



## Forum communication

## Reply to: A critical appraisal of the phylogenetic proposals for the South American Gomphotheriidae (Proboscidea: Mammalia) by M.A. Cozzuol, D. Mothé and L.S. Avilla

María Teresa Alberdi<sup>a,\*</sup>, José Luis Prado<sup>b</sup>, Edgardo Ortiz-Jaureguizar<sup>c</sup>, Paula Posadas<sup>c</sup>

<sup>a</sup>Departamento de Paleobiología, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain

<sup>b</sup>INCUAPA, Departamento de Arqueología, Universidad Nacional del Centro, Del Valle 5737, B7400JWI Olavarría, Argentina

<sup>c</sup>LASBE, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque S/N°, B1900FWA La Plata, Argentina

## ARTICLE INFO

## Article history:

Available online 22 August 2011

## ABSTRACT

The objective of this paper is to reply the recent comments on our papers made by Cozzuol et al. (2011) about the phylogeny and biogeography of South American Gomphotheres. We addressed the methodological criticism and concluded that *Sinomastodon* is the sister group of the South American gomphotheres, as we originally proposed, despite the weighting scheme adopted to analyze the data. Therefore, we argue that our conclusions based on this phylogenetic hypothesis on the evolution and biogeography of this group is not properly refuted by Cozzuol et al. (2011).

© 2011 Elsevier Ltd and INQUA. All rights reserved.

Cozzuol et al. (2011) challenge two of our papers about the phylogeny and biogeography of gomphotheres and suggest there are many errors in many points which invalidate our conclusions. Before addressing the core issue we will perform a number of clarifications.

Cozzuol et al. (2011) questioned the systematics of gomphotheres in South America and synthesizes them as follows: "...is confused, and the status of some taxa is still subject to discussion..." This was a vague and poorly founded assertion. We certainly recognize some problems recently suggested by Lucas (2009) in regard to the status of one genus name, "*Haplomastodon*", that we considered as a junior synonym of *Stegomastodon* but this does not mean the systematic was confused. Recently, Lucas (2009) proposed the use of the genus name "*Haplomastodon*", named by Hoffstetter (1950), and characterized by the absence of *foramina transversa* in the atlas. Such a name was assigned as a subgenus of *Stegomastodon*. Also, Lucas (2010) and Pasenko (2010) proposed *Mastodon waringi* as a neotype of the genus "*Haplomastodon*", contradicting Ferretti (2009) who proposed *Mastodon chimborazi* as the neotype. The problem is the diagnostic characters indicated by Hoffstetter (1950, 1952) for "*Haplomastodon*" which are not significant, because they are the same that for the genus *Stegomastodon*, and some of those (e.g., open foramina) are quite variable, as was pointed out by Simpson and Paula Couto (1957). These authors remark that the character of the *foramina transversa* in

the atlas and axis vertebrae is variable in the specimens from the Araxá locality in Brazil, that is it could be either present or absent (Simpson and Paula Couto, 1957, pp. 167–168). The distinguishing characters between these genera vary greatly in respect to the animal's age and are, therefore, not very good; both genera are very similar on the skull shape – elephantoid type –, adult tusks usually straight or slightly curved in the tip; and the mesial part of the maxilla with hemimaxilla straight and in contact (not divergent as in *Cuvieronius*). These authors also looked in detail for the differences between *Stegomastodon* and "*Haplomastodon*", finding that there were really few. Prado et al. (2005), in agreement with Simpson and Paula Couto (1957), considered that the genus "*Haplomastodon*" could not be clearly differentiated from *Stegomastodon*. Alberdi and Prado (1995) accepted the synonymies and species-level nomenclature proposed by Simpson and Paula Couto (1957), but included *waringi* within *Stegomastodon*, considering "*Haplomastodon*" a junior synonym of the former.

Prado and Alberdi (2008) observe that the only differences between both genera ("*Haplomastodon*" and *Stegomastodon*) are found on the morphology of premolar and molar occlusal surfaces, where drawings (trefoils) are more complicated or present more accentuated plications (*pticodonty*) on *Stegomastodon* than in "*Haplomastodon*", and also there are certain angulations on the loph(id)s more accentuated in *Stegomastodon* than in "*Haplomastodon*". The differential characters on both genera are not enough to separate those taxa at the genus level, but as specific. Consequently, Prado et al. (2005) synonymized the genus name "*Haplomastodon*" under the genus *Stegomastodon*, and two species: *Stegomastodon waringi* and

\* Corresponding author. Fax: +34915644740.

