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A critical appraisal of the phylogenetic proposals for the South American Gomphotheriidae (Proboscidea: Mammalia)

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ABSTRACT

The systematics of gomphotheres in South America is confused, and the status of some taxa is still subject to discussion. Recently, Prado and Alberdi published a cladistic analysis of the trilophodont gomphotheres, with emphasis on the South American species. Unfortunately, the paper has problems in many points, which invalidates the phylogeny itself and the biogeographic analysis of Alberdi et al. based on it. This paper reviews the problems of the analysis of Prado and Alberdi. The main problems of their analysis are: poor taxon sampling, exclusion of non-South American species of genera present in South America, inadequate choice of outgroup, use of outdated software and methodology, and several mistakes in coding of characters. Rebuilding of the original character matrix and analysis using TNT software resulted in a new consensus tree from five equally parsimonious trees. In the analysis, *Rhynchotherium*, *Sinomastodon*, *Gnathabelodon*, *Eubelodon* and a clade containing the three South American taxa form a polytomy that have *Gomphotherium* as a sister group. *Sinomastodon* and *Gnathabelodon* were successive branches toward the South American taxa in Prado and Alberdi's result. The main point of this contribution is to correct the errors in the original analysis and character coding, including polymorphism when necessary, and to use updated software and weighting strategy. The result is much less resolved than that of Prado and Alberdi, but it has a strong influence on the conclusions that those authors drew from the original phylogeny and the biogeographic implication presented in Alberdi et al.

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1. Introduction

Gomphotheres are to date the only group of Proboscidea known in South America. The systematics of gomphotheres in this continent was a little confused, and for many years the status of some species and even genera were matters of discussion. In a detailed monograph of the gomphotheres from Águas de Araxá, Minas Gerais State, Brazil, Simpson and Paula-Couto (1957) reviewed the systematics of the group and all the literature up to that time. These authors concluded that four genera were present in South America: *Cuvieronius* is distributed mainly along the Andean region; *Stegomastodon* occurs in the southern end of the continent; *Haplomastodon* is distributed in the north of the continent at the east of the Andes, with a record in the western Ecuador; and *Notiomastodon* is restricted to a small area in the Argentinean Pampean region. For *Notiomastodon*, Simpson and Paula-Couto

(1957) expressed some reservations, suggesting that might be a variation of *Stegomastodon*.

With few modifications this was the systematic scheme that prevailed until the work of Alberdi and Prado (1995), where they proposed a simplified scheme, including both *Haplomastodon* and *Notiomastodon* in *Stegomastodon*, reducing the number of genera to two, with only three species, *Cuvieronius hyodon*, *S. waringi* (north-east South America) and *S. platensis* (south end of the continent). This scheme was not universally accepted (Ferretti, 2010; see also Shoshani et al., 2006, whom included the four genera recognized by Simpson and Paula-Couto, 1957 in their matrix in the additional data), but was generally used by South American researchers. Therefore, when the South American “*Stegomastodon*” is cited on this paper, it will be written with quotation marks. Both genera in this scheme originated in North America. *C. hyodon* was present throughout the Americas, but “*Stegomastodon*” *warangi* and “*Stegomastodon*” *platensis* are endemic to South America.

Recently, Prado and Alberdi (2008) published a cladistic analysis of the trilophodont gomphotheres, with emphasis on the South

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American species. In a paper that was published before the one mentioned above (Alberdi et al., 2007), but that was produced later, those authors and other collaborators proposed an interpretation of the biogeographic history of the same group using a dispersion–vicariance analysis based on their phylogeny.

These are certainly much needed studies on one of the most conspicuous and ecologically and evolutionary important group of mammals that inhabited the Americas and participated in the Great American Biotic Interchange (GABI) at the end of the Cenozoic. Previous phylogenies were, at best, done at generic level. Shoshani et al., (2006) include 125 taxa at generic level in their matrix, although they published only a simplified cladogram at family level.

Unfortunately, both papers, but especially the proposed phylogeny, have errors in many points, which invalidate both the phylogeny itself and the biogeographic analysis based on it. The current paper reviews the problems of the analysis of Prado and Alberdi (2008) to show why these are serious enough to reject their propositions for both the phylogeny and biogeography.

2. General problems

2.1. Poor taxon sampling

Prado and Alberdi (2008) selected 13 terminals plus the outgroup. Most of the characters were taken from Tassy (1996) and Shoshani (1996), which in turn was the basis for Shoshani et al. (2006). Except for the South American species, all the other taxa were treated at generic level. The reduction of the number of taxa may force the formation of artificial groups by transforming homoplastic characters into synapomorphies.

