Late Pleistocene Stegomastodon (Mammalia, Proboscidea) from Uruguay

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Maria Teresa Alberdi
Spanish National Research Council
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Jose Luis Prado
National University of the Center of the Buenos Aires Province
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Late Pleistocene *Stegomastodon* (Mammalia, Proboscidea) from Uruguay

Mercedes Gutiérrez, St. Louis, Maria Teresa Alberdi, Madrid, José Luis Prado, Olavarría and Daniel Perea, Montevideo With 6 figures and 2 tables

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Abstract: Fossil Proboscidea remains from the Dolores Formation, Montevideo, Uruguay, are described and taxonomically identified. We compared these remains with those of *Stegomastodon waringi* and *Stegomastodon platensis* from several localities in Brazil and Argentina using multivariate analysis. The results indicate that *Stegomastodon waringi* (HOLLAND, 1920) is represented in the quarry. Enamel tooth sample of gomphothere was dated to 17,620 :!: 100 BP by AMS 14C so we confirm the late Pleistocene age for this fauna. To reconstruct the paleodiet and habitat preference we measured the carbon and oxygen isotope composition of the teeth dentine. Of the two different adaptations attributed to *Stegomastodon waringi,* we found that at this latitude they were mixed-C3 feeders, closely related with the Brazil population.

Zusammenfassung: Fossile Proboscidier-Reste aus der Dolores-Formation von Montevideo, Uruguay, werden beschrieben und bestimmt. Wir haben sie unter Zuhilfenahme von multivariaten statistischen Analysen mit *Stegomastodon waringi* und *Stegomastodon platensis* verschiedener Lokalitiiten in Brasilien und Argentinien verglichen. Dadurch konnte die Art *Stegomastodon waringi* (HOLLAND, 1920) identifiziert werden. Zahnschmelz wurde mit 14C auf 17,620:!: 100 Jahre datiert und so ein spatpleistozanes Alter der Fauna bestiitigt. Zur Rekonstruktion der einstigen Emahrung und der Habitatansprüche maBen wir die Kohlenstoff- und SauerstoffIsotopie des Dentins. Von den beiden der Art *Stegomastodon waringi* zugeordneten Anpassungsformen stellten wir fest, dass sie in diesen Breiten gemischte C3-Fresser waren und enge Bezüge zur brasilianischen Population aufweisen.

Key words: *Stegomastodon waringi*, Mammalia, Proboscidea, Upper Pleistocene, Uruguay, South America.

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1. Introduction

Numerous remains of gomphotheres have been cited from Uruguay, since W ALTHER (1914) to the present. But most of these records were assigned to several species that do not reflect the homogeneity of this group in South America.

Gomphotheres (family Gomphotheriidae) are known in South America from the early-middle Pleistocene (Ensenadan South American Land Mammal Age, hereafter SALMA) to the late Pleistocene (Lujanian SALMA). 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* and *Stegomastodon* (ALBERDI & PRADO 1995).

Recently, PRADO et al. (2002, 2003, 2005) presented a simplified classification modified after SIMPSON & PAULA COUTO (1957) and recognized one species of *Cuvieronius:* C. *hyodon* (FISCHER, 1814), and two species of *Stegomastodon:* S. *waringi* (HOLLAND, 1920) that was recorded in Brazil and Ecuador (ALBERDI et al., 2002), and S. *platensis* (AMEGHINO, 1888) that was recorded in Argentina, Uruguay and probably in Paraguay. Concerning *Stegomastodon* genus there is a nomenclatorial controversy that is not yet closed, because FICCARELLI et al. (1993, 1995) considered it as *Haplomastodon* genus.

New remains of gomphotheres from a good stratigraphic section in Montevideo (Fig. 1) offer an opportunity for studying and comparing them with remains from other sites in Brazil and Argentina (PEREA et al. 2001; GUTIÉRREZ 2002). The purpose of this study is to investigate which species of *Stegomastodon* is present in Uruguay during the late Pleistocene. Another aim of this study is to confirm whether change in the gomphotheres paleodiet and habitat preference occurred at this latitude as already suggested by SÁNCHEZ et al. (2004).

2. Stratigraphic setting and age

In southern Uruguay it is difficult to distinguish the Dolores Formation from the Libertad Formation because of their very similar lithology. Before the formal definition of these units, all mammal Quaternary remains from southern Uruguay were referred to the "Pampean", an informal term that may include both Libertad and Dolores formations for that region (UBILLA & PEREA 1999).

The Dolores Formation was formally defined by Goso (1 *972Jide* ANTÓN & Gasa 1974). It is composed mainly of siltstones, pelites, sandy to gravely pelites and sandstones with argillaceous matrix. Cálcium carbonate is