E-mail address: [malberdi@mncn.csic.es](mailto:malberdi@mncn.csic.es) (M.T. Alberdi).

*Stegomastodon platensis*. However, it is true that this position is pending now to the decision of International Commission on Zoological Nomenclature (Alberdi et al., 2011).

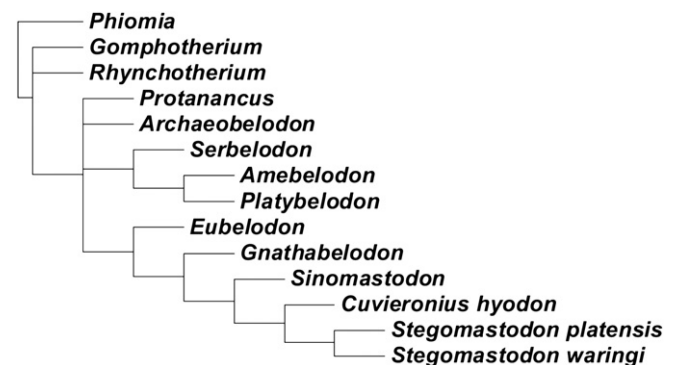
Another point in discussion is the phylogenetic relationships among gomphotheres that have generated a great deal of interest and controversy over the past few years, with various studies testing different character sets and phylogenetic methods (Shoshani, 1996; Tassy, 1996; Prado and Alberdi, 2008; Ferretti, 2010). One of the main problems with the assumed objective methodology is that it depends on the author's previous character selection, which is subjective by its very nature. Another problem emerges from the use of large sets of discrete, atomized characters without functional and structural considerations.

Cozzuol et al. (2011) criticize our recent hypothesis that *Sinomastodon* is a sister group of South American Gomphotheres on methodological grounds, including use of a biased taxon selection and differences in the coding of characters. One criticism referred to the taxon sampling. They say "...the reduction of the number of taxa may force the formation of artificial groups by transforming homoplastic characters into synapomorphies..." However, if it is true that including all or most constituent taxa and large set of characters in analyses attempting to resolve relationships among higher taxa is desirable, it may result impractical. This is especially problematic when the characters are coded from general descriptions and photographs instead of from the original material, as in the case of several analyses. Prado and Alberdi (2008) selected 13 terminals plus outgroup, and 43 characters. Some of these are either identical to, or modified from, those used by Tassy (1996) and Shoshani (1996), but were coded specifically for this analysis. Indeed, after the publication of our analysis, Ferretti (2010) published another analysis about gomphotheres phylogeny that used 11 terminal taxa only (a selection of species in 9 genera but not the total species in the genera) and 25 characters to evaluate the relationships. The analysis of Ferretti (2010) support the hypothesis that *Rhynchotherium* is the sister group of South American gomphotheres; this hypothesis does not agree with those of Prado and Alberdi (2008), who propose that *Sinomastodon* is the sister group of the South American gomphotheres. We believe that both are a more realistic solution than that obtained by Shoshani (1996) and Tassy (1996) using a large sample of taxa and a larger set of characters that do not resolve the node of trilophodon gomphotheres. Ferretti (2010) is right, there is a typo in the data matrix of Prado and Alberdi (2008) in character number 5. Both genera, *Gnathabelodon* and *Eubelodon* possess tuskless mandibles. Accordingly, we have corrected the original data matrix of Prado and Alberdi (2008) and reanalyze the data (see below). *Eubelodon* is a rare genus known from a skull with mandible and associated skeletal elements of *Eubelodon morrilli* (type specie of the genus described by Barbour, 1914) deposited in the University Nebraska State Museum under collection number 1416. This specimen is characterized by the absence of lower tusks with the mandibular symphysis elongated and highly tapered (Barbour, 1914). *Gnathabelodon* have a spoon-shaped symphysis with absence of lower tusk. The type species of the genus is *Gnathabelodon thorpei* described by Barbour and Sternberg (1935); there is a complete skull at Sternberg Museum of Natural History (Kansas).

