



Isotopic paleoecology of mammals and the Middle Miocene Cooling event in the Madrid Basin (Spain)

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ABSTRACT

The Middle Miocene underwent profound climatic perturbations detected in worldwide marine and continental records. The Miocene Climatic Optimum (~17 to 14 Ma), a warm and humid period, was followed by the Middle Miocene Cooling (~14–13.8 Ma) characterized by a sharp drop in temperatures and an increase in aridity triggered by the reestablishment of the Eastern Antarctica ice sheet. The Madrid Basin, located in the central Iberian Peninsula, has furnished a considerable number of Miocene fossil sites with a very complete succession of localities from the Lower Middle Miocene to the Upper Middle Miocene (Middle and Upper Aragonian, MN5 and MN6, local zones Db to G). Mammalian fossil tooth enamel of different taxa including rhinoceros, equids, gomphothere, suids and ruminants from 16 fossil sites spanning from ~15.9 Ma to ~13.2 Ma were analyzed for $\delta^{13}\text{C}$, $\delta^{18}\text{O}_{\text{CO}_2}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values with the aim of determining regional paleoecological, paleoenvironmental and paleoclimatic changes across this important climate transition. The $\delta^{13}\text{C}$ values vary between -11.9% and -6.4% (VPDB), indicating a C_3 environment ranging from woodlands to more open conditions. The rhinoceros *Alicornops simorreense* and *Hoploaceratherium tetradactylum*, the gomphothere *Gomphotherium angustidens*, the cervid *Heteroprox moralesi* and the paleomyricid *Triceromeryx pachecoi* may be regarded as browsers inhabiting more closed environments, whereas the equid *Anchitherium*, the rhinoceros *Hispanotherium matritense* and the bovid *Tethytragus langai* show a mixed feeding diet related to more open conditions. Furthermore, the variation in $\delta^{13}\text{C}$ values across the fossil sites and local zones indicates drier conditions in local zones Db and Dc (~15.9–14.8 Ma), a more humid period in local zone Dd (~14.8–14.1 Ma), before a return to a drier environment in local zones E, F and G (~14.1–13.2 Ma). The $\delta^{18}\text{O}_{\text{CO}_2}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ values and calculated $\delta^{18}\text{O}_w$ values all track a declining trend from local zones Db to Dd (~15.9–14.1 Ma), with minimum values in local zone E ($\delta^{18}\text{O}_{\text{CO}_2} = 26.5 \pm 2.1\%$, $\delta^{18}\text{O}_{\text{PO}_4} = 18.4 \pm 2.4\%$, and $\delta^{18}\text{O}_w = -5.3 \pm 2.9\%$). The minimum in $\delta^{18}\text{O}$ values in local zone E (~14.1–13.7 Ma) appears to coincide with a drop in temperature at the time of the Middle Miocene Cooling (~14–13.8 Ma). After this minimum, $\delta^{18}\text{O}_{\text{CO}_2}$, $\delta^{18}\text{O}_{\text{PO}_4}$ and $\delta^{18}\text{O}_w$ values recover in local zones F and G (13.7–13.2 Ma). The calculation of $\Delta^{13}\text{C}_{\text{leaf}}$ values allowed us to determine plausible biomes that might have existed in the Madrid Basin during the Middle Miocene (i.e., a tropical rain forest, a tropical deciduous forest, a temperate evergreen forest and a xeric woodland–scrubland), although this method was not able to detect more savanna-like environments. Finally, $\delta^{13}\text{C}_{\text{diet, meq}}$ values were used to infer mean annual precipitation, with values ranging from ~250 mm/yr (local zone Dc) to ~670 mm/yr (local zone Dd) which are in accordance with the proposed biomes suggested by the $\Delta^{13}\text{C}_{\text{leaf}}$ values and fossil mammal assemblages.

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1. Introduction

The Middle Miocene was a period of substantial paleoenvironmental and paleoclimatic change (Flower and Kennett, 1994; Zachos et al., 2001; Böhme, 2003). The Miocene Climatic Optimum (MCO; ~17 to 14 Ma) was the warmest period since the Middle Eocene, with high

temperatures worldwide and humid tropical and subtropical conditions reaching to middle latitudes (e.g., the presence of crocodiles and palm trees in the Vienna Basin; Agustí and Antón, 2002). According to Böhme (2003), who studied ectothermic vertebrates from Central Europe, the lower limit for mean annual temperature (MAT) during the MCO was 17.4 °C and paleobotanical data and bauxite records point to MAT as high as ~22 °C (Price et al., 1997). This global warming was followed by a sharp and short-term (~200 ka) drop in temperatures known as the Middle Miocene Cooling (MMC; 14–13.8 Ma), the first step toward the cold climatic regime of the late Neogene (Lear et al.,