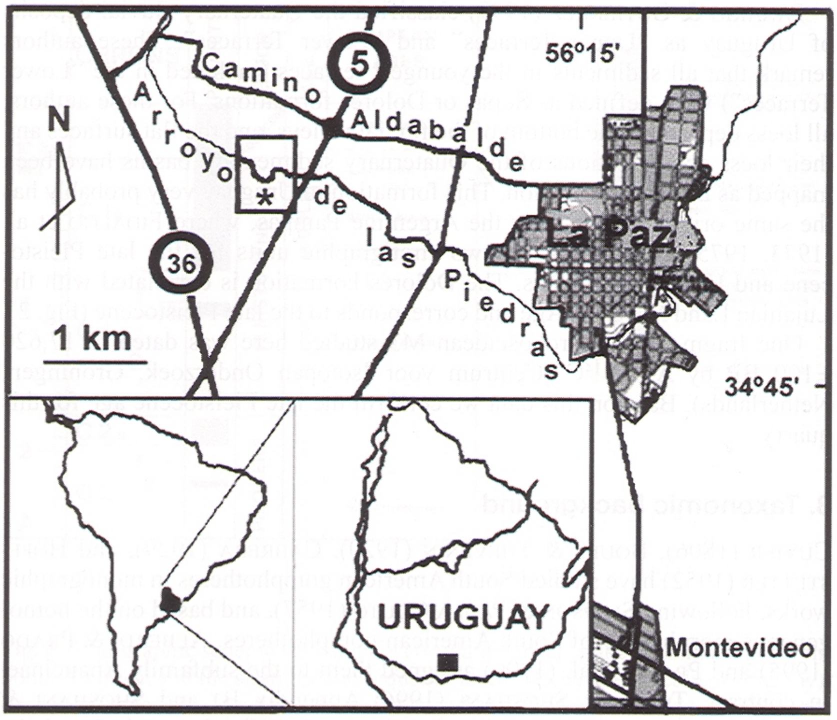

Fig. 1. Geographical location of the Montevideo locality (Uruguay, South America) with *Stegomastodon waringi* in which is indicated an approximate location of the collecting site.

abundant in various forms. The prevailing colour is brown with local changes to grey and greyish green (Bossi & Navarro 1991). Radiometric dates for the Dolores Formation in southern Uruguay indicates an age of ca. 10,500 years (Ubilla 1999).

In northern Uruguay, the Dolores Formation can be distinguished lithologically from the other Quaternary unit as the older Sopas Formation. Radiocarbonic ages indicate more than 40,000 years for the latter and nearly 11,500 years for the former (Ubilla & Perea 1999).

PANARIO & GUTIÉRREZ (1999) classified the Quafernary fluvial deposits of Uruguayas "Upper Terraces" and "Lower Terraces". These authors remark that all sediments in the youngest terraces (included in the "Lower Terraces") were defined as Sopas or Dolores formations. For these authors, allloess deposits at the bottom ofthe fluvial valleys, and the flat surfaces and their loess accumulations of the Quaternary sedimentary basins have been mapped as Dolores Formation. This formation in Uruguay very probably has the same origin as that from the Argentine Pampas, where FIDALGO et al. (1973, 1975, 1991) proposed two stratigraphic units for the late Pleistocene and Holocene deposits. The Dolores Formation is correlated with the Lujanian Land Mammal Age and corresponds to the late Pleistocene (Fig. 2).

One fragment of a proboscidean M3 studied here was dated to 17,620 ::1:: 100 BP by AMS 14C (Centrum voor Isotopen Onderzoek, Groningen, Netherlands). Base on this data we confirm the late Pleistocene age for this quarry.

3. Taxonomic background

CUVIER (1806), BOULE & THEVENIN (1920), CABRERA (1929), and HOFFSTETTER (1952) have studied South American gomphotheres in monographic works. Following SIMPSON & PAULA COUTO (1957), and based on the homogeneous morphology of South American gomphotheres, ALBERDI & PRADO (1995) and PRADO et al. (1999) assigned them to the subfamily Anancinae. In contrast, TASSY & SHOSHANI (1996: Appendix B) and SHOSHANI & TASSY (2005) proposed a new proboscidean classification and placed the South American gomphotheres in the subfamily Cuvieroniinae CABRERA, 1929 (family Gomphotheriidae HAY, 1922). We do not consider it accurate to include all South American species in the subfamily Cuvieroniinae, because CABRERA (1929) defined this subfamily based on *Cuvieronius*, and included *Stegomastodon* in another subfamily. The relationship between them is not yet clear. In the same book, TASSY (1996) proposed a phylogeny ofthe order Proboscidea that includes two gomphothere 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 (SHOSHANI & TASSY 2005).

In agreement with SIMPSON & PAULA COUTO (1957), we believe there is not sufficient supporting evidence to place South American gomphotheres into two distinct subfamilies. Also, in any case, the nomenclature is unclear. Therefore we tentatively include both genera *(Stegomastodon* and *Cuvieronius)* in the family Gomphotheriidae *(PRADO* et al. 2001, 2005) and refrain from placing them in subfamilies until we will have finished the cladistic analysis.

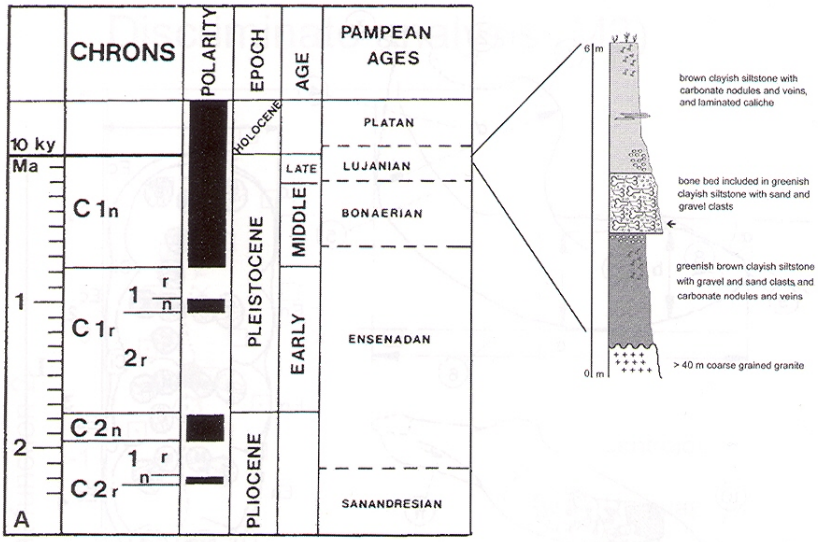

Fig. 2. Stratigraphic scheme showing the correlation of the Land Mammal Ages from South America, and the stratigraphic sequence at the Montevideo locality (Uruguay). Arrow indicates the location where the mandible of *Stegomastodon waringi* was collected.