*Phiomia* is not an outgroup as far from gomphotheres, as could be seen in Fig. 4 of Cozzuol et al. (2011). It also presents bunodont molars allowing better definition of the characters of the molars to the ingroup defined by Prado and Alberdi (2008). For instance, *Mammuth* is phylogenetically closer but the specializations of the molars complicate the definition of the characters. Prado and Alberdi (2008) follow *Phiomia major* described by Sanders et al. (2004) for definition of characters. For the rest of taxa Prado and Alberdi (2008) used the following species: for genus *Gomphotherium* they used *Gomphotherium angustidens*; for genus

*Rhynchotherium* they used *Rhynchotherium tascalae*; for genus *Protanancus* they used *Protanancus macinnesi*; for genus *Archaeobelodon* they used *Archaeobelodon filholi*; for genus *Serbelodon* they used *Serbelodon barbourensis*; for genus *Amebelodon* they used *Amebelodon fricki*; for genus *Platybelodon* they used *Platybelodon davoni*; for genus *Eubelodon* they used *E. morrilli*; for genus *Gnathabelodon* they used *G. thorpei*; and for character of genus *Sinomastodon* they follow Tobien et al. (1986), which considered *Sinomastodon intermedius* as type species.

Cozzuol et al. (2011) considered that the program Hennig86 (Farris, 1988) is outdated. However, being an exact search, the results are similar to those obtained using more recent software like TNT (Goloboff et al., 2008) with the same type of search except the fact that TNT allows collapsing unsupported branches during or after the search. The set of trees obtained Prado and Alberdi (2008) was run to an iterative process of characters weighting with hindsight (successive weighting) that finally allowed to choose a single topology for one of those included in the set of equally parsimonious cladograms obtained under equal weights. Thus, the object of the application of successive weights was only a strategy to select one of the equally parsimonious hypotheses obtained under equal weights. This error concept is common in people who only use the program without knowing in detail the method and its many options. For example, Cozzuol et al. (2011) modify the matrix proposed by Prado and Alberdi (2008) and analyzed it with TNT using an implied weights option different than that chosen by Prado and Alberdi (2008). One of the major discussions about the use of implied weights involves the choice of the value of K, since results may vary if this value is changed. Cozzuol et al. (2011) do not specify the value of K they selected, and they do not justify a choice. We have reanalyzed the data matrix of Cozzuol et al. (2011) with TNT, and we found that the results shown by these authors are those corresponding to  $K = 3$ , i.e., the default option in the software. The use of  $K = 3$  resulted in five trees with same fit, but whose strict consensus results in one hypothesis with much lower resolution than that obtained by Prado and Alberdi (2008). Moreover, analysis of the matrix proposed by Cozzuol et al. (2011) with other values of K give different results to those presented by these authors. For example, with  $K = 1$  we obtained six trees, and with  $K = 6$  we obtained four trees. The strict consensus are shown in Figs. 1 and 2, and both have better resolution than those obtained with  $K = 3$ . Also, not any of the consensus tree obtained for the three tested values of K is inconsistent with the hypothesis that *Sinomastodon* is the sister group of *Cuvieronius* + *Stegomastodon*. In fact, this hypothesis is explicit in the strict consensus tree obtained for the analysis with  $K = 1$ , that also is the most resolved one. On the other



**Fig. 1.** Strict consensus tree of six cladograms obtained from the data matrix of Cozzuol et al. (2011) applying implied weights with  $K = 1$ . Search was carried out with TNT. The topology of this tree is equal to the one obtained from the strict consensus of the ten cladograms obtained applying successive weighting to the data matrix corrected from Prado and Alberdi (2008).

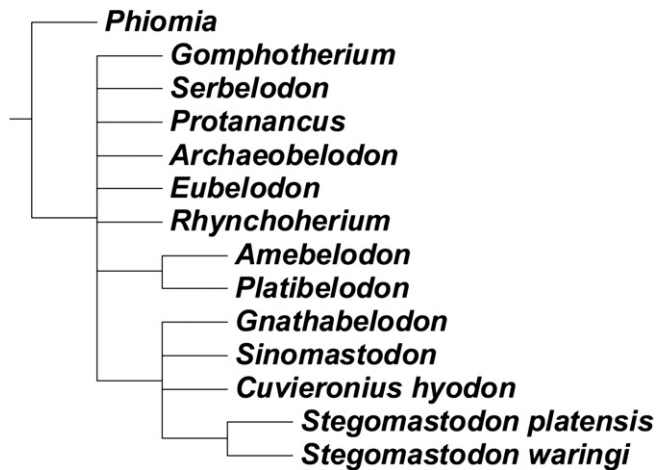


Fig. 2. Strict consensus tree of four cladograms obtained from the data matrix of Cozzuol et al. (2011) applying implied weights with  $K = 6$ . Search was carried out with TNT.

