



Contents lists available at SciVerse ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Extinction of a gomphothere population from Southeastern Brazil: Taphonomic, paleoecological and chronological remarks

Leonardo dos Santos Avilla^{a,*}, Ana Maria Graciano Figueiredo^b, Angela Kinoshita^c,
Cristina Bertoni-Machado^d, Dimila Mothé^e, Lidiane Asevedo^a, Oswaldo Baffa^f, Victor Hugo Dominato^g

^a Laboratório de Mastozoologia, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Estado do Rio de Janeiro, Avenida Pasteur 458, sala 501, Rio de Janeiro, RJ 22290-240, Brazil

^b Comissão Nacional de Energia Nuclear, Instituto de Pesquisas Energéticas e Nucleares, Avenida Professor Lineu Prestes 2242, Caixa Postal 11049, Pinheiros, São Paulo, SP 05508-900, Brazil

^c Universidade do Sagrado Coração, PRPPG – Biologia Oral, Rua Irmã Armanda 10-50, Campus Universitário, Bauru, SP 17011-160, Brazil

^d Instituto de Geociências, Universidade Federal da Bahia, Rua Barão de Jeremoabo s/n, Campus Universitário de Ondina, Salvador, Bahia 40170-020, Brazil

^e Programa de Pós Graduação em Zoologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, Rio de Janeiro, RJ 20940-040, Brazil

^f Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Departamento de Física, Avenida Bandeirantes, 3900, Monte Alegre, Ribeirão Preto, SP 14040-901, Brazil

^g Programa de Pós Graduação em Geologia, Universidade Federal do Rio de Janeiro, Avenida Athos da Silveira Ramos, 274, Ilha do Fundão, Rio de Janeiro, RJ 21949-900, Brazil

ARTICLE INFO

Article history:

Available online xxx

ABSTRACT

During the Quaternary in South America, the gomphotheres were one of the most common elements in the mammal megafauna. They went extinct in an evolutionary event known as the Late-Pleistocene Megafaunal Extinction, of which climate changes and human hunting are commonly claimed as the main possible causes. Most of the Brazilian Pleistocene fossil mammals did not preserve collagen, so alternative dating techniques are needed. In this case, the only option for dating such fossils is via Electron Spin Resonance (ESR) dating. The aim of this paper is (i) to place the Quaternary Águas de Araxá's *Notiomastodon platensis* population in a chronological context through ESR dating and, (ii) to investigate its paleoenvironmental context and extinction causes. The ESR analysis was made on both crushed tooth enamel and sediment from the study area. They were subjected to Neutron Activation Analysis to determine the concentration of U, Th and K. The ESR dating indicated an age somewhere between 60,000 and 55,000 a for this *N. platensis* population (Lujanian, the last age of the Late Pleistocene South American Land Mammal Ages – SALMA). The date found for these gomphotheres is included in the Middle Pleniglacial, which is characterized by a cold and arid climate. Previous paleodiet studies suggest that the feeding habits of those individuals were basically opportunistic/generalist herbivores (C_3 grasses and woody plants). Taphonomically, it was observed that the gomphotheres carcasses were transported by a high-energy water stream, typical of fluvial systems, and that the large amount of individuals in the fossil record is due to a mass death event related to a dry period. Based on taphonomical, paleoecological and chronological evidence, it is possible to assume that the gomphothere population from the Quaternary of Águas de Araxá is probably an example of individuals that suffered from climate changes during the Late Pleistocene in South America.

© 2012 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

During the Quaternary, the proboscideans were one of the most common element of the American megafauna. They probably

migrated to South America after the uplift of the Isthmus of Panama, during the biogeographic event called the Great American Biotic Interchange (GABI; Webb, 1991). During the Pleistocene, the South American gomphotheres were represented by the genera *Cuvieronius* and *Notiomastodon*, and only *Notiomastodon platensis* is present in the Brazilian fossil record (Gadens-Marcon, 2008; Mothé et al., 2011).

The South American proboscideans went extinct in an evolutionary event known as the Late-Pleistocene Megafaunal Extinction (Ferretti, 2008). The causes for this extinction event are still

* Corresponding author.