4. Material and methods

The gomphothere remains from Montevideo are stored at the Vertebrate Palaeontology Collection of Facultad de Ciencias, Universidad de la República, Uruguay, and consist of the following: a complete mandible with left and right m1, m2 and m3 (FCDPV-1370) and a left upper M3 (FCDPV-1803).

We studied the characteristics of the jaw and teeth of the gomphotheres following Alberdi et al. (2002; Figure 3). Most of these characters were taken based on overviews by Mazo (1977), Tassy (1983) and Boeuf (1983, 1992). For comparative analysis we used the remains from selected localities in Brazil (Pains, Minas Gerais; Toca dos Ossos, Bahia; and Bonito, Mato Grosso) and Argentina (mainly in the Pampean Region) with good

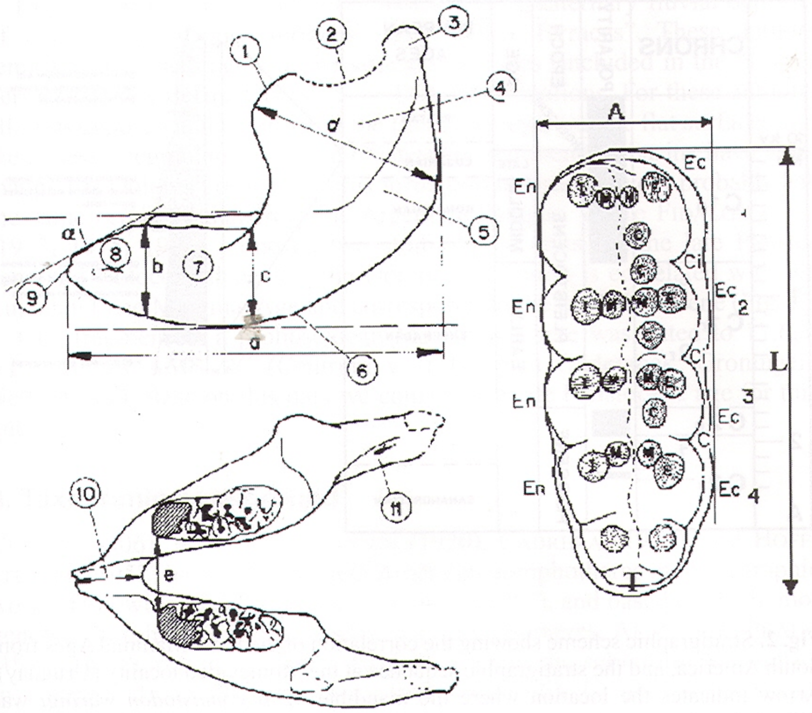

Fig. 3. Nomenclature and graphic representation of the measurements of the Gomphothere mandible and tooth following Alberdi et al. (2002). At left, a gomphothere mandible: **1** – coronoid process; **2** – mandibular incisure; **3** – articular condile; **4** – maseteric fossa; **5** – ascending mandibular ramous; **6** – mandibular border; **7** – dental row length; **8** – mentonian foramens; **9** – mandibular symphysis; **10** – symphysis length in sagittal plane; **10 bis** – height at the same level; **11** – pterigoid fossa; a: maximal mandibular length in sagital plane; b: mandibular height at anterior level of molar series; c: mandibular height at posterior level of molar series; d: maximal width of the ascending ramous; e: minimal distance between antero-internal molar edges; α-angle formed by the lateral edge of symphysis with the occlusal surface dental line. At right, a schematic graphic of the gomphothere last molar, M3, in occlusal view. L: maximal length; A: maximal width at each loph (1, 2, 3, and 4); En: entocones (lingual main cusp of each loph); Ec: labial main cusp of each loph; I: the main cusp internal; M: mesocones or the cusp close to the median sulcus; E: the main cusp external; C: central conules; Ci: cingulum; T: talon; Dashed line: median sulcus.

