to −4	24.45	2.19	21.21–28.02
<i>Stegomastodon</i>	38	−7.98	2.28	−12.11 to −0.78	30.26	1.49	28.25–36.61
<i>S. platensis</i>	32	−8.63	1.47	−12.11 to −5.9	30.00	1.07	28.25–33.19
<i>S. waringi</i>	6	−4.53	2.84	−8.2 to −0.78	31.61	2.61	28.95–36.61

N: number of samples; SD: standard deviation.

related to the altitudinal and latitudinal distribution of this species.

The different feeding preferences among the gomphotheres in South America shed considerable light on the dispersion and extinction of these groups in America. About 2.5 Ma ago, tectonic activities along the Pacific margin caused the connection of the American continent. As a result, a habitat corridor opened that facilitated the dispersal of terrestrial plants and animals into and out of South America, precipitating an event known as the “Great American Biotic Interchange” (GABI; Webb, 1976, 1991). This land bridge functioned as an ecologically selective dispersal corridor (Webb, 1978; Simpson, 1980). Biogeographic data indicate three major types of Plio-Pleistocene habitat corridors existed on the Panamanian land bridge: mesic tropical forest, mesic savanna, and xeric scrub savanna (Webb, 1978). During the humid interglacial phase, rain forests dominated the tropics, and the principal biotic movement was from Amazonia to Central America (south to north). During the more arid glacial phase, when savanna habitats predominated and extended well into tropical latitudes, the directional pattern reversed, and biotic forms moved from north to south (Webb, 1991). We do not believe that gomphotheres were present in South America in the late Miocene (c.f. Campbell et al., 2000).<sup>2</sup>

Before the interchange, *Cuvieronius* and *Stegomastodon* (Gomphotheriidae) *Mammuthus* (Elephantidae) and

*Mammut* (Mammutidae) were recorded in Florida and Honduras. There appears to be no biological explanation why *Mammuthus* and *Mammut*, which might have been expected to cross the Panamanian land bridge, did not reach South America. The reason may be found in the diet and habitat preferences of these genera. Mastodont (*Mammut*) have relatively low-crowned molars with cusps arrayed in widely spaced lophs. This dental morphology led to the recognition of mastodons as browsers (King and Saunders, 1984; Webb et al., 1992). Mammoths (*Mammuthus*) have high-crowned molars with closely spaced enamel lophs coated with cementum, which identifies them as grazers (Davis et al., 1985). Isotopic analyses confirm this hypothesis (MacFadden and Cerling, 1996). The gomphotheres from West Palm Beach, Florida, and from middle Pleistocene of South America have  $\delta^{13}\text{C}$  values (Table 1) that are intermediate isotopic values between browsers and grazers (Koch et al., 1998; Connin et al., 1998). Mammoth and mastodon species were more specialized feeders than *Cuvieronius*, which was a mixed-feeder. These observations do not match the predictions of Vrba's (1992) model, which specifies 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. We propose that the different feeding preferences among mastodons, mammoths, and gomphotheres could explain why only the bunodont forms reached 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. Currently, 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 North America, South America and Australia are related to various, sudden human impacts. This “overkill” hypothesis is supported by the synchronism of extinction with the arrival of large numbers of humans to these continents. The archaeological record from South America shows that gomphotheres were common in Paleo-Indian sites.

<sup>2</sup> Alberdi et al. (2004) discuss the Late Miocene data from Peru (Romero-Pittman, 1996; Campbell et al., 2000) and present serious doubts about this age. They consider that the forms described as *Amahuacatherium peruvium* (Romero-Pittman, 1996) from Madre de Dios Formation are very difficult to identify at the species level, because the available remains are not sufficient to make an identification of this type nor do they reveal significant morphological differences. They assign these remains to *Stegomastodon* sp. because: (1) they are unable to determine the exact provenance of these remains, (2) the remains are practically identical to those of *Stegomastodon*, and (3) the only real difference is that “lower tusks are present, rooted under and immediately medial posterior portion of M2, with roots with relatively large dorsal groove above longitudinal axes” (Campbell et al., 2000, p. 10). None of the material in these remains corresponds to the tusks, nor are there any signs that would indicate the presence of tusks. On the mandibular remains, a “large dorsal groove” can be observed, but this groove corresponds to the area where blood vessels, nerves and lymphatic tissues pass.



Gomphotheres appear to have been a human food resource in central and southern Chile (Dillehay and Collins, 1988; Montané, 1968), Colombia (Correal Urrego, 1981), and Venezuela (Bryan et al., 1978) between ca. 13,000 and 11,000 yrs BP. Gomphotheres are also present in the Pampean Region during this time but no association with human remains has yet been recorded. Therefore, it is possible that human activities, such as hunting pressure or habitat disturbance, affected the Pleistocene population of gomphotheres (Politis et al., 1995). Other authors suggest that climatic and ecological changes, particularly nutritional stress induced by rapid change in plant communities, may have been the principal cause of gomphothere extinction (Janzen and Martin, 1982; Graham and Lundelius, 1984; King and Saunders, 1984). With this in mind, Guthrie (1984) hypothesized that plant diversity was greater and the growing season was longer in the Pleistocene than in the Holocene. Specimens from middle Pleistocene in South America exhibit feeding strategies similar to those of modern elephants. They live in diverse habitats, are opportunists, and therefore are capable of living on nearly any dietary mixture (Bocherens et al., 1996). In contrast, populations from late Pleistocene show more selective dietary adaptations, which suggest that gomphotheres were driven to extinction because they were specialized feeders, adapted to a kind of plant that disappeared during the Holocene. The record from the Pampean Region shows that large mammal extinctions were correlated with climate change, a process that began prior to the arrival of humans (Prado et al., 2001).

## 5. Final remarks

The South American gomphotheres must be included in only one family: Gomphotheriidae. However, this assignment is only tentative until we can perform a cladistic analysis to further clarify its position. We recognize two genera, *Cuvieronius* and *Stegomastodon*; and three species, *C. hyodon*, *S. waringi*, and *Stegomastodon platensis*.

*Cuvieronius* genus arrived in South America first, during the early Pleistocene, and lived to the late Pleistocene, utilizing the Andes corridor for its dispersal. The genus *Stegomastodon* appeared later, during the middle Pleistocene, and dispersed through the eastern route and some coastal areas.

*Cuvieronius* was a mixed feeder, and *Stegomastodon* was a mixed-feeder with tendencies toward both browsing and grazing. *C. hyodon* inhabited high grasslands with cold to temperate climatic conditions, and *Stegomastodon* would have been adapted to more open grasslands with warm to temperate conditions.

Early *Cuvieronius* and *Stegomastodon* apparently entered South America during the more arid glacial phase, when savanna habitats extended broadly through tropical latitudes. The most likely explanation for the absence of *Mammuthus* and *Mammuthus* in South America was that they were highly specialized feeders with habitat preferences not represented in the Panamanian land bridge.

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