E-mail addresses: mastozoologiaunirio@yahoo.com.br (L.dosS. Avilla), anamaria@ipen.br (A.M. Graciano Figueiredo), angelamitie@gmail.com (A. Kinoshita), cristina.bertoni@gmail.com (C. Bertoni-Machado), dimothe@hotmail.com (D. Mothé), baffa@usp.br (O. Baffa), victordominato@gmail.com (V.H. Dominato).

unknown, but climate changes and human hunting have been commonly claimed as the main plausible hypotheses (Ficcarelli et al., 2003; Barnosky et al., 2004).

Gomphotheres fossils have been found in almost all Brazilian states, but the Quaternary of Águas de Araxá (QAA) outcrop is noted for its great abundance of dental and postcranial fossils of *N. platensis* (Simpson and Paula Couto, 1957; Mothé et al., 2010). Previous studies suggested that the gomphothere remains from the QAA outcrop represents a single *N. platensis* population (Simpson and Paula Couto, 1957; Mothé et al., 2010). These papers are the basis for several other studies that investigated aspects of the taphonomy and paleoecology of South American gomphotheres (e.g. Dominato et al., 2009; Avilla et al., 2010; Asevedo et al., 2010; Dominato et al., 2011; Asevedo et al., 2012). However, all those studies lack dating information.

Geochronological studies are rare in Brazil, particularly those involving Pleistocene Megafauna (Baffa et al., 2000; Lopes et al., 2010). Only a few studies based on Electron Spin Resonance (ESR) dating included southeastern Brazilian mammalian fossils [Toxodon] (Baffa et al., 2000; Lopes et al., 2010). However, since collagen is not preserved in most of the Brazilian Pleistocene mammals, dating techniques such as ESR are very effective and sometimes the only option available for dating these fossils. ESR dating can be applied in a wide interval of geologic time, extending from hundreds to millions of years (Skinner, 2000, 2006; Grün, 2006) but this method can be even more significant in the time range between 40,000 and 200,000 a, by filling up the gaps of the two most used dating techniques, ^{14}C and $^{40}\text{Ar}/^{39}\text{Ar}$ (Rink, 1997). ESR dating proved to be very efficient in archeological and paleontological studies because only small quantities of material are necessary in this procedure, and it is possible to use this technique on samples that do not have sufficient collagen for ^{14}C dating (Kinoshita and Baffa, 2005; Lopes et al., 2010).

The aim of this study is to place the QAA gomphothere population in a chronological context using ESR dating. Furthermore, based on previous paleoecological and taphonomic studies (e.g. Dominato et al., 2009; Asevedo et al., 2010; Avilla et al., 2010; Dominato et al., 2011; Asevedo et al., 2012), inferences are made about the paleoenvironment and the cause of extinction of the *N. platensis* population from the QAA.

2. Geological setting

The QAA fossiliferous assemblage was discovered in 1944 during the construction of a resort hotel at the locality of Águas de Araxá ($19^{\circ}38'45.77''\text{S}$; $46^{\circ}56'59.99''\text{W}$), in Minas Gerais State, South-eastern Brazil (Fig. 1). The resort hotel was constructed over the outcrop in which the gomphotheres remains were discovered. The fossils were found in a cavity and they were probably deposited there by a Pleistocene stream (Price, 1944; Simpson and Paula Couto, 1957). This stream runs on a large mass of metamorphic rock, common in the outcrop area (Price, 1944). The cavity is 6 m long, 4 m wide, and 1.2 m deep (Simpson and Paula Couto, 1957). The fossiliferous deposit was irregular, consisting of a confluent series of rounded and polished depressions produced by fluvial abrasion. The cavity is filled by clay, sand, pebbles and bioclastic conglomerate (Price, 1944) and displays a typical cut-and-fill structure. The best-preserved bone and tooth remains were found at the bottom of the deposit, and the most abundant fragmentary fossils were found at the top, near the surface of the deposit, associated with finer sediments (Simpson and Paula Couto, 1957) (Fig. 2).

The uppermost layer is composed of well-rounded pebbles (some are small) and by various waterworn bone fragments



Fig. 1. Location map of the Quaternary Águas de Araxá (QAA) outcrop.

cemented by iron oxide, forming a hard cover that sealed and preserved the deposit (Price, 1944). There were no bones associated with the same individual, except for radius and ulna (Simpson and Paula Couto, 1957).



Fig. 2. Original image of fossil remains from QAA site, made by Simpson and Paula-Couto in the 1950s, which is the only known outcrop overview.

