



Understanding climate's influence on the extinction of *Oreopithecus* (late Miocene, Tusco-Sardinian paleobioprovince, Italy)

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ABSTRACT

Despite its long history of scientific study, the causes underlying the extinction of the insular hominoid *Oreopithecus bambolii* are still a matter of ongoing debate. While some authors consider intense tectonism and invading species the cause of its extinction ca. 6.7 Ma, others propose climatic change as the main contributing factor. We rely on long-term patterns of tooth wear and hypsodonty of the Baccinello and Fiume Santo herbivore-faunas to reconstruct changes in habitat prior to, during and after the extinction. While a mosaic of habitats was represented in Baccinello V1 (as shown by a record of browsers, mixed feeders and species engaged in grazing), more closed forests (higher proportion of browsers, shortage of mixed feeders and lack of grazers) characterised Baccinello V2. Finally, there was a partial loss of canopy cover and development of open-patches and low-abrasive grasses in Baccinello V3 (as denoted by new records of taxa involved in grazing)—although still dominated by a forested habitat (since browse was a component in all diets). Our results provide evidence for two perceptible shifts in climate, one between 8.1 and 7.1 Ma and other ca. 6.7 Ma, though this latter was not drastic enough to lead to intensive forest loss, substantially alter the local vegetation or affect *Oreopithecus* life-style—especially if considering the growing evidence of its versatile diet. Although the disappearance of *Oreopithecus* is complex, our data reject the hypothesis of environmental change as the main factor in the extinction of *Oreopithecus* and Maremma fauna. When our results are analysed together with other evidence, faunal interaction and predation by invading species from mainland Europe seems to be the most parsimonious explanation for this extinction event. This contrasts with European hominoid extinctions that were associated with major climatic shifts that led to environmental uniformity and restriction of the preferred habitats of Miocene apes.

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1. Introduction

The late middle and late Miocene is an important time period for understanding the radiation of hominoids in Eurasia. Although much recent progress has been made in examining their dispersal from Africa into Eurasia during the middle Miocene (Andrews and Kelley, 2007), their subsequent radiation (see Alba, 2012 and references therein) and the drivers of their gradual extinction in the late Miocene (Merceron et al., 2010; Casanovas-Vilar et al., 2011; DeMiguel et al., 2014), the causes that underlie the disappearance

of *Oreopithecus bambolii*—the latest surviving Western Eurasian ape—still remain open to debate.

Oreopithecus was a large-bodied hominoid from the late Miocene of the Tusco-Sardinian paleobioprovince (Italy) that lived in conditions of insularity (Bernor et al., 2001; Rook et al., 2006) between ca. 8.1 Ma and 6.7 Ma (Rook, 2016) and evolved a unique mixture of primitive and derived anatomical features which precludes interpretations of its phylogeny, history and paleobiology. Despite this apparent lack of connection with most other European hominoids, *Oreopithecus* has a crucial role for understanding stem hominoid evolution and, particularly, the mechanism driving the extinction of late Miocene apes (DeMiguel et al., 2014).

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Oreopithecus went extinct at ca. 6.7 Ma (Rook, 2009; Rook et al., 2011), which contrasts strongly with most other ape extinctions in Eurasia, ultimately related to an increase in environmental uniformity and the resulting loss of habitat suitability (Merceron et al., 2010; DeMiguel et al., 2014). In Western and Central Europe, this sharp decline has been related to changes towards increased seasonality and lower temperatures, with the substitution of fruit-rich evergreen (sub)tropical forests by more deciduous trees (Alba, 2012; DeMiguel et al., 2014). At least in the Catalan coastal basins (with a large and outstanding record of Miocene primates, including among others *Pierolapithecus*, *Anoiapithecus*, *Dryopithecus* and *Hispanopithecus*) this process was gradual, implying the fragmentation of habitats in which (sub)tropical elements became progressively restricted to lowland humid areas (see DeMiguel et al., 2014 and references therein). The last occurrence (ca. 10 Ma) of *Hispanopithecus (Rudapithecus) hungaricus* at Rudabanya (Hungary) was also related to climate change and final regression of Lake Pannon (Bernor et al., 2004; Armour-Chelu et al., 2005 and relevant references therein). In Eastern Europe, *Oreopithecus* survived longer than these other Western and Central European counterparts (ca. 8.0–7.5 vs. 9.5 Ma), probably due to specialised dietary and anatomical adaptations to more open and arid habitats (Merceron et al., 2010). Although its extinction did not coincide with any major climatic shift, it might be similarly related to strong seasonal fluctuation (Merceron et al., 2013).

Oreopithecus survived this major (Vallesian-Turolian) extinction event in the latest Miocene Tusco-Sardinian paleobioprovince, but its extinction does not offer much insight with regard to that of these other hominoids from mainland Europe. Research findings, indeed, have yielded conflicting results regarding its disappearance. While some works attribute its extinction and the replacement of its endemic associated fauna to a marked shift from warm and humid conditions to an inconsistent climate regime (Benvenuti et al., 1994; Bernor et al., 2001; Ligios et al., 2008), others show no relation to any significant change in climate or habitat, but rather to the connection of its insular ecosystem to the mainland ca. 6.7 Ma (Rook et al., 2011; Matson et al., 2012; Nelson and Rook, 2016) and intensive interaction with invading non-endemic fauna like *Hippotherium*, *Dicerorhinus*, *Propotamochoerus*, *Machairodus*, etc. (Bernor et al., 2001; Rook et al., 2011).

