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## Journal of Human Evolution

journal homepage: [www.elsevier.com/locate/jhevol](http://www.elsevier.com/locate/jhevol)

## Late Miocene insular mice from the Tusco-Sardinian palaeobioprovince provide new insights on the palaeoecology of the *Oreopithecus* faunas

Isaac Casanovas-Vilar<sup>a,\*</sup>, Jan A. van Dam<sup>a,b</sup>, Salvador Moyà-Solà<sup>a,c</sup>, Lorenzo Rook<sup>d</sup>

<sup>a</sup> Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, E-08193 Cerdanyola del Vallès, Barcelona, Spain

<sup>b</sup> Department of Sedimentology and Marine Biology, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, de Boelelaan 1086, 1081 HV Amsterdam, The Netherlands

<sup>c</sup> Unitat d'Antropologia Biològica, Departament BABVE, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, E-08193 Cerdanyola del Vallès, Barcelona, Spain

<sup>d</sup> Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira, 4, I-50121 Firenze, Italy

## ARTICLE INFO

## Article history:

Received 4 August 2010

Accepted 29 January 2011

## Keywords:

*Oreopithecus bambolii*

Late Miocene

Italy

Insular ecosystems

Palaeoecology

Palaeoenvironmental reconstruction

Evolution

## ABSTRACT

*Oreopithecus bambolii* is one of the few hominoids that evolved under insular conditions, resulting in the development of unique adaptations that have fueled an intensive debate. The palaeoenvironment associated with this great ape has been the subject of great controversy as well. On the one hand, palaeobotanical data indicate that *Oreopithecus* likely inhabited mixed mesophytic forests interrupted by swamps; on the other hand, an abundance of hypsodont bovids points towards the existence of dry and open environments. Here, we provide a new approach based on the ecomorphology of the extinct endemic Muridae (rats and mice) of the so-called *Oreopithecus* faunas. Our results show that the successive species of endemic insular murids (*Huerzelerimys* and *Anthracomys*) evolved a number of adaptations observed only in extant family members that include significant proportions of grass in their diet. While this fits the pattern exhibited by large mammals, it contrasts with the available palaeobotanical information, which indicates that grasses were minor components of the vegetation. This contradiction may be explained because these endemic murids may have been adapted to the consumption of particular food items such as hard parts of aquatic plants (as shown by some extant murid species). However, because it is unlikely that the remaining herbivore mammals were adapted to this diet as well, we favour an alternative hypothesis that takes into account the peculiar ecological conditions of insular ecosystems leading to a density-dependent selective regime with strong competition. Such a regime would promote the selection of dental adaptations to increase feeding efficiency and durability of the dentition (such as hypsodonty) as seen in some fossil insular ruminants. This hypothesis requires further testing, but may partly account for parallel evolution of dental traits in phylogenetically unrelated insular mammals.

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## Introduction

*Oreopithecus bambolii* is one of the few hominoids known to have evolved in insular conditions. This Late Miocene great ape inhabited Tuscany and Sardinia (Italy), which at that time were isolated from the European mainland (Sartori, 2001; Rook et al., 2006a) and defined a unique faunal palaeobioprovince, the so-called Tusco-Sardinian palaeobioprovince. *Oreopithecus* shows a number of anatomical features that successive authors have qualified as “unique” or “bizarre” and that may be related to its evolution under insular conditions (Moyà-Solà and Köhler, 1997). Recent reviews have interpreted its postcranial anatomy as indicative of habitual bipedality combined with some climbing adaptations (Köhler and

Moyà-Solà, 1997; Moyà-Solà et al., 1999; Rook et al., 1999). Also, its phylogenetic relationships have been a matter of great controversy. *Oreopithecus* has been considered a cercopithecoid, a hominoid, or a hominid. Most probably, however it is related to the Late Miocene hominoid *Hispanopithecus* representing an insular offshoot of this taxon (Moyà-Solà and Köhler, 1997).