3. Methodology

The QAA *N. platensis* had been previously recognized as a single population (Simpson and Paula Couto, 1957; Mothé et al., 2010) and its age was established by dating a single tooth (DGM104-M) and its associated sediment, representing the dating for the entire population. This *N. platensis* tooth is currently housed at the paleontological collection of Departamento Nacional de Produção Mineral, Rio de Janeiro State, Brazil. The dating analysis was performed by the Physics Department at the Universidade de São Paulo (FFCLRP-USP). An enamel sample was removed from the tooth and separated from the dentine using the thermal expansion technique. Due to the differences in the thermal expansion coefficient between both tissues, the enamel was eventually detached from the dentine after repeating the procedure a few times. The remaining dentine was mechanically removed with low-rotation diamond drills. The enamel was then subject to chemical etching in an acid solution (HCl 1:5).

The thickness of the enamel before treatment was about 4.6 cm, and 4.0 cm afterwards. Once dry, the enamel was manually ground in an agate mortar until a powder ($\varphi < 0.5$ mm) was formed. The dentine and associated sediment were also crushed. The sediment was then sampled in 3 parts, and along with the enamel and dentine, and subjected to Neutron Activation Analysis (NAA) at the IPEN (Instituto de Pesquisas Energéticas e Nucleares), to determine the concentrations of U, Th, and K.

The spectrum of powdered enamel was recorded in a X-Band ESR spectrometer (JEOL FA-200) and compared with a sample of bovine enamel, previously irradiated with a known dose (150 Gy) for prior assessment of the cumulative dose (D_e). Subsequently, 10 aliquots of about 70 mg were selected and then irradiated with doses ranging from 0 to 7 kGy.

After registering the spectrum of all the aliquots, the intensity peak-to-peak of signal dosimetric at g_{\perp} was associated with the added dose for posterior construction of the dose–response curve. The experimental data points were fitted using the following equation (Ikeya, 1993):

$$I = I_0 \left\{ 1 - e^{-\left[\frac{(D + D_e)}{D_0} \right]} \right\} \quad (1)$$

The conversion of the D_e s to ages was made using ROSY software (Brennan et al., 1999), which calculates the ages through the rates of internal and external doses given by the radioisotope concentrations and cosmic rays. The rate of 240 μ Gy/year was used, after correcting for the appropriate latitude and longitude (19°38'45.77"S; 46°56'59.99"W) and altitude (997 m), as proposed by Prescott and Hutton (1994).

4. Results and discussion

Fig. 3 shows the initial ESR spectrum of enamel, without the additive dose. The signal of a main radical produced by ionizing radiation in hydroxyapatite (CO_2) with the spectral features $g_{\perp} = 2.0025$ and $g_{\parallel} = 1.9973$ can be observed, as well as the radical Isopropyl (*) and the 3rd and 4th lines of Mn^{2+} (#) marker, used to calibrate the magnetic field. Fig. 4 shows the dose response curve and the D_e found of $7 (\pm 0.4) \cdot 10^2$ Gy. Table 1 shows the concentration of U, Th and K in the sediment, enamel and dentine obtained by NAA; whereas Table 2 exhibits the age results according to the U-uptake model. Although the results are similar, the result given by the Combination Uptake model, defined as Linear uptake for

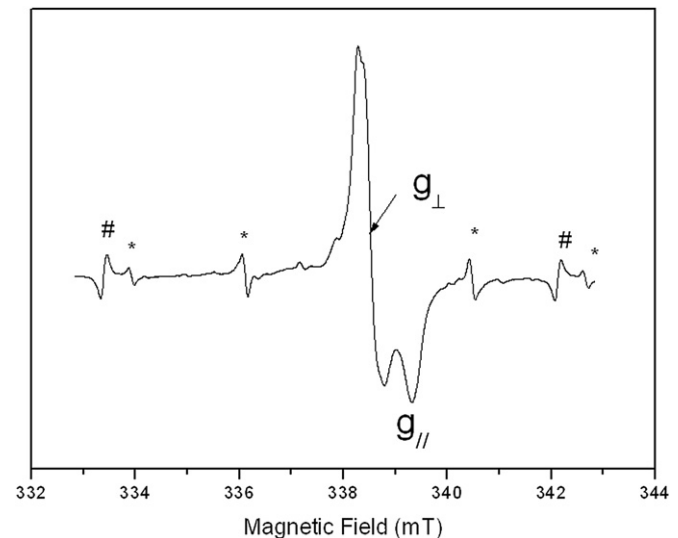


Fig. 3. ESR spectrum of enamel without additive doses showing the components of CO_2 (g_{\perp} and g_{\parallel}), the Isopropyl radical (*) and the 3rd and 4th Mn^{2+} marker.

enamel and Early uptake for dentine, was the adopted value as the age of the tooth, considering that dentine is porous while enamel is more compact. The data show low dispersion and a good fitting of the exponential curve.