Together with this controversial hominoid, there is a substantial record of fossil herbivorous mammals and a preponderance of ruminants, which are particularly suitable for the reconstructions of terrestrial environments and habitat, and the evolution of climate (DeMiguel et al., 2010, 2011). Given such unusual abundance of late Miocene plant-eating taxa (mostly bovids belonging to the genus *Maremmia* and to Antilopini species—such as *Tyrrhenotragus*—, but also other ruminants and equids) during the Baccinello–Cinigiano sequence, this investigation relies on evidence of their diets (through quantitative analyses of tooth wear) and ecologically-dependent traits to search for signs of the existence of changes in climate during the whole sequence and reconstruct *Oreopithecus*' habitat and changes in habitat that may have ultimately led to its extinction (our working hypothesis here). Our investigation thus yields direct data on the feeding behavior and dietary guilds of the herbivorous faunas, thereby providing evidence of the vegetation composition and habitat structure of the local ecosystems. To do so, dental wear and hypsodonty are first examined for the interval belonging to V1, V2 and Fiume Santo to provide a reconstruction of the vegetation mosaic and environments at a time when *Oreopithecus* was present. Then, results are reported for V3 biozone to reconstruct the habitat just after *Oreopithecus* went extinct. Finally, we analyse our data together with previous results from other works for this late Miocene taxon to re-evaluate and further refine

the most likely mechanisms driving the eventual extinction of the last European hominoid.

2. Materials and methods

2.1. Sample

We sampled for analysis a total of 183 individuals from 12 fossil ungulate taxa (artiodactyls and perissodactyls) (see Table 1) from the Baccinello–Cinigiano sequence (Tuscany, Central Italy), which comprises three local vertebrate biozones (from oldest to youngest: V1, V2 and V3) (Lorenz, 1968; Engesser, 1989; Rook, 2016), and other localities of the so-called Tusco Sardinian paleobioprovince (Fig. 1). *O. bambolii* is reported in zones V1 and V2, which include a very peculiar and highly endemic faunal complex as well—referred to as the “Maremma fauna” or “*Oreopithecus* Zone Faunas”—, very different from coeval faunas either from European or African continental realms (Benvenuti et al., 1994; Bernor et al., 2001). The material considered for study belongs to different localities and reflects differences in faunal composition (Table 1). i) Fauna (*Maremmia haupti*, *Tyrrhenotragus casteanensis* and *Umbrotherium azzarolii*) from V1 level including Ribolla, Casteani and Serrazzano (ca. 8.3–8.1 Ma, upper part of chron C4r). ii) V2 fauna (such as *Maremmia lorenzi*, *Maremmia cf. lorenzi*, *Tyrrhenotragus gracillimus*, *T. casteanensis*, ?Antilopini gen. and sp. indet., *Etruria viallii* and *U. azzarolii*) that account for the last representatives (that is, the pre-extinction interval) of the Maremma assemblage and *Oreopithecus*, represented by Podere la Crocina and Montebamboli, and the comparable in age Fiume Santo assemblage (ca. 7.1–6.7, chron C3Ar) (Abbazzi et al., 2008). iii) V3 assemblage (*Hippotherium malpassii*, *Paracervulus cf. australis*, *Procapreolus cf. loczyi* and *Tuscomeryx huerzeleri*) records a great faunal renewal of mainland origin, including the post-extinction interval localities of Ribaldella, Podere Firenze, Podere La Locca, Podere Le Pigne, Cinigiano, Fosso del Pian Calcinaio and Galassi (ca. 6.7–6.4 Ma, chron C3An.2n) (Rook et al., 1999a; Bernor et al., 2001, 2011). The last updated chronology of the Baccinello Basin sediments is used following magnetostratigraphic data (Rook et al., 2011) based on the geopolarity timescale GPTS 2004 (Lourens et al., 2004). Note that small bovids previously considered as belonging to Neotragini by Abbazzi et al. (2008) are here considered Antilopini according to the updated revision of the group by Bärmann et al. (2013) and Bärmann and Schikora (2014). All studied specimens from the Baccinello–Cinigiano Basin are housed at the Museo di Storia Naturale (Sezione Geologia e Paleontologia) of the University of Florence (Italy), while the specimens from Fiume Santo belong to the Soprintendenza per i Beni Archeologici per le Province di Sassari e Nuoro (sample studied while on loan to the Vertebrate Paleontology Laboratory of the Earth Sciences Department, University of Florence).

2.2. Long-term patterns of tooth wear

The study of diets has received increasing attention in paleontological research over the past several decades. Among the various methods of paleoenvironmental and paleoecological reconstruction, analyses based on either stable isotope geochemistry or dental wear are the most widely used as they provide direct information on the properties of the foods consumed and are independent from adaptation. Geochemical methods, such as carbon isotopic ratios derived from fossil tooth enamel are based on the carbon isotopic distinction between C₃ and C₄ photosynthetic pathways. Carbon and oxygen stable isotope analyses from matter and paedogenic carbonate in paleosols from the Baccinello Basin (Matson et al., 2012) and inorganic carbonate in tooth enamel (Nelson and Rook, 2016) have been

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