Another issue that should be considered here is that it was not made explicit which species were used to score the taxa when only the genus is given. This is important because some genera have more than one species, and some are long-lived, such as *Rhynchotherium* and *Sinomastodon*, to cite two particularly crucial taxa.

As well, for the case of *Gnathabelodon*, no source for the data is presented, which is particularly important because this genus is designated as the sister group of the “brevirostrine” group because it is the only one with “reduced lower tusks” (state 1 of character 5, but see character discussion and Ferretti, 2010).

2.2. Exclusion of non-South American species of genera present in South America

The exclusion of the North American representatives of the South American species left unclear their position in the phylogeny. It seems that the authors assume that they are identical to the South American ones in the character considered. In the genus *Stegomastodon*, two additional species are known, *S. mirificus* (the type species) and *S. primitivus*. As stated above, *Cuvieronius hyodon* (the type species) is recorded for Mexico, but another two species are also included in this genus, *C. tropicus* and *C. priestleyi*.

2.3. Inadequate choice of the outgroup

The use of *Phiomia* Andrews and Beadnell (1902), as the outgroup for this subset of Proboscidea has the effect of a “plesiomorphic artificial group”, as if it were built by hand, because it has 0 for all the states, forcing this as the plesiomorphic condition for the rest. The choice was based on, “it was considered by Tobien (1973) to be the most probable ancestor of gomphotheres” (Prado and Alberdi, 2008), but immediately after this, the authors recognized that this hypothesis is no longer favored in the more recent revisions, which considered *Phiomia* a basal proboscidian. Despite this, they insist in using this genus because “we consider *Phiomia* to be

the most suitable outgroup”. This is particularly important because as Maddison et al. (1984) and Nixon and Carpenter (1993) noted, the use of an outgroup taxon very distant from the ingroup basal node may cause misinterpretation of homologies.

2.4. Use of outdated software and methods

The authors used the Hennig86 program, written by S. Farris, to run the analysis. This software is outdated, lacking some of the functions, routines and modern algorithms that are in use in computer assisted phylogenetic systematic analysis (Goloboff et al., 2008a). It may be argued that this software may still be useful for a small matrix such as the one examined here: however, the fact that it lacks some capabilities, including coding polymorphic characters, makes this inappropriate in this case. As well, the use of the successive weighting routine has better options at present (see Goloboff, 1995, 1997; Goloboff et al., 2008b).

3. Problems in characters

This section discusses, reviews, and comments on some of the characters used by Prado and Alberdi (2008).

3.1. Character 0

Presence of an enamel band in the second lower incisor. This character refers to the presence of an enamel band in i2, and consequently is not applicable to taxa in which this tooth is not present and should be coded as ? or –. However, it was coded as 0 in the matrix for *Sinomastodon*, both “*Stegomastodon*” species, and *Cuvieronius*.

3.2. Character 2

Upper tusks with helicoidal twisting. This character was coded as 0, with torsion (the condition found in *Cuvieronius*) and 1 without torsion (all the other terminals), but was coded inversely in the matrix. In any case, since only one terminal has the derived condition, this character is uninformative. Some species of *Rhynchotherium* may have a similar helicoidal enamel band (Lucas and Morgan, 2008).

3.3. Character 3

The position of the alveoli for the upper tusk in premaxillae. This character has three states (Prado and Alberdi, 2008: Fig. 2), with “*Stegomastodon*” *waringi* as 0, “*Stegomastodon*” *platensis* as 1 and *Cuvieronius hyodon* as 2. However, in the matrix both “*Stegomastodon*” are coded 1, as well as all terminals except *Phiomia* (0) and *C. hyodon* (2).

3.4. Character 4

Presence of enamel band in I2. State 1 of this character (absence of enamel band) seems to define the node 7 (*Gnathabelodon*, *Sinomastodon*, *Cuvieronius hyodon*, “*Stegomastodon*” *platensis* and “*Stegomastodon*” *waringi*). However, an enamel band was mentioned as one of the diagnostic characters in *Cuvieronius* (Prado et al., 2005; Alberdi et al., 2007) and in some juvenile specimens of *Stegomastodon* (Alberdi et al., 2004, 2008; Fig. 1A and B; Prado et al., 2005).