Table 1
Radioisotopes concentration assessed by Neutron Activation Analysis.

Sample	U (ppm)	Th (ppm)	K (ppm)
Enamel	6.4 ± 0.9	0.30 ± 0.05	<750
Dentine	240 ± 35	0.37 ± 0.06	<750
Soil sample 1	36 ± 5	135 ± 22	<750
Soil sample 2	32 ± 2	154 ± 7	<750
Soil sample 3	29 ± 2	139 ± 6	<750

Table 2
Age results according to Uranium uptake model.

Model	Age (ka)
Early Uptake (EU)	58 ± 4
Linear Uptake (LU)	66 ± 5
Combination Uptake (CU)	64 ± 5

The ESR dating of the tooth of the QAA outcrop indicates that the age of this *N. platensis* population falls in the interval between 60,000 and 55,000 a. This interval of time is part of the Lujanian (120,000–8500 a) (Cione and Tonni, 1995, 1999). The date found for the QAA gomphotheres is included in the glacial age called Middle Pleniglacial, ranging from 65,000–26,000 a, characterized by a cold and arid environment until 50,000 a (Ledru, 1993; Ledru et al., 1996). Previous studies suggest that, afterwards, a gradual increase in the environmental humidity occurred (between 45,000 and 33,000 a), which is also inferred by the increase in semi-deciduous tree taxa (*Alchornea*, *Casearia*, *Celtis*, *Gallesia*, *Melastomataceae*, *Miconia-type*, *Mimosaceae*). Thereafter, and over the past 17,000 y, a rapid succession of climate changes started as reflected by different forest categories (Ledru, 1993; Ledru et al., 1996). These changes in climate were also evidenced by analyses of a complete palynological sequence at the Salitre locality (19°S46°46'W, and altitude of 980 m), near Araxá (19°S46°56'W) (Ledru, 1993; Ledru et al., 1996). Additionally, Asevedo et al. (2012) recovered information about the latest meals of adult

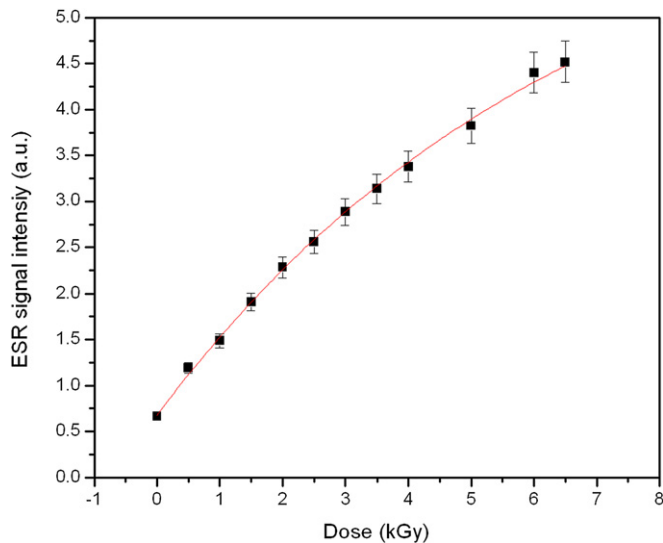


Fig. 4. Dose Response Curve. The experimental data points were fitted by Equation (1) using instrumental weighing.