hand, we reanalyzed the data matrix after corrected the typos aforementioned (Character 5 in *Eubelodon* from state 0 to 2 and in *Gnathabelodon* from 1 to 2 at Prado and Alberdi, 2008), using and exact search algorithm under equal weights both in TNT and Hennig86, and obtain the same results with both software (52 equally parsimonious trees  $L = 71$ ;  $CI = 78$ ;  $RI = 70$ ). The strict consensus tree is showed on Fig. 3. One of the most parsimonious trees obtained correspond to that published by Prado and Alberdi (2008) which is the one used for biogeographical analysis applying DIVA in Alberdi et al. (2007). In sum, the strict consensus tree obtained for the implied weights option in analysis of the matrix proposed by Cozzuol et al. (2011) with  $K = 1$ ,  $K = 3$  and  $K = 6$  are consistent with the phylogenetic hypothesis proposed by Prado and Alberdi (2008). Cozzuol et al. (2011) only apply the default option in the software to implied weights ( $K = 3$ ) that in this case produces the less resolved consensus tree. The analysis that obtained the most resolved consensus tree is when we use value of  $K = 1$  (Fig. 1). This consensus tree maintains the relationship as following (*Gnathabelodon* (*Sinomastodon* (*Cuvieronius* (*S. waringi*, *S. platensis*))))). Finally, the analysis of the matrix of Prado and Alberdi (2008) with modifications resulted in a set of equally parsimonious cladograms that included the hypothesis published by these authors in the original work. Also, the application of successive weights to this set of trees

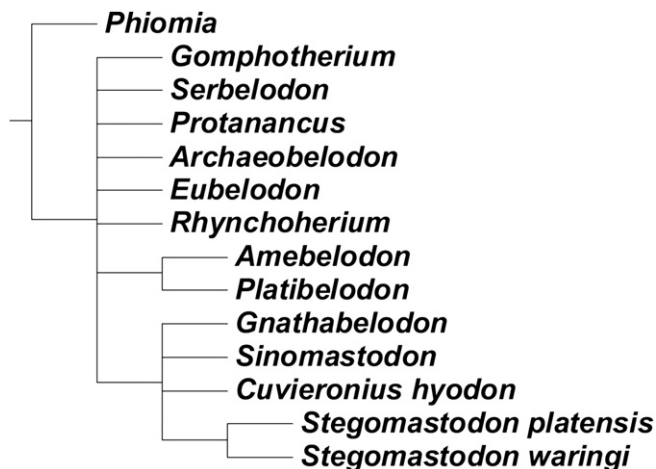


Fig. 3. Strict consensus tree of 52 cladograms obtained from the data matrix corrected from Prado and Alberdi (2008) under equal weights. Search was carried out with TNT.

produces a set of ten trees ( $L = 71$ ) which strict consensus coincided with the obtained from the analysis under  $K = 1$  in the matrix published by Cozzuol et al. (2011, Fig. 1), in which the relationships of *Sinomastodon* and *Gnathabelodon* with respect to South American gomphotheres is the same that Prado and Alberdi (2008) proposed and therefore the same that Alberdi et al. (2007) used for paleobiogeographic analysis.