3.5. Character 5

Presence or absence of the lower tusks. State 2 (absence of lower tusks) has the same distribution as character 39 (*brevirostrine*

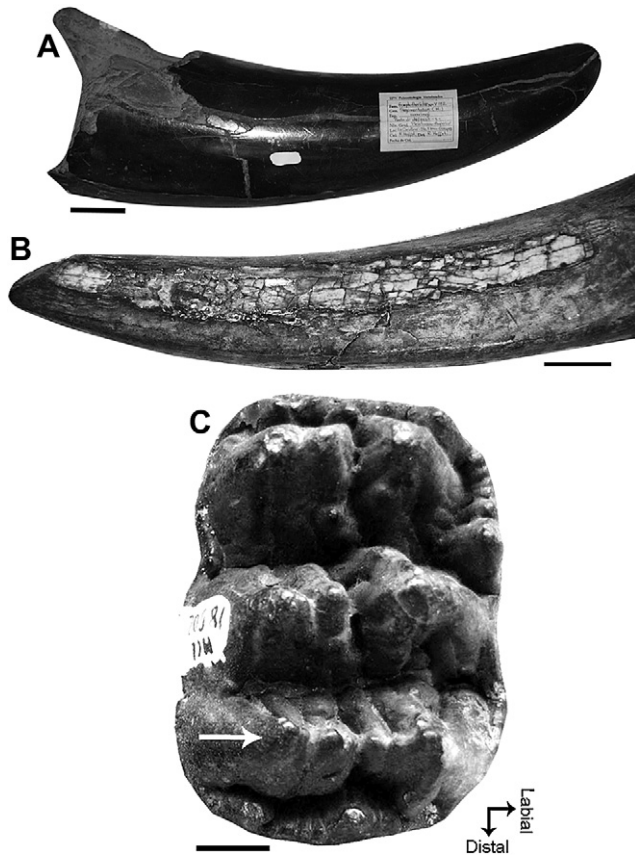


Fig. 1. Incisors and Molars of “*Stegomastodon waringi*”. A – incisor fragment of “*Stegomastodon waringi*” from Equator (V. 162, Museo de Historia Natural ‘Gustavo Orces’ mammalian fossil collection, Quito, Ecuador) with enamel. B – incisor fragment of “*Stegomastodon waringi*” waringi from Colombia (without collection number, Instituto Colombiano de Geología y Minería mammalian fossil collection, Colombia) with an enamel band. Scale bar = 5 cm. C – left DP3 without posterior loph obliquity (MCL 18502, Pontificia Universidade Católica de Minas Gerais mammalian fossil collection). Scale bar = 1 cm.

(Fig. 1C). Of course, the possibility that this condition exists in some specimens cannot be absolutely rejected, but if not all specimens exhibit it, the character should be coded as polymorphic at best.

3.7. Character 21

Cingulum on medial side on the upper molar. This character was coded as 1 only for *Gnathabelodon* and unknown for three other taxa, with all the others coded 0. That makes this character uninformative.

3.8. Character 22

Mesial and lateral cingulum on the molars, and 23: Central conules on the upper and lower teeth. These two characters have states defined subjectively, and it is very hard to recognize such differences in real specimens. These are subjective characters, quite difficult to identify. Some degree of subjectivity is inherent to the process of choosing characters. However, when defining the states it should be done in a way that anyone can determine if one of other is present in a specimen. This is not possible for those two characters.

Additionally, Prado and Alberdi (2008) coded character 23 as having two states (p. 908): 0 and 1. However, in the matrix (Table 2) and in the cladogram (Fig. 9), “*Stegomastodon*” platensis was coded as 23(2). Correcting this make the derived condition present in all the terminals except the outgroup.

3.9. Character 25

Anancoidy. This refers to alternate position of the pretrite and postrite cusps in molars. The condition 2 is defined as “always present” and only the two species of “*Stegomastodon*” have this state. However, in Prado and Alberdi (2008): Figs. 5D and 7A, where molars of “*Stegomastodon*” waringi are represented, this condition

condition) in Prado and Alberdi’s (2008) matrix, which gives the impression that those two characters are correlated. This is, the loss of the lower tusks determine the brevisrostrine condition. This would be a violation of the principle of independence of the characters required by the phylogenetic analysis. However, recently Ferretti (2007, 2008) recorded vestigial lower incisors for a juvenile *Cuvieronius hyodon* from the late Pleistocene of Tarija, Bolivia. In this individual the lower incisor was present until the eruption of m1, which in extant proboscideans occurs about the age of 11 years (Moss, 1996). Consequently this character should be coded as polymorphic for *C. hyodon*. Ferretti (2010:710) noted that both *Eubelodon* and *Gnathabelodon* had no lower tusk, contrary to the coding of Prado and Alberdi (2008) which codes it as present for *Eubelodon* and reduced for *Gnathabelodon*. Besides this, one implication derived from this observation is that the loss of the lower incisor may have occurred independently more than once, making it an homoplastic character, which also occurred within Elephantidae. This was corrected in the revised matrix.