gomphotheres from the QAA population through both tooth enamel microwear analysis and plant microfossils preserved in tooth calculus. They concluded that the diet of those individuals was basically composed of C_3 grasses and woody plants. Fragments of conifer tracheids and secondary xylem corroborate with the suggestion of a woody plants-based diet. Pollen grains (Polygonaceae) and spores (Polypodiaceae) could be associated with secondary elements ingested by chance (Asevedo et al., 2012). The botanical groups of C_3 grasses, conifers and Polygonaceae dicots are primarily found in temperate zones, and the Polygonaceae family of polypod ferns is mostly distributed throughout tropical humid environments, but it also occurs in temperate climates. Plant remains preserved in teeth calculi of *N. platensis* were represented by fibrous (hard to assimilate) parts (Asevedo et al., 2012), a low-quality food. Hence, since those gomphotheres had a low-nutritious diet, they would potentially feed on a great amount of food. Similar behavior can be observed in the feeding habits of extant proboscideans that ingest different types of vegetation according to the climatic season (see Sukumar, 1990; Stokke and du Toit, 2000; Tchamba and Seme, 2008; Short, 2009). Consequently, the gomphotheres' diet might be based on the availability of plants in their habitats, so they may be considered as opportunistic/generalist herbivorous regarding their feeding habits. The climate in the QAA region was possibly cold and dry, since groups of plants that are typical of temperate environments were abundant in the area. This assumption reinforces previous palynological studies done in samples from the region, dated around 60,000–55,000 a (Ledru, 1993; Ledru et al., 1996).

Mothé et al. (2010) estimated that about 40 individuals comprised the gomphothere population of the QAA. Living proboscideans (*Loxodonta* and *Elephas*) are commonly found in small family groups of no more than six or eight individuals. However, when this population experiences severe environmental conditions, such as a colder/warmer or drier climate than they accustomed to, or when food and water are scarce, they can gather in herds of more than 50 individuals (Haynes, 1991). Dominato et al. (2011) and Mothé et al. (2010) suggested that *N. platensis* would have a similar survival strategy. Consequently, one explanation for the great number of individuals of the *N. platensis* population from the QAA outcrop is that they were perhaps facing a severe climate or scarcity of resources during 60,000–55,000 a. For example, if modern populations of proboscideans suffer with lack of water,

then a large amount of individuals (sometimes more than a hundred), migrate together and gather around water resources (Haynes, 1988, 1991).

Price (1944) and Dominato et al. (2011) suggested that these animals had been transported by a large stream, which is demonstrated by the fact that these fossils are poorly selected and by the presence of a variety of bony elements with different densities (long bones, vertebrae, ribs, teeth, jaw fragments, basin debris and others) in the same deposit. The absence of preserved skulls may be related to their destruction by weathering, trampling or other processes. The final agent of transportation was a high-energy fluvial system and the fossils underwent brief transport (Dominato et al., 2011).

According to Simpson and Paula Couto (1957) and Mothé et al. (2010), the QAA gomphothere fossil bones can be assigned to a mass death event related to a dry period, together with scarcity of water and food resources. Firstly, the QAA gomphothere deposit holds characteristics of a catastrophic event, where individuals of all age classes were found together (Mothé et al., 2010). Secondly, this hypothesis of a death population related to a severe climate exposure is supported by estimations of the environmental conditions around Águas de Araxá during the Late Pleistocene, based on palynological analysis conducted by Ledru et al. (1996). According to the authors, a glacial maximum, characterized by extremely cold and dry environmental conditions, probably occurred around 60,000–50,000 a. Thirdly, the study of the organic composition of the latest meal of the gomphothere individuals from the QAA shows a low-nutritious diet (Asevedo et al., 2012), which can be related with the scarcity of resources at the glacial maximum around 60,000–50,000 a. Therefore, the extinction of the QAA gomphotheres was probably related to a catastrophic regional event, related to an extreme cold and dry climate associated with shortage of water and food resources.

The gomphotheres, together with some northern hemisphere immigrants (all of the species of horses, most of the camelids, some cervids, amongst others) and most of the South American native mammals, became extinct at the end of the Late Pleistocene (Ficcarelli et al., 1997; Alberdi et al., 2002). There are several possible explanations for this extinction event. However, the two most plausible hypotheses are (i) human overhunting (Martin, 1984; Whittington and Dyke, 1984; Alroy, 2001) and (ii) climate changes (Graham and Lundelius, 1984; King and Saunders, 1984; Sánchez et al., 2003; Vivo and Carmignotto, 2004). The literature brings good arguments in defense of both hypotheses (Barnosky, 1989; Cione et al., 2003; Barnosky et al., 2004), but this debate still stands. Nonetheless, all hypotheses for the extinction of South American Megafauna share the assumption that the extinction was a single event, and it occurred at around 11,000 a, near the Pleistocene/Holocene boundary. However, the extinction hypotheses suggested by Ficcarelli et al. (1997) and Cione et al. (2003) argue that no massive extinction was observed in large mammals through the Pleistocene Glaciations in South America.