The mammal faunas from the Tusco-Sardinian palaeobioprovince are also known as *Oreopithecus* faunas and consist in an endemic and taxonomically poor assemblage that does not include carnivores except for crocodiles (Delfino and Rook, 2008) and otters (Hürzeler, 1987). Hürzeler and Engesser (1976) were the first to recognize the insular character of these faunas and noted the peculiar adaptations of some mammals. These include the markedly hypsodont molars, ever-growing incisors, and shortened metapodials of some bovids (e.g., *Maremmia*; Hürzeler, 1983). The rodents also tend to develop higher crowned teeth and to become larger than their mainland

\* Corresponding author.

E-mail address: [isaac.casanovas@icp.cat](mailto:isaac.casanovas@icp.cat) (I. Casanovas-Vilar).

relatives (Engesser, 1983, 1989). Mainly thanks to the rodent faunas, it has been possible to subdivide the succession of the *Oreopithecus* faunas from the Baccinello–Cinigiano basin (Tuscany) into different local biozones (named V-0 to V-3) and to constrain their age (see Lorenz, 1968; Engesser, 1989; Rook et al., 1996). The endemic faunas existed from about 8.5 Ma to 6.5 Ma, and went extinct when a connection with the mainland was established in the late Messinian.

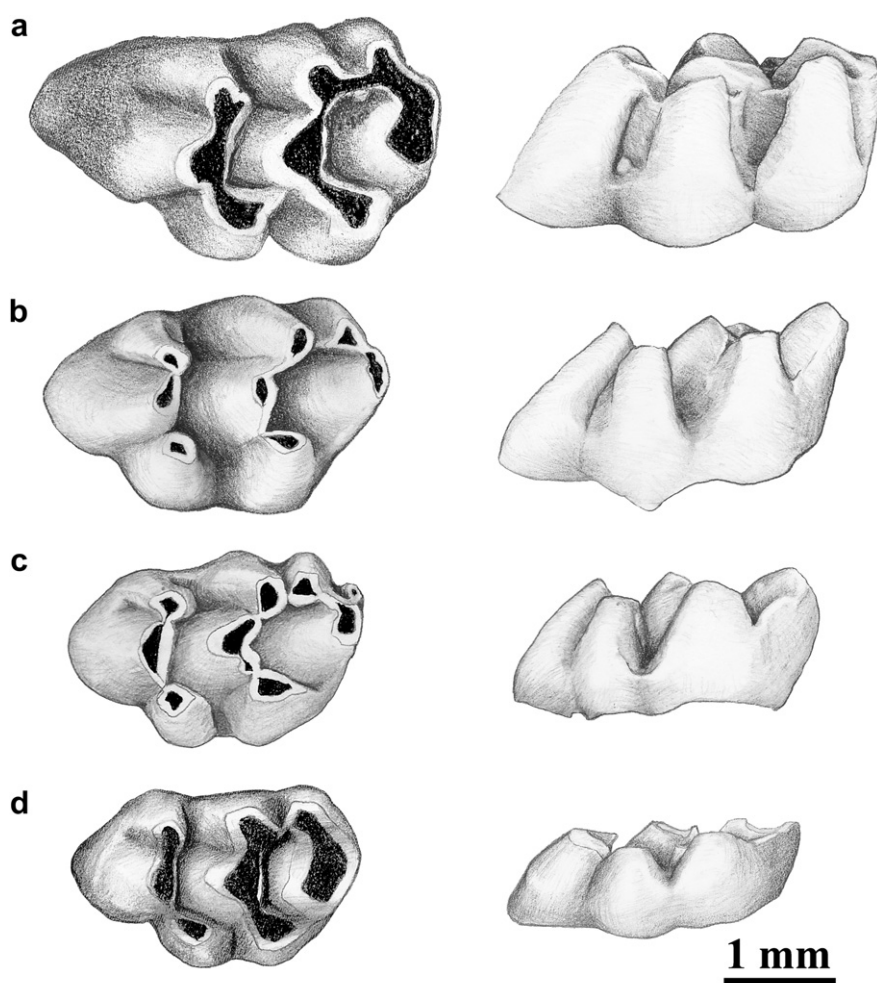
As with almost every other aspect of the *Oreopithecus* faunas, the reconstruction of the palaeoenvironment of the Tusco-Sardinian palaeobioprovince is controversial. While palaeobotanical data (Harrison and Harrison, 1989; Benvenuti et al., 1994) indicate that small swamps interrupted mixed mesophytic forests, the study of the herbivorous mammals points in a markedly different direction. Specifically, the high diversity and abundance of hypsodont bovids have been related to the occurrence of dry and open environments (Bernor et al., 2001; Abbazzi et al., 2008).