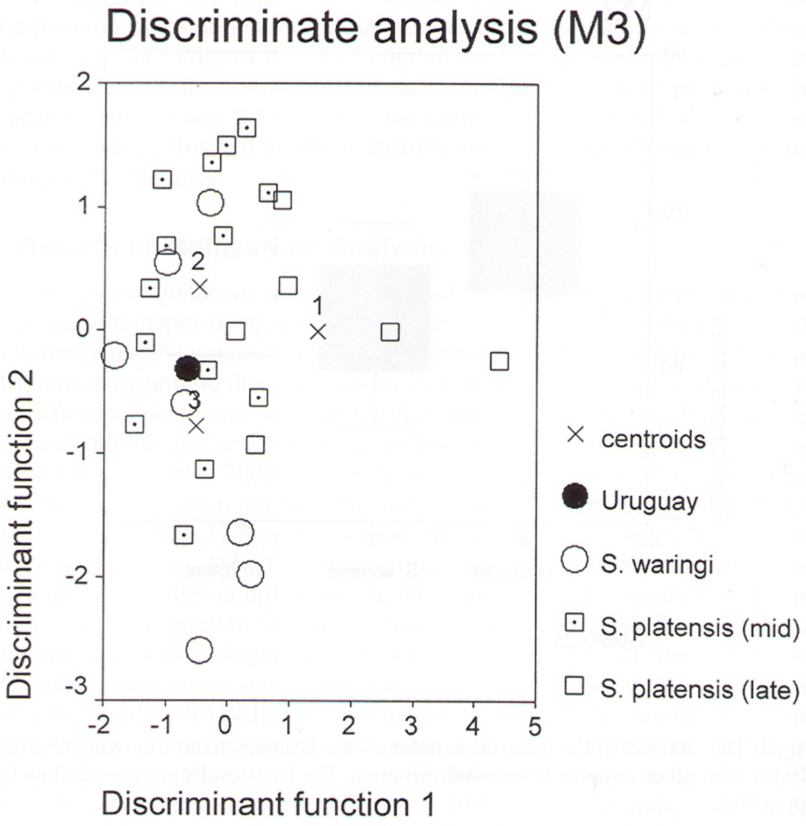

Fig. 4. Discriminant analysis (DA) of upper M3 samples of *Stegomastodon platensis* from Ensenadan SALMA in Argentina (*S. platensis* (mid)); *Stegomastodon platensis* from Lujanian SALMA in Argentina (*S. platensis* (late)); and *Stegomastodon waringi* from Lujanian SALMA in Brazil and Ecuador (*S. waringi*). Upper M3 from Uruguay is noted as a black circle.

stratigraphic data. These remains belong to the following collections: MLP: Museo de La Plata, Argentina; MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MHNBH: Museo de Historia Naturais de Belo Horizonte, Brazil; MUCBH: Museo

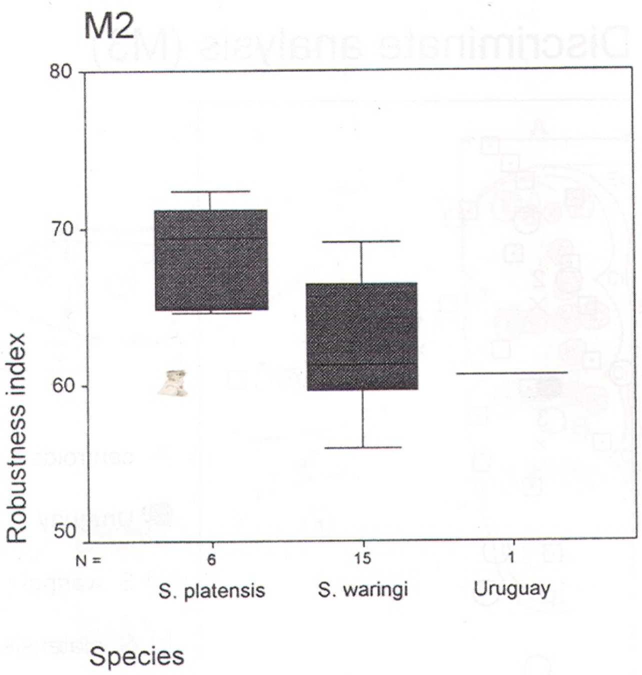

Fig. 5. The analysis of the robustness index of the Uruguay teeth following Osborn (1936) with other samples from South America. The best results are provided by the upper M2.

de la Pontifical Universidad Católica de Belo Horizonte, Brazil; MNHNP: Museum National d'Histoire Naturelle de Paris, France; MZK: Museum of Zoology, Copenhagen, Denmark; and NMB: Museum für Naturkunde in Berlin, Germany.

All dimensions are expressed in millimetres; 31 M3, 40 m3, 24 M2 and 17 m2 were analysed. The computational work was carried out using SPSS version 11.5. The authors will provide the original data underupon request. Data were analysed by Discriminant Analysis (hereafter, DA). Further details of this method are in Reyment (1991).

Two samples were measured to obtain the oxygen and carbon isotopic composition of tooth dentine carbonate. We extracted dentine samples from the anterior basal edge of the first lophid of the M3. The isotopic results were reported against the V-SMOW standard and the analytical precision for repeated analyses was 0.1 %0. Also, one sample was dated by AMS. Isotopes analysis was performed in the Centrum voor Isotopen Onderzoek, Groninguen, Netherlands.

5. Results of Multivariate Analysis

Stegomastodon platensis and *Stegomastodon waringi* have been identified in a previous paper using teeth morphology and bivariate analysis of teeth measurements (ALBERDI et al. 2002). Now we used DA to establish a rule for differentiating among these species base on teeth measurements. To compare the different specimens, we divided the samples into three groups, taking into account the species and the age of the corresponding deposit following PRADO et al. (2003, 2005): (1) *Stegomastodon platensis* from Ensenadan SALMA in Argentina (2) *Stegomastodon platensis* from Lujanian SALMA in Argentina; and (3) *Stegomastodon waringi* from Lujanian SALMA in Brazil and Ecuador. DA of the three groups provided a correct identification especially from M3 sample (Fig. 4). The material from Lujanian in Brazil and Ecuador assigned to *Stegomastodon waringi* is clearly different from the Lujanian material in Argentina. DA of both populations of *Stegomastodon platensis* in Argentina shows them as clearly distinguished; the population from Ensenadan SALMA has a smaller size than the population from Lujanian SALMA. We compared also the Uruguayan teeth with the rest of the sample, using the robustness index defined by OSBORN (1936). We found that when measuring maximum width x 100/length, especially the second molar provided a correct identification of both species of *Stegomastodon* (Fig. 5).

