

Spanish Pleistocene Proboscidean diversity as a function of climate

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SUMMARY: Around 0.9 Ma ago, the 100 ka Milankovitch cycles forced global climate, causing glaciations, and created new ecological niches. It is at this time that *Elephas antiquus* arrived in Europe and occupied the temperate environments, while *Mammuthus* became increasingly adapted to cold environments.

1. INTRODUCTION

Fossil proboscideans have been among the first fossils that lead to palaeoclimatic interpretations. Interest focussed mainly on their value as a indicators of glacial and interglacial conditions in central Europe. Two genera and four species occur in the Pleistocene of western and central Europe: *Mammuthus meridionalis*, *M. trogontherii*, *M. primigenius*, and *Elephas antiquus*. The species of *Mammuthus* have historically been seen as a lineage, but present opinions are more inclined to see them as subsequent species, that arrived by dispersal (Lister 1996).

One of the first occurrences of *Mammuthus meridionalis* in western and central Europe is from Montopoli, in sediments overlying the top of the Gauss Epoch (Azzaroli 1977), suggesting an age for the entry of some 2.6 Ma. One of the last occurrences of the species is in Voigtstedt (Von Koenigswald & Heinrich 1999), a locality believed to be corelative of OIS 17 (Van der Made in press). *Mammuthus trogontherii* appeared not later than in Süssenborn (Von Koenigswald & Heinrich 1999) and is a common constituent of glacial faunas, until the level (OIS 10) below the “*antiquus* Schotter” at Steinheim (OIS 9). In the overlying “*primigenius*-Schotter” (OIS 8) *M. primigenius* appeared. This species survived in Europe till around the Pleistocene-Holocene transition.

The first record of *Elephas antiquus* in Germany and surrounding areas and in France is in the Middle Pleistocene of Mosbach 2 and Soleilhac (both OIS 15), while in Italy it is around 0.9 Ma (Bout 1964; Palombo 1995 Sardella *et al.* 1998; Von Koenigswald & Heinrich 1999).

2. THE SPANISH RECORD

The localities with *M. trogontherii*, *M. primigenius* and *E. antiquus*, as well as isolated finds, are indicated in Figure 1. Those localities and finds of which the approximate age could be estimated on the basis of geological, palaeontological or archaeological criteria have been indicated in Figure 2.

The first appearance of *Mammuthus meridionalis* in Spain is from Huelago carretera (Mazo 1989) from normally polarized sediments attributed to the Gauss epoch and an estimated age of some 2.7 Ma, and is slightly earlier at Montopoli, in sediments on top of the Gauss. The last record is in Atapuerca TD6 in sediments just below the Brunhes-Matuyama boundary (Van der Made in press) and is much older than the last record in Voigtstedt.

The oldest Spanish record of *M. trogontherii* is at Cúllar de Baza-1 (Mazo 1989). This locality has *Megaloceros savini*, and material assigned to *Bison* sp. (Azanza & Morales 1989). This bison possibly represents *Bison voigtstedtensis*, suggesting an age not later than that of

Süssenborn, otherwise the last locality with that bison, contrasting with a AAR date of 476+24 ka (Ortiz *et al.* 2000). Martín Penela (1988) described the fauna from Solana del Zamborino and attributed part of the proboscidean material to *Mammuthus trogontherii*. The rich fauna is interpreted to be correlative of Atapuerca TG10 and OIS9-10 (Van der Made, in press).

Most or all Spanish records of *M. primigenius* are of the Late Pleistocene. Though the species entered Europe two cycles earlier, there is no evidence of it having entered Spain at that time. The southernmost record of this species is

at El Padul (Granada).

The earliest record of *Elephas antiquus* in Spain is in Huescar-1 (Mazo, 1989). The locality has *Stephanorhinus etruscus*, *Mimomys savini*, *Microtus brecciensis*, *Microtus gregaloides* and *Castillomys crusafonti* is placed below Atapuerca TD4-6 (Sesé *et al.* 2001), with a probable age between some 0.9 and 1 Ma. This contrasts with a datation based on amino acid racemisation of 491+84 ka (Ortiz *et al.* 2000). The latest records are Late Pleistocene in age and are at Cova Negra, Buelna and Olha (Mazo 1995, 1998; Altuna 1984).