The death event of the QAA gomphotheres at about 60,000–55,000 a disputes the argument that the extinction of South American Megafauna occurred at 11,000 a. The extinction of the QAA gomphotheres is an independent event and brings a new horizon to understand the mammalian megafaunal loss during the Late Pleistocene in South America. Perhaps there had been several prior extinctions during the Lujanian, and not only a single event at its end. Ficcarelli et al. (1997) suggest that the climatic changes during the Lujanian affected the distribution of foraging and arid areas in South America, which may have impacted the survival of gomphothere populations, which disappeared in a mosaic way. They were probably forced to concentrate in restricted areas where water and foraging resources remained sufficient and, as result, the

increase in selective pressure may have given rise to delays in sexual maturity and decrease in fertility, which has been observed in living elephant herds confined within restricted areas (Haynes, 1991). These aspects were also observed in the *N. platensis* population from QAA, such as a declining population profile, with rare presence of immature and young individuals (Mothé et al., 2010), low-nutritious diet of adults (Asevedo et al., 2012), and a death event close to water resources. Two explanations are suggested for the absence of juvenile individuals: 1) predation or scavenging (Dominato et al., 2011); and, 2) destruction by transportation or other taphonomic processes that preferentially destroy the smaller individuals because young skeletal elements are more fragile than those of adults.

The gomphothere population from Araxá probably is an example of individuals that were suffering with the climate changes during the Late Pleistocene. This is demonstrated by the declining age profile of their individuals (Mothé et al., 2010), which became extinct before the Pleistocene/Holocene transition.

Uncertainty exists in accepting the extinction of megafauna during the Pleistocene/Holocene transition based on Brazilian records, because, until now, only a few fossils and deposits were dated. In this manner, a very detailed dating program for the Quaternary mammalian fossils is critical for Brazil and for some other South American bearing fossil sites, such as the ones in the northern and Andean regions of the continent.

5. Conclusions

These taphocoenoses has a peculiar origin. The QAA gomphotheres were a result of a death mass event which happened before the extinction of the megamammals in the Pleistocene/Holocene transition. This is a regional event related to scarcity of water and food resources during the Middle Plenigalcial interval, ranging from 65,000 to 26,000 a, characterized by a cold and arid environment until 50,000 a. The gomphothere population has an age between 60,000 and 55,000 a, which coincides with that interval. The population size is related to a survival strategy, where a great number of individuals of *N. platensis* were perhaps facing a severe climate or scarcity of resources. The extinction of the QAA gomphotheres was probably due to a catastrophic regional event, related to an extreme cold and dry climate associated with shortage of water and food resources.

Acknowledgments

The authors are thankful to the Departamento Nacional de Produção Mineral (DNPM) for permitting access to the fossil collection. LSA would like to thank the Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for the grant E-26/110.591/2011. VHD would like to acknowledge the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the master's scholarship granted.