In this research, we focus on the functional morphology of the murid (rats and mice) molars from the *Oreopithecus* faunas. Several morphological characters of murid molars have been related to a diet, which, at least partly, consists of fibrous components such as grasses (Crabb, 1976; Braithwaite, 1979; van Dam, 1997). The murids are the only mammal family from the Tusco-Sardinian

palaeobioprovince for which phylogenetic relationships are well resolved (Engesser, 1989; Casanovas-Vilar et al., 2011). The occurrence of the non-endemic murid *Huerzelerimys vireti* (Fig. 1d) in the oldest (V-0) faunal assemblages of Tuscany has allowed placing the age of the colonization of the Tusco-Sardinian area in the Early Turolian (European Mammal Neogene zone MN11). Later on, this species gave rise to the endemic *Huerzelerimys oreopitheci* (from local zones V-1 and V-2), which differs from its ancestor by its larger size, and wider and higher crowned molars (see Fig. 1c). Finally, this trend culminates into the endemic genus *Anthracomys* (from local zones V-2 and V-3; see Fig. 1a and b). Here, we discuss whether or not the changes in molar morphology seen in these endemic murids were related to a dietary adaptation with a grass component. This has important implications, because it would either support or challenge previous mammal-based reconstructions of the environment of *Oreopithecus* as a dry and open landscape.

### Geological and taphonomical background

In Tuscany, the *Oreopithecus* faunas were initially recovered from a series of lignite mines, including Monte Bamboli, Serrazano, Ribolla, and Casteani. Nevertheless, most localities have been found in the small Baccinello–Cinigiano basin, which comprises



**Figure 1.** Occlusal (left) and lingual (right) views of the upper first molars of the murid species from the genera *Huerzelerimys* and *Anthracomys* recorded in the Tusco-Sardinian palaeobioprovince. The material is stored within the collections of the Earth Sciences, Department of the University of Florence (B5, FS-779, FS-831) and the Faculty of Earth Sciences of the Utrecht University (VP-1). (a) *Anthracomys majori* from Monte Bamboli B5. (b) *Anthracomys lorentzi* from Fiume Santo FS-779 (reversed). (c) *Huerzelerimys oreopitheci* from Fiume Santo FS-831. (d) *Huerzelerimys vireti* from Vivero de Pinos (Teruel basin, Spain) VP-1. Note the increase in the height of the crown from *Huerzelerimys vireti* to *Huerzelerimys oreopitheci* and the two *Anthracomys* species. Original artwork by Marta Palmero.

a succession of fluvial and lacustrine sediments (Rook et al., 1996). Several of the mentioned classical *Oreopithecus*-bearing sites have been correlated to lignite layers interbedded in the lower part of the Baccinello-Cinigiano succession (Azzaroli et al., 1986; Rook et al., 1996). In Sardinia, *Oreopithecus* faunas are known from one site only: Fiume Santo. The fossils were recovered from mostly uncemented sands and gravels of fluvial or alluvial origin (Cordy et al., 1995; Rook et al., 2006b).