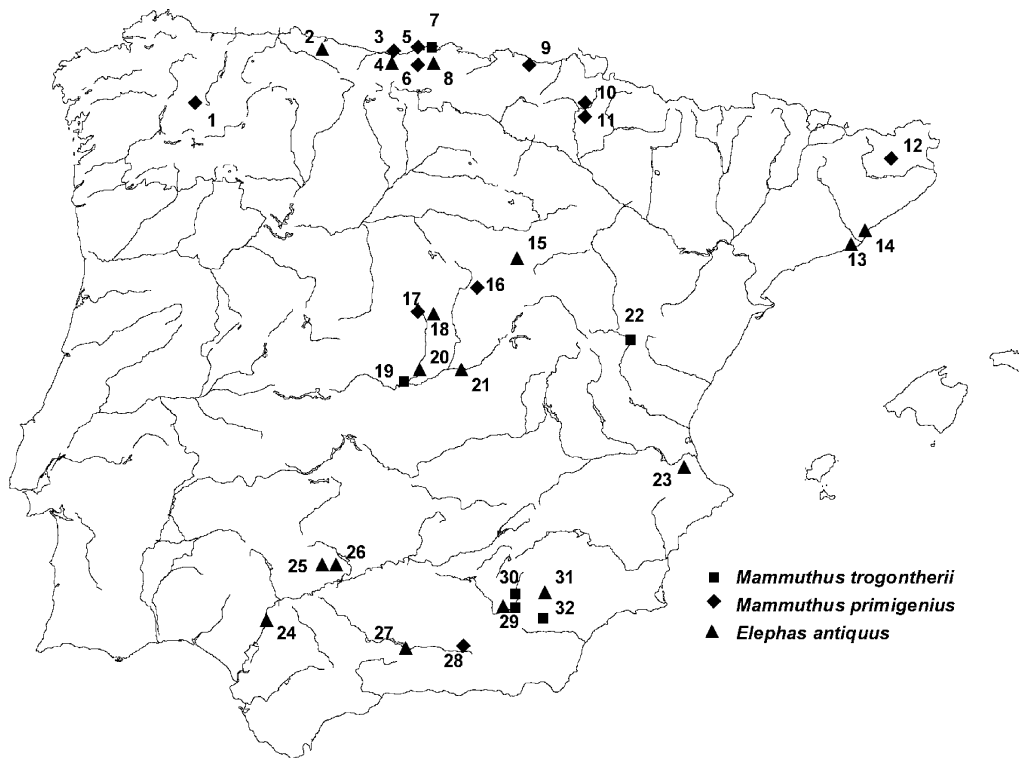


Fig.1 - Location map of sites with proboscidean remains. *Mammuthus trogontherii*: 7 = Peña Cabarga (Santander); 19 = Toledo (Toledo); 22 = Teruel (Teruel); 29 = Solana del Zamborino (Granada); 30 = Cúllar de Baza-1 (Granada); 32 = Daimuz (Granada). *Mammuthus primigenius*: 1 = Incio (Lugo); 3 = El Pindal & Cueto de la Mina (Asturias); 5 = Pámanes (Santander); 6 = Altamira & Cueva Morín (Santander); 9 = Itziar and Labeko Koba (País Vasco); 10 = Olha (País Vasco); 11 = Isturitz (Navarra); 12 = Olot (Gerona); 16 = Cueva de los Casares (Guadalajara); 17 = La Aldehuela (Madrid); 28 = El Padul (Granada). *Elephas antiquus*: 2 = Llanera (Asturias); 4 = Buelna (Asturias); 15 = Torralba & Ambrona (Soria); 18 = Madrid (Transfesa/Villaverde, San Isidro, Los Rosales, Arriaga, Orcasitas, Aridos, Ciempozuelos); 20 = Pinedo (Toledo); 21 = Aranjuez (Madrid); 23 = Cova Negra y Bolomor (Valencia); 24 = La Rinconada (Sevilla); 25 = Hornachuelos (Córdoba); 26 = Almodóvar del Río (Córdoba); 27 = Loja (Granada); 29 = Solana del Zamborino (Granada); 31 = Huescar-1 (Granada).