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2000; Zachos et al., 2001; Shevenell et al., 2004). The MMC coincided with the reestablishment of the Eastern Antarctica ice cap; its impacts have been recorded in marine and continental sections worldwide (Kennett and Barker, 1990; Flower and Kennett, 1994; Zachos et al., 2001; Shevenell et al., 2004; Lewis et al., 2008; Domingo et al., 2009). This cooling led to a stronger meridional temperature gradient and establishment of new climatic zonations (Pickford and Morales, 1994; Böhme, 2003). Estimates of temperature change range from a drop in MAT of more than 7 °C in Central Europe (Böhme, 2003), to a 6 to 7 °C drop in high-latitude (~55°S) southwest Pacific sea surface temperatures (Shevenell et al., 2004), to a decline of 8 °C in mean summer temperatures in Antarctica (Lewis et al., 2008). Although more difficult to quantify, an increase in aridity accompanied this global cooling. According to palynological studies, a replacement of evergreen forests adapted to humid tropical and subtropical conditions by drought-adapted vegetation occurred in mid-European latitudes (Agustí and Antón, 2002; Jiménez-Moreno, 2006). While the causes for these profound climatic and environmental changes remain mostly unknown, several mechanisms have been invoked as triggering factors such as a drawdown in atmospheric pCO₂ levels (Kürschner et al., 2008) either via organic carbon sequestration on mid-latitude continental margins ("Monterey hypothesis"; Vincent and Berger, 1985; Flower and Kennett, 1994) or a boost in silicate weathering rates (Raymo, 1994) as a consequence of Himalaya uplift. Milankovitch cycles may have been also responsible for the drop in temperatures and the enhancement of aridity around the MMC (Shevenell et al., 2004). Finally, tectonic factors and the reorganization of gateway regions may also have played a role (Pagani et al., 1999; Wang et al., 2006).

The relationship between these climate changes and shifts in mammalian faunal assemblages is controversial. The MMC triggered environmental changes, such as the development of more open, less forested habitats. Some authors argued these changes had profound consequences on mammalian terrestrial herbivores, including a trend towards a larger body size, more hypsodont teeth, and more elongated distal limb segments (Janis and Damuth, 1990; Agustí and Antón, 2002). Other authors have argued that there is no direct relationship between climatic change and mammalian turnover rates (Costeur et al., 2004; Legendre et al., 2005; Costeur et al., 2007). Costeur et al. (2007) cautioned that this lack of synchronicity might be due to flaws in the Mammal Neogene (MN) biochronology and urged a revision of the geochronology of some European fossil sites, an issue that has been already dealt with by recent studies (Gómez Cano et al., 2011; van der Meulen et al., 2011).

Studies of environmental and climatic fluctuations in long terrestrial sequences are rare in comparison to the more complete sedimentary sequences of the marine record. The Madrid Basin contains well preserved Middle Miocene vertebrate localities in continuous temporal succession. Most of the fossil mammals from this basin correspond to the Middle Miocene Aragonian continental stage (Daams et al., 1977), spanning from ~17 to 11 Ma. The abundance and variety of macromammal taxa in these deposits make the Madrid Basin an ideal location in which to use stable isotope analysis to study palaeoenvironmental and paleoecological change in the Middle Miocene.

1.1. Isotopic reconstruction of continental environments

Analyses of the carbon isotope ($\delta^{13}\text{C}$) composition of mammalian tooth enamel have provided information about paleodiets, permitting reconstruction of habitat preferences and ecological niche dimensions (for a review see Koch, 1998, 2007). The $\delta^{13}\text{C}$ values of herbivore tooth enamel bioapatite ($\delta^{13}\text{C}_{\text{enamel}}$) track the $\delta^{13}\text{C}$ values of the plants they consume ($\delta^{13}\text{C}_{\text{diet}}$), offset by a consistent +12 to +14‰ due to fractionations associated with carbonate equilibria and metabolic processes (Cerling and Harris, 1999; Passey et al., 2005).