Taphonomical analyses have been conducted for Fiume Santo (Abbazzi et al., 2008; Casanovas-Vilar et al., 2011). Both small and large vertebrate remains show bone decortication and dissolution of dentine and roots in the teeth, which has been interpreted as the result of their burial in a highly alkaline environment (Fernández-Jalvo et al., 2002). The dentine is only preserved in four *Anthracomys lorenzi* molars. Interestingly, these molars also show conspicuous evidence of digestion similar to those produced by diurnal raptors or mammal carnivores (Andrews, 1990): the enamel is specially affected and has even disappeared from some cusps, while dentine is affected but to a lesser degree. Crocodiles can be excluded as predators because they strongly demineralise calcified tissues leading to the complete disappearance of the enamel but leaving dentine intact (Fisher, 1981). The rest of the small mammal remains of this site do not show evidence of predation.

Regarding the Tuscan material, the fossils from the lignite beds often show extensive crushing and deformation. In the Baccinello-Cinigiano basin microvertebrate remains are not particularly common, although low concentrations occur in certain horizons. Consequently, screen washing of these sediments has been mostly unproductive and the majority of the micromammal remains has been recovered from the outcrop surface. This material mostly consists of isolated teeth and mandibles not showing traces of predation.

Evidence for predation in the case of the Fiume Santo material may have been obscured by the burial of the remains in a highly alkaline environment, but this explanation cannot be assumed for the Tuscan material. All the available evidence indicates that predators were not significant accumulation agents, although the activity of raptors, such as nocturnal owls, cannot be totally excluded since these animals only produce light digestion of the teeth and bone (Andrews, 1990). Islands are characterized by a lack of terrestrial carnivores, but, on the other hand, aerial predators are often present. These sometimes attain a much larger size than their continental relatives in order to cope with the larger-sized micromammals of the insular ecosystems (see, for example, the giant owls *Tyto balearica* from the Balearic Islands and *Tyto robusta* from Gargano, Italy) (Ballmann, 1973; Mourer-Chauviré et al., 1980). However, fossil raptors are not yet known from Tuscany and the only known potential predators are aquatic otters and crocodiles, which do produce extensive signs of digestion on both bones and teeth.