6. Systematic paleontology

We observed that all South American gomphotheres present a generalized pattern that includes the following features: abrachycephalic skull with a tendency towards an elephantoid skull, a brevirostrine jaw with a slightly curved symphysis elongate upper tusks which vary from straight or slightly curved to very twisted, and that may or may not be present an enamel bando Within South American gomphotheres, only adult *Cuvieronius hyodon* conserve a true enamel bando The alternate contact between successive pretrite and postrite half-loph(id)s (anancoidy) is present frequently in the last loph(id)s on M3 and m3. These molars are brachyodont or sub hypsodont, with simple or slightly complex trefoils on the occlusal surface. M2 is trilophodont and occasionally has a developed talon. M3 varies from tetralophodont to heptalophodont.,

Family Gomphotheriidae CABRERA, 1929
Genus *Stegomastodon* POHLlG, 1912

Synonyms:
1842 *Mastodon;* LESSON: 157,
1906. *Mastodon;* WINGE: 48.
1928 *Bunolophodon;* SPILLMANN: 67.
1929 *Notiomastodon* CABRERA: 90 ff., figs. 2-4.
1950 *Stegomastodon (Haplomastodon)* HOFFSTETTER: 22, figs. 2-3. 1952 *Haplomastodon (Aleamastodon)* HOFFSTETTER: 208 (in part), 1957 *Haplomastodon* HOFFSTETTER; SIMPSON & PAULA COUTO: 166. For more detail see CABRERA (1929) and OSBORN (1936).

Type species: *Mastodon mirificus* LEIDY, 1858,

Geographical distribution: The South America records of *Stegomastodon* began with the Taima-Taima site in Venezuela (BRYAN et al. 1978; BRYAN 1986; CASAMIQUELA et al. 1996). It was also found on the Santa Elena Peninsula and in Quebrada Pistud in Ecuador (HOFFSTETTER 1952; FICCARELLI 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 localities) (ALBERDI et al. 2002). SIMPSON & PAULA COUTO (1955, 1957) indicated the presence of *Stegomastodon* in temperate southwestern Brazil. This genus extended as far south as Argentina, and was particularly abundant in the Pampean region, as well as in Uruguay and Paraguay (CABRERA 1929; SIMPSON & PAULA CauTo 1957; MONES & FRANCIS 1973; PRADO et al. 2002) and possibly in Chile (CASAMIQUELA et al. 1996).

Stratigraphic range: The genus was recorded in the late Pliocene and the early Pleistocene in central and western regions of North America. In South America, it

Fig. 6. *Stegomastodon waringi* remains stored at the Vertebarate Paleontology Collection of Facultad de Ciencias, Universidad de la República (Montevideo). 1 - mandible with left and right mI, m2 and m3 (FCDPV-1370), in lateral view; 2 - detailed the left ramus mandible (FCDPV-1370), in occlusal view; 3 -left upper M3 (FCDPV-1803), in occlusal view.