References

- Alberdi, M.T., Prado, J.L., Cartelle, C., 2002. El registro de *Stegomastodon* (Mammalia: Gomphotheriidae) en el Pleistoceno Superior de Brasil. *Revista Espanhola de Paleontologia* 2 (17), 217–235.
- Alroy, J., 2001. A multispecies overkill simulation of the end Pleistocene megafaunal mass extinction. *Science* 292, 1893–1896.
- Asevedo, L., Winck, G.R., Mothé, D., Avilla, L.S., 2010. Paleoeecologia alimentar do gonfoteriídeo *Stegomastodon waringi* (Mammalia, Proboscidea, Gomphotheriidae) de planícies de latitudes medianas do Pleistoceno da América do Sul. In: Simpósio Brasileiro de Paleontologia de Vertebrados, VII, 2010, Rio de Janeiro. Resumos. Paleontologia em Destaque. UNIRIO, Rio de Janeiro, pp. 76–77.
- Asevedo, L., Winck, G.R., Mothé, D., Avilla, L.S., 2012. Ancient diet of the Pleistocene gomphothere *Notiomastodon platensis* (Mammalia, Proboscidea, Gomphotheriidae) from lowland mid-latitudes of South America: stereomicroscopy and tooth calculus analyses combined. *Quaternary International* 255, 42–52.
- Avilla, L.S., Mothé, D., Dominato, V., Asevedo, L., Bittencourt, N., Winck, G.R., 2010. Vie et mort de *Stegomastodon waringi* (Proboscidea, Gomphotheriidae) du Pléistocène supérieur du Brésil. In: International Conference on Mammoths and their Relatives, V, 2010, Puy en Velay. Résumés. Quaternaire: Revue de l'Association Française pour l'Etude du Quaternaire, Puy en Velay, Musée Crozatier, pp. 162–164.
- Baffa, O., Brunetti, A., Karmann, I., Dias-Neto, C.M.E., 2000. ESR dating of a Toxodon tooth from a Brazilian karstic cave. *Applied Radiation and Isotopes* 52, 1345–1349.
- Barnosky, A.D., 1989. The late Pleistocene event as a paradigm for widespread mammal extinction. In: Donovan, S.K. (Ed.), *Mass Extinctions: Processes and Evidence*. Columbia University Press, pp. 235–254.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306, 70–75.
- Brennan, B.J., Rink, W.J., Rule, E.M., Schwarcz, H.P., Prestwich, W.V., 1999. The ROSY ESR dating program. *Ancient TL* 17, 45.
- Cione, A.L., Tonni, E.P., 1995. Biostratigraphy and 'Land-Mammal Ages' in the Cenozoic of southern South America: principles, practices and the 'Uquian' problem. *Journal of Palaeontology* 69 (1), 135–159.
- Cione, A.L., Tonni, E.P., 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean Area, Argentina. In: Rabassa, J., Salemme, M. (Eds.), *Quaternary of South America and Antarctic Peninsula*, vol. 12. A.A. Balkema Press, Rotterdam, pp. 23–51.
- Cione, A.L., Tonni, E.P., Soibelzon, L., 2003. The broken zig-zag: Late Cenozoic large mammal and tortoise extinction in South America. *Revista del Museo Argentino de Ciencias Naturales* 5, 1–19.
- Dominato, V.H., Mothé, D., Avilla, L.S., Bertoni-Machado, C., 2009. Ação de insetos em vértebras cervicais de *Stegomastodon waringi* (Gomphotheriidae: Mammalia) do Pleistoceno de Águas de Araxá, Minas Gerais, Brasil. *Revista Brasileira de Paleontologia* 12 (1), 77–82.
- Dominato, V.H., Mothé, D., Silva, R.C., Avilla, L.S., 2011. Evidence of scavenging on remains of the gomphothere *Haplomastodon waringi* (Proboscidea: Mammalia) from the Pleistocene of Brazil: Taphonomic and paleoecological remarks. *Journal of South American Earth Sciences* 31 (2–3), 171–177.
- Ferretti, M., 2008. A review of South American proboscideans. *New Mexico Museum of Natural History and Science Bulletin* 44, 381–439.
- Ficcarelli, G., Azzaroli, A., Bertini, A., Coltorti, M., Mazza, P., Mezzabotta, C., Moreno-Espinoza, M., Rook, L., Torre, D., 1997. Hypothesis on the cause of extinction of the South American Mastodonts. *Journal of South American Earth Sciences* 10, 29–38.
- Ficcarelli, G., Coltorti, M., Moreno-Espinoza, M., Pieruccini, P.L., Rook, L., Torre, D., 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. *Journal of South American Earth Sciences* 15, 835–845.
- Gadens-Marcon, G.T., 2008. Contribuição ao estudo dos Proboscidea (Mammalia, Gomphotheriidae) do Quaternário do Estado do Rio Grande do Sul, Brasil. *Revista Universidade Guarulhos* 7, 93–109.
- Graham, R.W., Lundelius, E.L., 1984. Coevolutionary disequilibrium and Pleistocene Extinction. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: a Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 223–249.
- Grün, R., 2006. Direct dating of human fossils. *American Journal of Physical Anthropology* 131, 2–48.
- Haynes, G., 1988. Mass deaths and serial predation: comparative taphonomic studies of modern large mammal death sites. *Journal of Archaeological Science* 15, 219–235.
- Haynes, G., 1991. *Mammoths, Mastodonts and Elephants: Biology, Behavior, and the Fossil Record*. Cambridge University Press, Cambridge, 428 pp.
- Ikeya, M., 1993. New Applications of Electron Paramagnetic Resonance. Dating, Dosimetry and Microscopy. Scientific World, New Jersey, 520 pp.
- King, J.E., Saunders, J.J., 1984. Environmental insularity and the extinction of the American Mastodont. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: a Prehistoric Revolution*. University of Arizona Press, Tucson, pp. 315–349.
- Kinoshita, A., Baffa, O., 2005. Datação por Ressonância do Spin Eletrônico. *Canindé Revista do Museu de Arqueologia do Xingó* 6, 47–66.
- Ledru, M.P., 1993. Late Quaternary environmental and climatic changes in central Brazil. *Quaternary Research* 39, 90–98.
- Ledru, M.P., Braga, P.I.S., Soubiès, F., Fournier, M., Martin, L., Suguio, K., Turcq, B., 1996. The last 50,000 years in the Neotropics (Southern Brazil): evolution of vegetation and climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123, 239–257.
- Lopes, R.P., Oliveira, L.C., Figueiredo, A.M.G., Kinoshita, A., Baffa, O., 2010. ESR dating of Pleistocene mammal teeth and its implications for the biostratigraphy and geological evolution of the coastal plain, Rio Grande do Sul, Southern Brazil. *Quaternary International* 212, 213–222.
- Martin, P.S., 1984. Prehistoric overkill: the global model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: a Prehistoric Revolution*. University of Arizona Press, pp. 354–403.
- Mothé, D., Avilla, L.S., Cozzuol, M.A., Winck, G.R., 2011. Taxonomic revision of the Quaternary gomphotheres (Mammalia: Proboscidea: Gomphotheriidae) from the South American lowlands. *Quaternary International*, 1–6. <http://dx.doi.org/10.1016/j.quaint.2011.05.018>.
- Mothé, D., Avilla, L.S., Winck, G.R., 2010. Population Structure of the gomphothere *Stegomastodon waringi* (Mammalia: Proboscidea: Gomphotheriidae) from the Pleistocene of Brazil. *Anais da Academia Brasileira de Ciências* 82 (4), 983–996.

