



Review of paleo-humidity parameters in fossil rodents (Mammalia): Isotopic vs. tooth morphology approach



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ABSTRACT

Paleoecology of fossil rodents is frequently inferred from the dental pattern of the teeth, attributing the habitat conditions of extant rodents to fossil species with similar dental pattern. This technique is common practice and has been in use for several decades. A relatively new technique is based on the carbon and oxygen isotope composition of the incisor enamel of fossil rodents to reconstruct paleoenvironmental scenarios. We combine these two methods, studying material from two Early Miocene Spanish sections, one in the Mediterranean coastal area and one in Northcentral inland Spain. Comparison of the humidity values obtained by means of these two proxies reveals discrepancies. Therefore, we analyzed the habitat preferences, especially humidity, of extant rodents and found that dental pattern is not very reliable to reconstruct the humidity preferences of fossil rodents and this kind of interpretation has to be taken with caution. We conclude that the isotopic composition of enamel of fossil teeth is a more reliable proxy in the studied sections.

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1. Introduction

Paleoecology of fossil rodents is fundamentally based on the ecology of related extant species; e.g. fossil beavers and fossil ground squirrels are attributed the same environment as their extant relatives. A more complex method is comparison of dental patterns (e.g. van der Meulen and de Bruijn, 1982; Daams et al., 1988, 1999). Van der Meulen and de Bruijn (1982) grouped living and fossil glirid species on the basis of morphological features of the upper molars and extrapolated the ecology of the living representatives to the fossil species with similar dental pattern. Daams et al. (1988) gave habitat preferences for Aragonian (Lower Miocene) rodents, using, among other things, this grouping of glirids. Their related abundance of supposedly forest-dwelling species to a greater degree of humidity. Eomyidae were assigned wet preference because of their association with supposedly forest-dwelling Gliridae. Daams et al. (1999) extended and refined the paleoecological interpretations of several taxa, especially Cricetidae, and that scheme is now generally accepted. Here we will analyze the habitat preferences of those extant rodent groups that are commonly found in European fossil faunas.

Agustí (1990) distinguished two bioprovinces in the Spanish Neogene faunas: The strictly continental Ibero-Central bioprovince and the Ibero-Levantine bioprovince with marine influences. A sharp definition was never given, but one may say that the first one comprises the central basins (e.g. Duero, Ebro, Madrid, Teruel) and the second one comprises the Mediterranean coastal basins like Valles-Penedes, the Valencia basins and the Betic basins in the South of Spain (Guadalquivir, Guadix-Baza, etc.) (Fig. 1). In this paper, we compare the paleohumidity reconstruction based on fossil rodents from these two bioprovinces.

In Daams et al. (1999, Fig. 7.6) one can observe between 50 and 75% of wet-habitat rodents in the second part of MN4 and the first part of MN5 in the type area of the Aragonian (Lower–Middle Miocene, Teruel Basin), coinciding with the Miocene Climatic Optimum (from ~17 to 15 Myr; Zachos et al., 2001). We applied the same habitat definitions of Daams (1999) to our material from Morteral (Valencia Basin) and found between 12 and 50% of wet components in the same time interval (Ruiz-Sánchez et al., 2012). This is surprising since Morteral belongs to the Ibero-Levantine bioprovince, supposedly more humid than the Ibero-Central bioprovince to which the Aragonian type area belongs. This led us to a re-evaluation of the habitat, especially humidity, of extant Gliridae, Cricetidae and Sciuridae that serves as a basis for the interpretation of fossil rodents, and its reliability for paleoecological inferences.

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Fig. 1. Cenozoic basins of Spain and the location of the Olmo Redondo section (OR) and Morteral section (MT).

Because of the inconsistencies of the traditional methodology of paleohumidity reconstruction of Daams et al. (1999), in this paper we contrast the results obtained from this method with another paleo-humidity proxy, the isotopic composition of rodent enamel, in order to validate the reliability of the traditional paleohumidity data. Small mammals are characterized by a restricted habitat and scarce migratory behavior, therefore their isotopic record faithfully reflects the local/regional environment (Royer et al., 2013).

The carbon isotopic composition of mammal tissues, such as collagen or hydroxylapatite, provides information about their diet (Vogel and van der Merwe, 1977; DeNiro and Epstein, 1978; Lee-Thorp and van der Merwe, 1987; Cerling et al., 1997a,b; Kohn and Cerling, 2002; among others). In herbivore mammals it reflects the composition of the ingested biomass; for example, it may indicate the preference for either C3 or C4 plants in their diet (DeNiro and Epstein, 1978; Quade et al., 1995; Cerling et al., 1997b; among others). In the case of specimens that feed upon the same type of plants, such as C3 plants (with $\delta^{13}\text{C}$ values ranging from -35 to -22‰), their carbon isotopic composition provides information about the environmental conditions, showing an isotopic enrichment related to water stress (aridity) and open environments (Farquhar et al., 1989; Ehleringer and Monson, 1993; Quade et al., 1995; Cerling et al., 1997a; among others), in contrast to wetter and closed canopy forest.