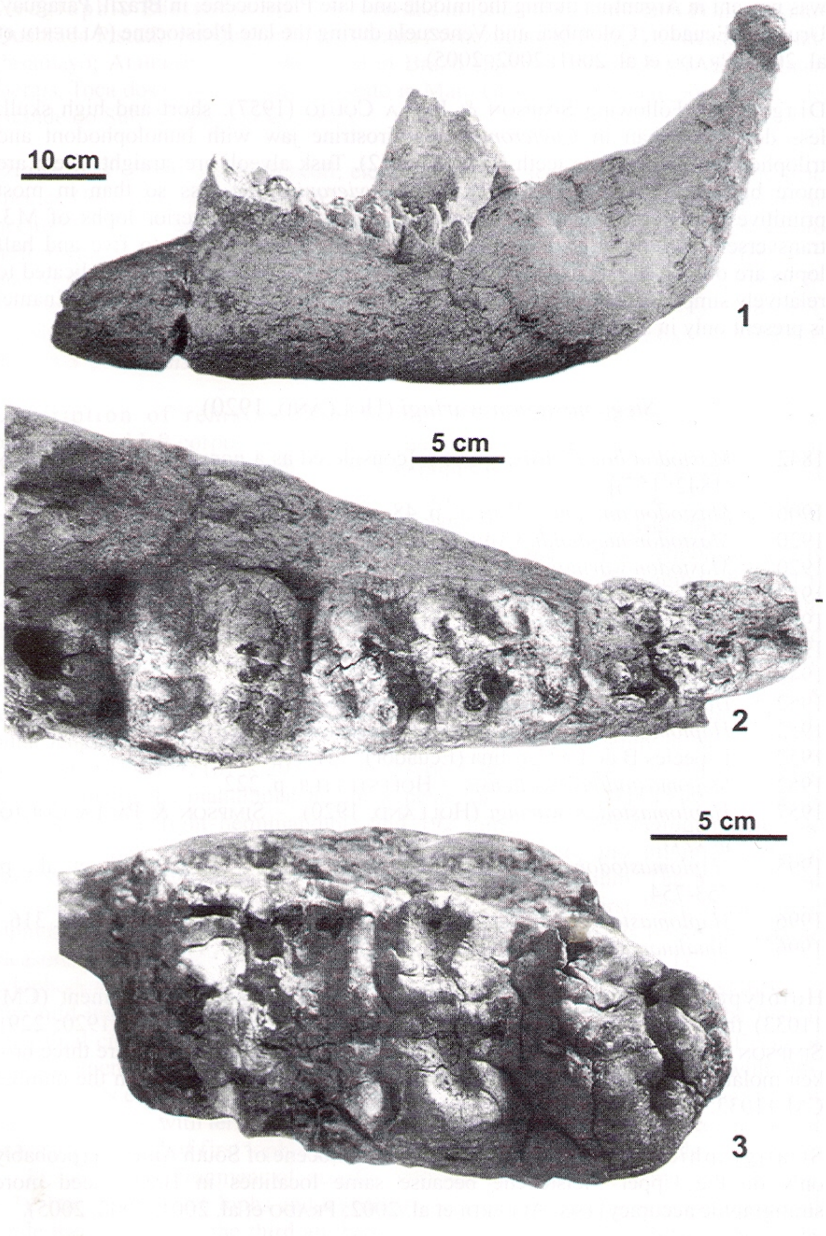

Fig. 6 (Legend see p. 650)

was present in Argentina during the middle and late Pleistocene; in Brazil, Paraguay, Uruguay, Ecuador, Colombia, and Venezuela during the late Pleistocene (ALBERDI et al. 2002; PRADO et al. 2001, 2002, 2005).

Diagnosis: Following SIMPSON & PAULA COUTO (1957): short and high skull; less depressed than in *Cuvieronius.* Brevirostrine jaw with bunolophodont and trilophodont intermediate teeth (D4, MI, M2). Tusk alveoli are straight. Teeth are more bunodont and choerodont than in *Cuvieronius* but less so than in most primitive Old World Anancinae. Moderate alternation in posterior lophs of M3, transversely slightly angled pretrite and postrite cusps, and five to five and half lophs are observable. Double trefoils vary in form and pattern from complicated to relatively simple. Tusks are simply curved to nearly straight, without enamel. Enamel is present only in some juvenile individuals.

Stegomastodon waringi (HOLLAND, 1920)

1842 *Mastodon brasiliensis.* - LUND [considered as a *nomen nudum* in LESSON (1842: 157)].
1906 *Mastodon andium.* - WINGE, p. 48, *nec* CUVIER, 1806, p. 413.
1920 *Mastodon humboldti* CUVIER. - BOULE & THEVENIN, p. 68.
1920 *Mastodon waringi.* - HOLLAND, p. 229.
1922 *Mastodon chimborazi.* - PROAÑO, p. 13.
1928 *Bunolophodon ayora.* - SPILLMANN, p. 70.
1931 *Bunolophodon postremus.* - SPILLMANN, p. 73.
1948 *Notiomastodon vidali.* - CASTELLANOS, p. 139.
1952 *Haplomastodon (Haplomastodon) chimborazi.* - HOFFSTETTER, p. 192.
1952 *Haplomastodon (Aleamastodon) guayasensis.* - HOFFSTETTER, p. 208.
1952 Especies B de La Carolina (Ecuador). - HOFFSTETTER, p. 224.
1952 *Stegomastodon brasiliensis.* - HOFFSTETTER, p. 222.
1957 *Haplomastodon waringi* (HOLLAND, 1920). - SIMPSON & PAULA COUTO, p.171.
1995 *Haplomastodon chimborazi* (PROAÑO, 1922). - FICCARELLI et al., p. 753-754.
1996 *Haplomastodon waringi* (HOLLAND, 1920). - CASAMIQUELA et al., p. 316.
1996 *Amahuacatherium peruvium* ROMERO-PITTMAN. - p. 171-178.

Holotype: Corresponds to an incomplete mandible and bone fragment (CM11033) from Pedra Vermelha, Bahía, Brazil described by HOLLAND (1920: 229). SIMPSON & PAULA COUTO (1957: 172) further commented that there were three broken molars, two tusk fragments, and the distal part of a tibia - all with the number CM-11033.

Stratigraphic range: Middle and Upper Pleistocene of South America (probably only on the Upper Pleistocene because same localities in Brazil need more stratigraphic accuracy) (see ALBERO! et al. 2002; PRADO et al. 2001, 2002, 2005).

Geographic Distribution: It is recorded in Ecuador (Santa Elena Peninsula and Quebrada Pistud), possibly in Taima-Taima (Venezuela), in Peru (La Huaca, Quipan, Pasamayo; ALBERDI et al. 2004) and in Brazil (Pains, Lagoa Santa are a in Minas Gerais, Toca dos Ossos in Bahia, Bonito in Mato Grosso do Sul, and possibly in Río Grande do Sul; ALBEÍillI et al. 2002).