- Prescott, J.R., Hutton, J.T., 1994. Cosmic ray contributions to dose rates for luminescence and ESR dating: large depths and long-term time variations. *Radiation Measurements* 23 (2–3), 497–500.
- Price, L.L., 1944. O depósito de vertebrados pleistocênicos de Águas de Araxá (Minas Gerais). *Anais da Academia Brasileira de Ciências* 16 (3), 193–195.
- Rink, W.J., 1997. Electron spin resonance (ESR) dating and ESR applications in quaternary science and archaeometry. *Radiation Measurements* 27 (5–6), 975–1025.
- Sánchez, B., Prado, J.L., Alberdi, M.T., 2003. Paleodiet, ecology, and extinction of Pleistocene gomphotheres (Proboscidea) from Pampean Region (Argentina). *Coloquios de Paleontología* 1, 617–625.
- Short, J., 2009. Diet and feeding behaviour of the forest elephant. *Mammalia* 45 (2), 177–186.
- Simpson, G.G., Paula Couto, C., 1957. The Mastodons of Brazil. *Bulletin of American Museum of Natural History* 112 (2), 1–65.
- Skinner, A.R., 2000. ESR dating: is it still an “experimental” technique? *Applied Radiation & Isotopes* 52, 1311–1316.
- Skinner, A.R., 2006. An introduction to electron spin resonance (ESR) dating in archaeology and paleontology. *The Review of Archaeology* 27, 87–97.
- Stokke, S., du Toit, J.T., 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23, 70–80.
- Sukumar, R., 1990. Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology* 6 (1), 33–53.
- Tchamba, M.N., Seme, P.M., 2008. Diet and feeding behaviour of the forest elephant in the Santchou Reserve, Cameroon. *African Journal of Ecology* 31 (2), 165–171.
- Vivo, M., Carmignotto, A.P., 2004. Holocene vegetation change and the mammal faunas of South America and África. *Journal of Biogeography* 31, 943–957.
- Webb, S.D., 1991. Ecogeography and the Great American Interchange. *Paleobiology* 17, 266–280.
- Whittington, S.L., Dyke, B., 1984. Simulating overkill: experiments with the Mosimann and Martin model. In: Martin, P.S., Klein, R.G. (Eds.), *Quaternary Extinctions: a Prehistoric Revolution*. University of Arizona Press, pp. 451–465.