3.6. Character 12

Obliqueness of the posterior loph of DP3. The obliquity of the posterior loph of DP3 is supposed to characterize all the ingroup. However, the present authors failed to find the derived state in both species of “*Stegomastodon*” and *Cuvieronius* from South America



Fig. 2. Mandible of *Cuvieronius hyodon* from Tarija, Bolivia (MNHN 1907-35/TAR 805, Museum National de Histoire Naturelle mammalian fossil collection, Paris, France) with molars showing plicate enamel (ptychodonty).

Fig. 3. The cladogram obtained after the character matrix revision from the [Prado and Alberdi \(2008\)](#) proposal. Character numbers above the filled and open circles correspond to the variables specified in the text. Filled circles indicate non-homoplastic steps; open circles denote convergences.

3.12. Character 31(32)

Premaxilla with posterodorsal process in the midline, at the floor of the nasal fossa. This character has only two states (0, 1) in the character list, but in the matrix *Eubelodon* was coded 2.

3.13. Character 37(38)

External shape of skull. This character is poorly defined and difficult to identify in practice. It has also a very poor behavior in the [Prado and Alberdi \(2008\)](#) cladogram. It changes from 0 to 1 at node 5, reverts to 0 at node 7, changes again to state 1 at node 9, and to state 2 in “*Stegomastodon*” species. Besides all this consideration, very few species have adult skulls suitable to allow identification of the state.

3.14. Character 39(40)

Brevirostrine condition. This character is present in its derived state only in “*Stegomastodon*” spp., *Cuvieronius* and *Sinomastodon*. Obviously this character will join the three genera if considered in this reduced context, since it occurs also in Elephantioidea. Moreover, [Lucas and Morgan \(2008\)](#) noted that *Rhynchotherium* has the brevirostrine condition along with lower tusks. This was corrected in the revised matrix.

4. Material and methods

After the analysis of the characters and methodology, the original matrix was modified according to the observations above (Table 1). The matrix was run with TNT software ([Goloboff et al.,](#)

2008a) using the “Implied weighting” strategy (see [Goloboff, 1993, 1995, 1997; Goloboff et al., 2008a](#)), more efficient and less flawed than the “successive weighting” strategy, and the “implicit enumeration” search strategy, as the number of terminals is low and allows the use of it. For the larger matrix, TNT and implied weights were also used, but as the number of terminals does not allow the use of an exact algorithm, the “New Technology search” strategy, particularly Sectorial Search and Tree Fusing (see [Goloboff et al., 2008b](#)) was used.

5. Results and discussion

A consensus tree was derived from five equally parsimonious trees (Fig. 3), in which *Sinomastodon*, *Gnathabelodon*, *Eubelodon*, and *Rhynchotherium*, along a clade with the three South American species, form a polytomy, having Gomphotherium as sister group. This differs from the original [Prado and Alberdi \(2008\)](#) result in which *Sinomastodon* and *Gnathabelodon* were successive branches toward the South American taxa. This was due mainly to the erroneous code of characters 0, 5, and 39.

The goal in this contribution was only to correct the errors in character coding, include polymorphism when necessary and use more updated software and weighting strategy, not to actually review the phylogeny. However, this result has a strong influence in the conclusions that the authors drew from the original phylogeny. *Sinomastodon* is not supported as the sister group of the South American gomphotheres, and the biogeographic derivations presented in [Alberdi et al., \(2007\)](#) are invalidated.

The source of most of the original characters were the datasets of [Tassy \(1996\)](#) and [Shoshani \(1996\)](#), which, in turn, were the bases