Diagnosis: Short and high skull, elephantoid type; less elephantoid than the type species *(Stegomastodon mirificus)* and less depressed than *Cuvieronius.* The molar occlusal surfaces are less complicated than in *Stegomastodon platensis.* The double trefoil pattern (on both pretrite and postrite) varies from simple to relatively complex due to the presence of secondary conules or conelets. Tusks are nearly straight to very slightly curved, with an enamel band in some juvenile individuals; usually simply curved and without enamel band in adults. All these features are less marked than in S. *plantensis.*

Description of remains from Montevideo: FCDPV-1370: mandible with both right and left corpus, with mI, m2 and m3 on each corpus, the last one still in the alveolus (Fig. 6-1). The right ascending ramus is broken and the left one is almost complete, as is the mandibular condyle (5) (see Fig. 3). The external masseteric fossa (4) is a slight depression that is more or less curved as following the left ramus. The pterygoid fossa is reconstructed (11) and the mandibular symphysis (9) is elongate and broken at its apex. Length of the symphysis at the sagittal plane (10) is approximate 190 mm. The angle a formed by the lateral edge of symphysis with the occlusal surface dental line is approximately *30°* (Fig. 6-1). The left coronoid process (1) and the mandibular incisure (2) have been lost; the left condyle (3) is not completely preserved; the mandibular border (6) is slight curved; the dental row length is 367 mm (7); with mentonian foramens below mI (8); the maximal mandibular length in the sagittal plane (a) is 840 mm, mandibular height at anterior level of molar series, mI, (b) is 205 mm in the right hemimandible and 201 mm in the left hemimandible, mandibular height at posterior level of molar series, m2, (c) is 163 mm in the right hemimandible and 192 mm in the left hemimandible; the maximal width of the ascending ramus (d) is broken; the minimal distance between antero-internal molar edges (e) is between 70-80 mm. The mI, m2 and m3 are conserved in both hemimandibles (Fig. 6-2). On first, second and third lophids both mi show signs of advanced wear. The right mI is broken and some measurements are not possible to take (measurements in Table 1). The m2 is trilophodont and has a talonid with occlusal trefoil figures which have faded by wear. The mid-line is clear and there are several, internal central conulids. The mesial and labial cingula are strongly marked and have a very significant layer of cement (measurements in Table 1). The m3 is recently erupted; showing no wear, with only three lophids erupted. There is some cement residue, an observable mid-line, several central conulids, with ternary division ofthe lingual conid offirst and second lophid in the left m3 and offirst lophid in the right m3 (measurements in Table 1).

FCDPV-1803: fragment of maxilla with left M3 from the same locality (Fig. 6-3). The M3 has five lophs and a pronounced talon, the first loph is not preserved while the second and the third are badly preserved. The postrite and pretrite cones

Table 1. Measurements, in millimetres, of the upper and lower teeth of *Stegomastodon* from Montevideo (Uruguay). L: maximal length; W1: width of the first loph; W2: width of the second loph; W3: width of the third loph; W4: width of the fourth loph; W5: width of the fifth loph; T: talon; >W: the maximum width; r = right; l = left. FCDPV: Facultad de Ciencias, Departamento de Paleontología de Vertebrados, Universidad de la República (Uruguay).

Col. Number	Locality	Tooth	L	W 1	W 2	W 3	W 4	W 5	T	W >
Stegomastodon										
FCDPV-1370	Canelones	m1 lower r	104	70 ca	72 ca	73 ca				
FCDPV-1370	Canelones	m1 lower l	111,7	68	69	76	78,5			78,5
FCDPV-1370	Canelones	m2 lower r	128	80	87	90,5			59	90,5
FCDPV-1370	Canelones	m2 lower l	132	80	86,3	89,2			59	89,2
FCDPV-1370	Canelones	m3 lower r		95,6						
FCDPV-1370	Canelones	m3 lower l		97,5						
FCDPV-1803	Canelones	M3 upper l	230-235		97	96,5	96	83	48,7	97
FCDPV-300	sin localidad	m2 lower r	139	83	84,2	89				89

Table 2. Univariate statistics for the two groups studied of *Stegomastodon*: *S. platensis* and *S. waringi*, from the results of $\delta^{18}O$ and $\delta^{13}C$ analysed and compared with samples studied by SÁNCHEZ et al. (2003, 2004).

Groups	*n*	Mean $\delta^{13}C$ (‰)PDB	SD (‰)	Range (‰)	Mean $\delta^{18}O$ (‰)V-SMOW	SD (‰)	Range (‰)
S. platensis from latest Pl. of Pampean Region	7	-10,74	0,97	-12,11 to -9,69	29,84	1,67	28,25 to 33,19
S. platensis from late Pl. of Pampean Region	18	-8,12	0,81	-9,56 to -6,09	30,27	0,80	28,15 to 32,76
S. platensis from early Pl. of Pampean Region	7	-7,80	1,24	-9,06 to –5,9	29,46	0,80	28,6 to 30,60
S. waringi from Ecuador, late Pleistocene	4	-3,49	2,73	-5,97 to -0,78	32,48	2,78	30,77 to 36,61
S.waringi from Brazil, late Pleistocene	2	-6,6	2,26	-8,2 to -5	29,88	1,31	28,9 to 30,80
S. waringi from Uruguay, late Pleistocene	1	-9,56			27,73		

form a slight angle on fourth and fifth lophs. The mid-line is lost on the first and second lophs, without remnants of cement, the mesial and lingual cingula are strongly marked in the last two lophs,(measurements in Table 1).

7. **Discussion**

HOFFSTETTER (1952) proposed the subgenus *Haplomastodon* based on the presence oftransverse foramina in the atlas and axis. We think that this taxon is not clearly differentiated from *Stegomastodon.* In agreement with SIMPSON & PAULA COUTO (1957) we consider this character high1y variable within species In addition, we observed several specimens with and without foramina from Argentina and Brazil.