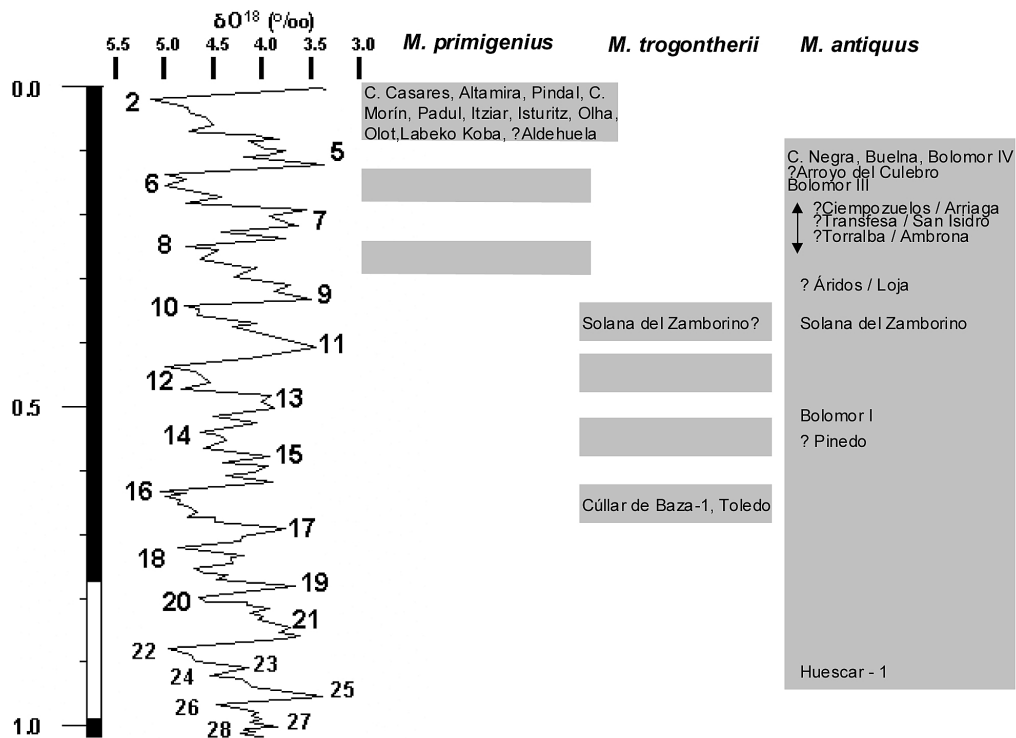


Fig.2 - Time and palaeomagnetic scales, δO^{18} values and stages (OIS) and approximate stratigraphic position of the Spanish localities with proboscideans remains. The grey areas indicate the known or expected temporal distribution of the proboscideans. Arrows and question marks indicate insecure stratigraphical position. Question marks behind a locality name indicate dubious taxonomy.

3. DISCUSSION

The Spanish proboscidean record resembles that from the rest of Europe, save for relatively early appearances of *M. meridionalis*, and *E. antiquus*, and the late appearance of *M. primigenius*. At present we are not able to establish whether the records of *M. trogontherii* and *E. antiquus* are of glacial or interglacial chronology, though it is possible that the presence of the former is restricted to glacial periods and that of the latter continuous. The most interesting parallel with the rest of Europe, is the long period with a single proboscidean species, between some 2.7 and 1 Ma, followed by a period when two species were present.

The appearance of both *Elephas antiquus* and the replacement of *Mammuthus meridion-*

alis by *M. trogontherii* occurred after a long relatively stable period and in the middle of important faunal changes. These changes started around some 1.2 Ma with the dispersal of a number of taxa that later were to become adapted to, or at least more common in, glacial environments: *Bison*, *Praeovibos*, *Soergelia*, *Capra alba* as well as a cervid that was probably adapted to relatively open environments, *Eucladoceros giulii*. During the Jaramillo Event, *Capreolus*, *Bison menniseri*, *Hemitragus bonali* and *Alces latifrons* dispersed into west and central Europe. During the latest Early Pleistocene, *Elephas antiquus*, *Sus scrofa*, *Cervus elaphus* and *Crocuta crocuta* dispersed into Europe. During the earliest Middle Pleistocene *Stephanorhinus hundsheimensis*, *Megaloceros savini*, *Ovibos suessenbornensis* and *Praeovibos priscus* dispersed into Europe.

At about the time that *Miomys savini* was replaced by *Arvicola cantianus*, *M. meridionalis* was definitively replaced by *M. trogontherii*. Various later waves of dispersals into Europe are recorded. These appearances are not matched by an equal number of extinctions, and biodiversity increased on a European wide scale. Part of these animals developed into glacial, others into interglacial taxa. (Van der Made 1999, in press.)

The Milankovich cycles are detected in oxygen isotopes and dust concentrations in deep sea cores, as well as by the sedimentological study of out crops. Around 1,2 Ma the amplitude of the Oxygen Isotope variations increased and around 0,9 Ma, the dominant period passed from 40 ka to 100 ka, which is the cyclicity of the glacials (Shackleton 1996).

These climatical changes lead to an important change in biogeography; a cyclic pattern of biogeographical changes was established. This apparently is what allowed for an increase in biodiversity in general, and in the proboscideans in particular. Due to the climatical changes, proboscidean diversity in Europe increased from one to two genera: *E. antiquus* filled the "interglacial" niche, while *Mammuthus* adapted progressively to the "glacial" niche.

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