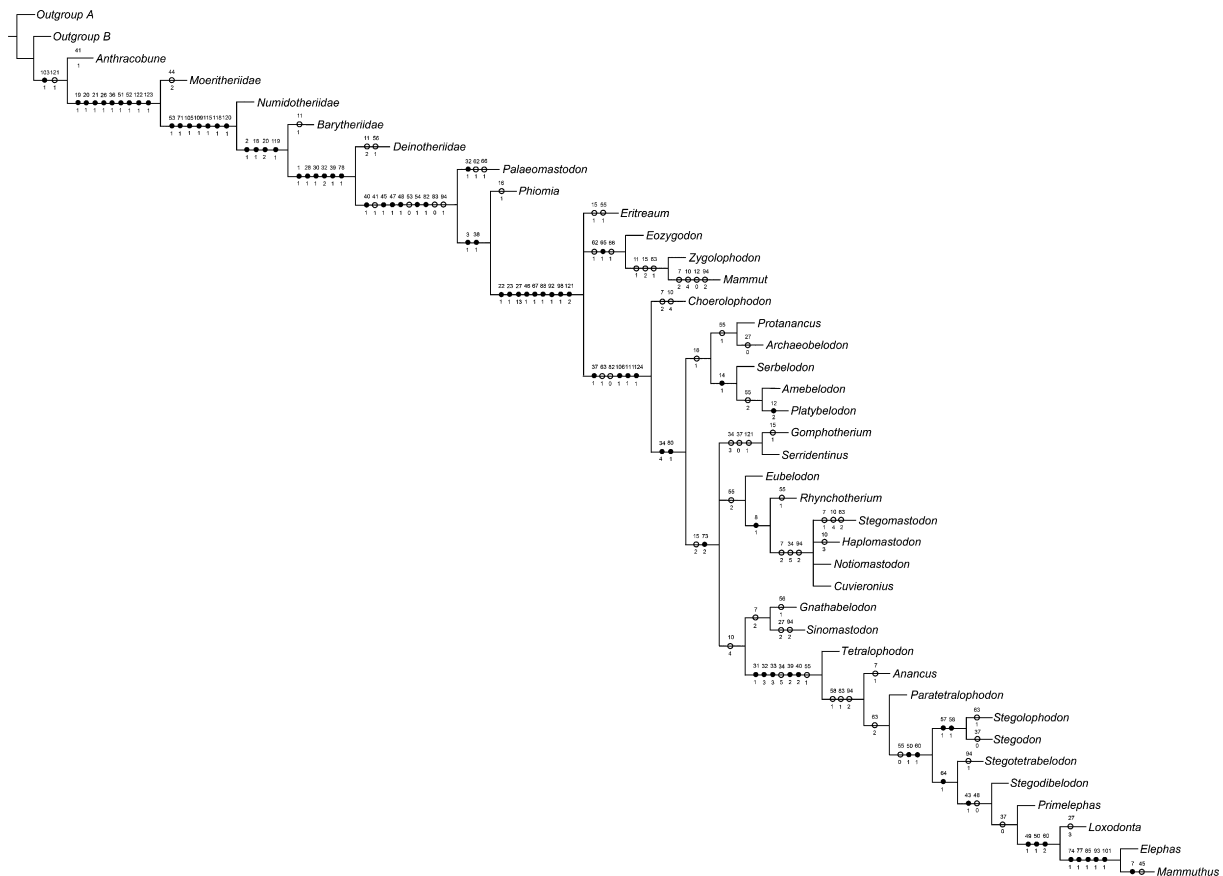


Fig. 4. Resulting tree based on the matrix modified from [Shoshani et al. \(2006\)](#).

for the dataset of Shoshani et al. (2006). This is available as Supporting Appendices at PNAS site (www.pnas.org/content/103/46/17296/suppl/DC1). The matrix was maintained in its original state, keeping the taxa as Shoshani et al., (2006) used them. For example, *Haplomastodon* and *Notiomastodon* were maintained for South American taxa, both sinonimized with “*Stegomastodon*” by Alberdi and Prado (1995). Even so, the results are important for the phylogeny and biogeography proposed by Prado and Alberdi (2008) and Alberdi et al. (2007).

In the resulting phylogeny (Fig. 4), *Sinomastodon* and *Gnathabelodon* are grouped with the Elephantoida Gray 1821, sensu Shoshani et al. (2006), and *Rhynchotherium* appears as the sister group of “*Stegomastodon*” (including *Haplomastodon* and *Notiomastodon*) and *Cuvieronius*, which remains in the Gomphotheriidae. This is particularly important because it makes clear that the position of *Sinomastodon* in the original proposition of Prado and Alberdi (2008) was a consequence of the inadequate taxon sampling. The intention here was only to test, under similar but updated conditions, the proposition made based on a reduced dataset and to correct errors in the original matrix.

6. Conclusion

The phylogeny, taxonomy and diversity of gomphotheres are an issue that needs clarification, and this is especially true for the South American representatives. Prado and Alberdi's (2008) analysis is the first attempt dedicated especially to the last group. Unfortunately, as shown above, this study has methodological and procedural errors that ultimately invalidate its conclusions. Recent propositions, even with relatively small number of terminals (Ferretti, 2010), reach similar conclusions.

Consequently, both the proposed phylogeny and its derived biogeographic analysis should not be considered and a more comprehensive analysis is still waiting. Such a study will help to understand some controversial points such as the time of arrival of gomphotheres to South America, the generic identity of some of the South American species, and the validity of some widely used characters in gomphothere species identification.

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