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 *Stegomastodon platensis* (following the International Code of Zoological Nomenclatues - ICZN 1999 - mIes). CABRERA retained *Stegomastodon superbus* as a separate species, based on his observations that it did not come from the same geological time periodo SIMPSON & 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 in the multivariate analysis a pattern of increased teeth size since Ensenadan remains from Argentina to the Lujanian remains but the morphological character in both populations are homogeneous. We think that the few differences observed are related to adaptation to different environmental conditions and correspond to intraspecific variations. ConsequentIy, we conserve only one species, *Stegomastodon platensis*, for Argentinean remains. We believe that differences in pattern of teeth morphology between *Stegomastodon platensis* and *Stegomastodon waringi* are sufficient evidence, plus the size differences, to conserve two distinct species.

RecentIy, a study on food adaptations of Pleistocene gomphotheres from South America (SÁNCHEZ et al. 2004) postulated that a relationship exists between the extinction of the gomphotheres species and their dietary preferences. Carbon isotope analyses reveal that middle Pleistocene *Stegomastodon platensis* recorded in Pampean Region had different food adap

tations (SÁNCHEZ et al. 2003). It fed on a mixed diet (Table 2), as their isotopic values are more homogeneous, ranging between -9.06 to -5.9 %0. These data indicate an isotopically mixed C3-C4 diet. Gn the other hand, late Pleistocene samples show a wider range of dietary adaptation (between -12.11 to 6.09 %0), with specimens from latest Pleistocene indicating an exclusively C3 or C4 diet, and others mixed feeders. SÁNCHEZ et al. (2004) believe that *Stegomastodon platensis* from middle Pleistocene exhibited opportunistic feeding strategies and consequently may have been adapted to diverse habitats, even though the majority of gomphotheres from the middle Pleistocene showed a preference for mixed-feeding. In contrast, populations from late Pleistocene appear to have been adapted to a more selective diet, which restricted their habitat preferences (SÁNCHEZ et al. 2003). They propose that Pampean gomphotheres were driven to extinction because they were specialized feeders, adapted to plants that may have disappeared during the Holocene.

Alternatively, *Stegomastodon waringi* shows two different adaptations. Samples from Brazil (Toca dos Ossos) indicate that this species were mixed-feeders while those from La Carolina (Ecuador) were mostly C4 feeders. Data for the specimens study here present a value (-9.56 %0) closely related with the Brazil population (Table 2).

MAcFADDEN et al. (1999), using the distribution of Pleistocene *Equus* in America, show a general o13C gradient that seems to be symmetrical on either side of the Equator. The isotopic transition between plants with C4 photosynthetic pathway to plants with C3 pathways is observed in the Southern hemisphere at around 35 to 4loS (SÁNCHEZ et al. 2004). The proportion of C3 and C4 grasses in modern ecosystems varies with latitude and the crossover between C3 versus C4 dominance in grasslands occurs at about 40-45° latitude in the northern hemisphere (EHLERINGER et al. 1997). This progression of more negative values south of the equator in *Stegomastodon waringi* (Table 2) confirms a latitudinal gradient for the Southern hemisphere similar to that observed by MAcFADDEN et al. (1999).

Isotopic oxygen values also varied according to latitude and were further influenced by altitude. In previous paper SÁNCHEZ et al. (2004), indicated that *Stegomastodon waringi* from Brazil and Ecuador show a range between 28.6 to 36.6 %0. The specimen form Uruguay show a value of27,73 %0 (Table 2). The isotopic oxygen value of samples from the late Pleistocene of Brazil, Uruguay and Buenos Aires were in the range expected for actual African herbivores inhabiting a semiarid and seasonal rainfall climate (KOCH et al, 1995; BocHERENs et al. 1996).

8. Conclusions

The gomphotheres remains from Montevideo are scarce, but characteristic enough to assign them without doubt to *Stegomastodon waringi*, thus confirming the previous assignment to *Stegomastodon* cf. S. *waringi* by GUTIÉRREZ (2002). The double trefoils pattern (on both pretrite and postrites) due to the presence of relatively simple secondary conulids or conelets is typical ofthis species. *Stegomastodon waringi* is one ofthe largest species of

South American gomphotheres, which appears tó have predominated at middle latitudes (in Uruguay, Brazil, Peru, and Ecuador), where it occupied savannas or xerophytic open areas, and consequently would have been better adapted to warm or temperate climatic conditions. Carbon isotope analyses for this individual reveal that *Stegomastodon waringi* specimens from Uruguay were possibly mixed-feeders similar to Brazil samples of this species. The presence of *Stegomastodon waringi* in this quarry represents a new local record and expands the known southern distribution of this species in South America. The radiometric data ofthis specimen (AMS 14C) confirm the late Pleistocene age for this quarry.

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Addresses of the authors:

MERCEDES GUTIÉRREZ, Department of Anthropology, Washington University in
St. Louis. Campus Box 1114. St. Louis, MO 63130;
e-mail: mgutierrez@wustl.edu
MERCEDES GUTIÉRREZ, DANIEL PEREA, Departamento de Paleontología, INGEPA,
Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay;
e-mails:macbeth@movinet.com.uyandperea@fcien.edu.uy
MARIA TERESA ALBERDI, Departamento de Paleobiología. Museo Nacional de
Ciencias Naturales, CSIC, José Gutiérrez Abascal2, 28006-Madrid, Spain;
e-mail: malberdi@mncn.csic.es
JOSÉ LUIS PRADO, INCUAPA-Departamento de Arqueología, Universidad Nacional
del Centro. Del Valle 5737. B7400JWI - Olavarría, Argentina;
e-mail: jprado@soc.unicen.edu.ar