## References

- Alberdi, M.T., Prado, J.L., 1995. Los mastodontes de América del Sur. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), *Evolución biológica y climática de la Región Pampeana durante los últimos 5 millones de años. Un ensayo de correlación con el Mediterráneo occidental*, vol. 12. Monografías Museo Nacional de Ciencias Naturales, CSIC, España, pp. 277–292.
- Alberdi, M.T., Prado, J.L., Ortiz-Jaureguizar, E., Posadas, P., Donato, M.H., 2007. Historical biogeography of trilophodont gomphotheres (Mammalia, Proboscidea) reconstructed applying Dispersion–Vicariance Analysis. *Cuadernos del Museo Geominero*, n° 8. In: Díaz-Martínez, E.I., Rábano, I. (Eds.), 4th European Meeting on the Palaeontology and Stratigraphy of Latin America. Instituto Geológico y Minero de España, Madrid, pp. 9–14.
- Alberdi, M.T., Prado, J.L., Corona, E.M., Prado, J.L., Polaco, O.J., 2011. Comments on the proposed conservation of usage of *Mastodon waringi* Holland, 1920 (currently *Haplomastodon waringi*; Mammalia, Proboscidea) by designation of a neotype. *Bulletin of Zoological Nomenclature* 68 (1), 80–81.
- Barbour, E.H., 1914. *Mammalian Fossils from Devil's Gulch*, vol. 4. Nebraska Geological Survey, pp. 177–190.
- Barbour, E.H., Sternberg, G., 1935. *Gnathabelodon thorpei*, gen. et sp. nov. A New Mud-grubbing Mastodon. *Bulletin of the Nebraska State Museum* 42, 395–404.
- Cozzuol, M.A., Mothé, D., Avilla, L.S., 2011. A critical appraisal of the phylogenetic proposals for the South American Gomphotheriidae (Proboscidea: Mammalia). *Quaternary International*. doi:10.1016/j.quaint.2011.01.038.
- Farris, J.S., 1988. Hennig86 reference, version 1.5 Port Jefferson, New York, (Published by the author).
- Ferretti, M.P., 2009. Comment on the proposal conservation of usage of *Mastodon waringi* Holland, 1920 (currently *Haplomastodon waringi*; Mammalia, Proboscidea) by designation of a neotype (Case 3480; see BZN 66: 164–167). *Bulletin of Zoological Nomenclature* 66 (4), 358–359.
- Ferretti, M.P., 2010. Anatomy of *Haplomastodon chimborazi* (Mammalia, Proboscidea) from the late Pleistocene of Ecuador and its bearing on the phylogeny and systematic of South American gomphotheres. *Geodiversitas* 32 (4), 663–721.
- Goloboff, P., Farris, S., Nixon, K., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Hoffstetter, R., 1950. Observaciones sobre los mastodontes de Sud América y especialmente del Ecuador. *Haplomastodon subgen. nov. de Stegomastodon*, 1. Publicaciones Escuela Politécnica Nacional, pp. 1–39.
- Hoffstetter, R., 1952. Les mammifères Pléistocènes de la République de l'Équateur. *Mémoires de la Société Géologique de France, Nouvelle Série* 31, 1–391.
- Lucas, S.P., 2009. Case 3480 *Mastodon waringi* Holland, 1920 (currently *Haplomastodon waringi*; Mammalia, Proboscidea): proposed conservation of usage by designation of a neotype. *Bulletin of Zoological Nomenclature* 66 (2), 164–167.
- Lucas, S.P., 2010. Comment on the proposed conservation of usage of *Mastodon waringi* Holland, 1920 (currently *Haplomastodon waringi*; Mammalia, Proboscidea) by designation of a neotype (Case 3480; see BZN 66: 164–167, 358–359; 67: 96). *Bulletin of Zoological Nomenclature* 67 (2), 181–182.
- Pasenko, M.R., 2010. Comment on the proposed conservation of usage of *Mastodon waringi* Holland, 1920 (currently *Haplomastodon waringi*; Mammalia, Proboscidea) by designation of a neotype (Case 3480; see BZN 66: 164–167, 358–359). *Bulletin of Zoological Nomenclature* 67 (1), 96.
- Prado, J.L., Alberdi, M.T., 2008. A cladistic analysis among trilophodont gomphotheres (Mammalia, Proboscidea) with special attention to the South American genera. *Palaeontology* 51, 903–915.
- Prado, J.L., Alberdi, M.T., Azanza, B., Sánchez, B., Frassinetti, D., 2005. The Pleistocene Gomphotheriidae (Proboscidea) from South America. *Quaternary International* 126–128, 21–30.
- Sanders, W.J., Kappelman, J., Rasmussen, D.T., 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica* 49 (3), 365–392.
- Shoshani, J., 1996. Para- or monophyly of the gomphotheres and their position within Proboscidea. In: Shoshani, J., Tassy, P. (Eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and their Relatives*. Oxford University Press, Oxford, New York, Tokyo, pp. 149–177.
- Simpson, G.G., Paula Couto, C., 1957. The mastodons of Brazil. *Bulletin of the American Museum of Natural History* 112, 125–190.
- Tassy, P., 1996. Who is who among the Proboscidea? In: Shoshani, J., Tassy, P. (Eds.), *The Proboscidea. Evolution and Palaeoecology of Elephants and their Relatives*. Oxford University Press, Oxford, New York, pp. 39–48.
- Tobien, H., Chen, G.F., Li, Y.Q., 1986. Mastodonts (Proboscidea, Mammalia) from the late Neogene and early Pleistocene of the People's Republic of China. Part 1. Historical account: the genera *Gomphotherium*, *Choerolophodon*, *Synconolophus*, *Amebelodon*, *Platybelodon*, *Sinomastodon*. *Mainzer Geowissenschaftliche Mitteilungen* 15, 119–181.