In terrestrial settings, the dominant control on the $\delta^{13}\text{C}$ value of plants is photosynthetic pathway (Bender, 1971; O'Leary, 1988;

Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993; Hayes, 2001). Plants following the C₃ or Calvin–Benson photosynthetic pathway (trees, shrubs, forbs and cool-season grasses) strongly discriminate against ¹³C during fixation of CO₂, yielding tissues with $\delta^{13}\text{C}$ values averaging –27‰ (VPDB) (ranging from –36 to –22‰). The most negative $\delta^{13}\text{C}$ values of this range (–36 to –30‰) reflect closed-canopy conditions due to recycling of ¹³C-depleted CO₂ and low irradiance. The highest values (–25 to –22‰) correspond to C₃ plants from high light, arid, or water stressed environments. C₄ plants (Hatch–Slack photosynthetic pathway) comprise grasses and sedges from areas with a warm growing season and some arid-adapted dicots. C₄ plants discriminate less against ¹³C during carbon fixation, yielding mean $\delta^{13}\text{C}$ value of –13‰ (ranging from –17‰ to –9‰). Crassulacean acid metabolism (CAM) is the least common pathway, occurring chiefly in succulent plants. CAM plants exhibit $\delta^{13}\text{C}$ values that range between the values for C₃ and C₄ plants.

Using the expected $\delta^{13}\text{C}$ ranges for C₃ and C₄ plants and a typical diet-to-enamel fractionation of +14.1 ± 0.5‰ (Cerling and Harris, 1999), we can estimate the expected $\delta^{13}\text{C}$ values for pure C₃ feeders in different habitats (closed-canopy, –22 to –16‰; mesic/woodland, –16 to –11‰; open, arid C₃, –11 to –8‰) and pure C₄ feeders (–3‰ to +5‰). Enamel $\delta^{13}\text{C}$ values between –8‰ and –3‰ represent mixed C₃–C₄ diets. When considering fossil taxa, however, it is necessary to account for shifts in the $\delta^{13}\text{C}$ value of atmospheric CO₂ (the source of plant carbon), including anthropogenic modification due to fossil fuel burning, which has decreased the $\delta^{13}\text{C}$ value of atmospheric CO₂ from –6.5 to –8‰ since onset of the Industrial Revolution (Friedli et al., 1986; Marino and McElroy, 1991). Using isotopic data from marine foraminifera, Tipple et al. (2010) reconstructed the $\delta^{13}\text{C}$ value of the atmospheric CO₂ for the Middle Miocene (~15.9–13.2 Ma) as ~–6‰, a difference of 2‰ relative to the modern value. Accounting for these shifts in baseline, closed-canopy $\delta^{13}\text{C}$ values would range from –20 to –14‰, mesic/woodland from –14 to –9‰, open, arid C₃ from –9 to –6‰, and pure C₄ feeders from –1‰ to +7‰.

Isotopic studies of ancient C₃-dominated ecosystems have provided evidence for niche partitioning among sympatric taxa (Feranec and MacFadden, 2006; Tütken et al., 2006; Domingo et al., 2009; Tütken and Vennemann, 2009). This is possible because of the wide range of $\delta^{13}\text{C}$ values in C₃ plants related to microenvironment and plant functional type. C₄ plants have a competitive advantage when atmospheric pCO₂ levels are low and at higher temperatures, and they have greater water use efficiency (Ehleringer et al., 1991). Undeniable C₄ vestiges have been found in fossil localities as old as ~14 Ma (Nambudiri et al., 1978; Retallack et al., 1990; Morgan et al., 1994), and the C₄ plants rose to dominance in different regions asynchronously from the late Miocene to late Pliocene (between ~8 Ma and ~2.5 Ma) (for a review see Strömberg, 2011).

Oxygen isotope values have also proven useful in paleoenvironmental and paleoecological reconstruction. The $\delta^{18}\text{O}$ values of both carbonate and phosphate fractions of the bioapatite in mammalian tooth enamel are a reflection of the $\delta^{18}\text{O}$ value of body water, which in turns records oxygen uptake (inspired O₂ and water vapor, drinking water, dietary water, oxygen in food dry matter) and loss (excretion, expired CO₂ and water vapor) during tooth development (Bryant and Froelich, 1995; Kohn, 1996). Within a taxon, variations in body water $\delta^{18}\text{O}$ values can be interpreted as chiefly reflecting changes in the isotopic composition of ingested water, which varies with mean annual temperature and aridity. Briefly, the $\delta^{18}\text{O}$ values of meteoric water, the ultimate source of drinking water, and water and oxygen in dry matter in plants, are positively correlated with mean annual temperature. In addition, as aridity increases, this water (especially the water in plants) becomes ¹⁸O-enriched due to evaporation (Luz et al., 1990; Ayliffe et al., 1992). Within a region, the $\delta^{18}\text{O}$ values of herbivore taxa will vary in relation to their physiology of water economy, which determines how much they need to rely upon drinking water, as well as dietary differences that affect the $\delta^{18}\text{O}$ value of water in plants.

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