2. Abbreviations

MAP	Mean annual precipitation (mm/yr)
OR	Olmo Redondo
MT	Morteral
MN	Neogene Mammal units

3. Material and methods

3.1. Ecological preferences of fossil and extant rodents

Van der Meulen and Daams (1992) listed three ways to analyze ecological preferences of fossil rodents:

- extrapolation of habitat preferences of extant relatives, applied in e.g. beavers and ground squirrels.

- functional morphological inferences from molar patterns, applied in e.g. Gliridae and Cricetidae.
- repeated association of species with certain sedimentary environments, applied in e.g. Eomyidae.

Mayr (1979) and van der Meulen and de Bruijn (1982) developed the second method for fossil Gliridae. They assembled ecological preferences of extant glirids and related these to the dental pattern; then they coined these preferences to fossil glirids with similar dental pattern. Daams and van der Meulen (1984) and Daams et al. (1988) extended this method to fossil cricetids, listing a number of the latter as catholic or unknown. Daams et al. (1999) introduced the length of the mesoloph (a transverse crest in the center of the upper molars) of cricetids as a paleoecological parameter and in that way concluded preferences for all cricetids. This scheme is now widely accepted.

Paleoecological interpretations of fossil rodents are usually based on the ecology of related extant species (e.g., van der Meulen and de Bruijn, 1982; Daams et al., 1988, 1999). Here we present an analysis of the habitat, especially humidity, of extant Gliridae, Cricetidae and Scuridae that serves as a basis for the interpretation of fossil rodents. Data are from a variety of sources, among which the IUCN redlist (<http://www.iucnredlist.org/>) is particularly important. More details about the habitat of extant taxa are explained in Section 3.

We use this analysis of the habitat and humidity of extant taxa to evaluate the validity of currently accepted paleohumidity interpretations based on dental pattern of fossil rodents. The fossil rodent data are from two Lower Aragonian (Lower–Middle Miocene, MN4/5) sections in Spain (Fig. 1): the Aragonian type area (Olmo Redondo section, Calatayud–Teruel Basin, prov. Zaragoza; Ibero-Central bioprovince) and the Rio Magro Basin (Morteral section, Valencia Basin, prov. Valencia; Ibero-Levantine bioprovince) and compare the results with those obtained from carbon isotopic analysis of rodent enamel from these sections. We have selected these two sections because they showed different humid conditions during the Aragonian (Lower–Middle Miocene) when applying the traditional paleoecological reconstruction based on the comparison of the dental patterns of related extant species (Ruiz-Sánchez et al., 2012).

3.2. Isotopic analyses

We have carried out isotopic analyses of rodent incisors from stratigraphically superposed levels: MT1, MT5, MT5C, MT17/18, MT20A, MT22, and MT19 (Morteral section) and OR1, OR2, OR5, OR8, and OR9 (Olmo Redondo section). The OR samples were obtained from the collections of Museum Naturalis (Leiden, The Netherlands); the MT samples are from the Department of Geology, University of Valencia (Spain).

Continuously growing teeth from the same rodent species should be selected (Royer et al., 2013) in order to avoid the plausible weaning effect in some rodent molars (Linders et al., 2001). This is possible in unrooted arvicolid molars from the Pleistocene, because their molars (diagnostic elements) are continuously growing. However, in older Muroidea, the only continuously growing teeth are incisors, where the species differentiation is complicated. These continuously growing teeth reflect the conditions during the last weeks of the specimens' life, which in the case of rodent incisors may reflect the last 4–9 weeks (Klevezal et al., 1990; Klevezal, 2002). For our analysis we selected incisors of Cricetidae, Gliridae and Eomyidae, which are the main components of the studied faunal associations. This combination does not bias the results, because a mean fractionation value of $\sim 11\text{‰}$ between diet and hydroxylapatite may be assumed in small- to mid-sized mammals (Koch, 1998; Passey et al., 2005). Although rodent incisors were scarce in the selected fossil levels, a minimum number of seven specimens was taken in order to gather a representative sample of the population.

Teeth were physically cleaned with de-ionized water, ultrasonication, and mechanical abrasion using a brush. Afterwards, dentine was physically separated from enamel, in order to analyze only the enamel because

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