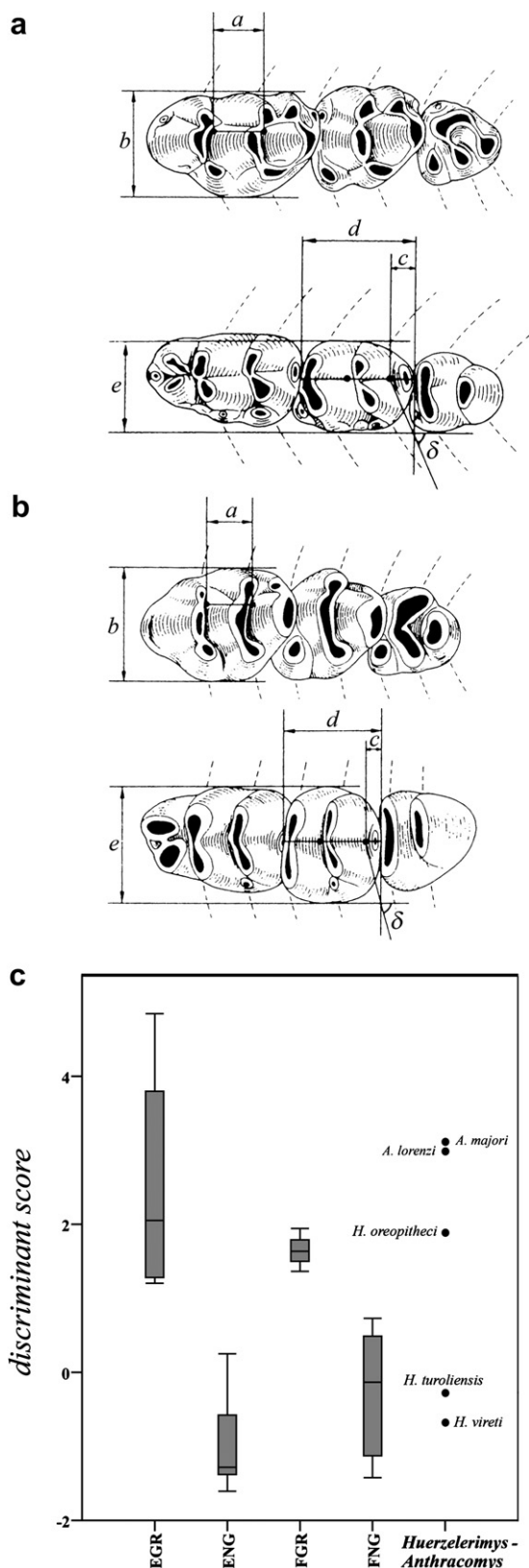
## Materials and methods

We calculated three dental parameters defined by van Dam (1997), Appendix C, for a sample of extant and fossil murid taxa as well as for the species present at sites from the Tusco-Sardinian palaeobioprovince (see Table 1 for the species included in this analysis). The sample size is ten molars (5 M1 and 5 m2) for each species except for *Anthracomys majori* for which fewer specimens were available. These morphometric parameters refer to the relative width of the molars and orientation of the transverse ridges as expressed by three different indices (see Fig. 2a and b): (1)  $b/a$ , an index of relative width of the M1. The measure  $a$  is the distance corresponding to one chevron measured between two landmarks: one in the anterior transverse valley between the labial and the

**Table 1**  
Mean values for  $b/a$ ,  $e/d$ , and  $2\delta$  for the species considered in the analyses. Extant species are indicated in bold. Extant species are classified into two dietary groups: species that include grass in their diet (GR) and those that do not (NG).

Species	Locality	Dietary group	$e/d$	$2\delta$	$b/a$
<b><i>Aethomys kaiseri</i></b>	Wangereze Forest (Uganda)	GR	0.94	143.51	2.46
<b><i>Arvicanthis niloticus</i></b>	Nakuru (Kenya)	GR	1.09	157.25	2.76
<b><i>Dasymys incomtus</i></b>	Chaya (D.R. Congo)	GR	1.20	178.80	2.88
<b><i>Lemniscomys striatus</i></b>	Queen Elizabeth Park (Uganda)	GR	1.11	145.52	2.74
<b><i>Oenomys hypoxanthus</i></b>	Namaganga Forest (Uganda)	GR	0.94	135.48	2.43
<b><i>Pseudomys hermannsburgensis</i></b>	Central Australia	NG	1.00	132.89	1.96
<b><i>Apodemus mystacinus</i></b>	Scalita (Turkey)	NG	0.96	130.38	2.08
<b><i>Apodemus sylvaticus</i></b>	Ethe (Belgium)	NG	0.94	131.41	2.06
<b><i>Grammomys dolichurus</i></b>	Namaganga Forest (Uganda)	NG	0.95	130.46	2.05
<b><i>Hybomys univittatus</i></b>	Wangereze Forest (Uganda)	NG	0.97	129.25	2.54
<b><i>Lenothrix canus</i></b>	Kepong (Malaysia)	NG	0.88	119.65	2.27
<b><i>Pseudomys higginsi</i></b>	Tasmania	NG	0.97	125.62	2.55
<b><i>Thallomys paedulus</i></b>	Stampriet (Namibia)	NG	0.96	129.14	2.12
<b><i>Thammomys rutilans</i></b>	Western Ghana	NG	0.94	131.13	2.13
<i>Anthracomys lorenzi</i> <sup>a</sup>	Fiume Santo (Sardinia, Italy)	–	0.95	163.04	2.39
<i>Anthracomys majori</i> <sup>a</sup>	La Pavolona (Tuscany, Italy)	–	0.98	160.06	2.59
<i>Apodemus gudrunae</i>	Valdecebro 3 (Spain)	–	0.89	128.76	2.10
<i>Huerzelerimys oreopithecii</i> <sup>a</sup>	Fiume Santo (Sardinia, Italy)	–	0.92	156.57	2.19
<i>Huerzelerimys turolensis</i>	Concud 3 (Spain)	–	0.89	133.64	2.23
<i>Huerzelerimys vireti</i> <sup>a</sup>	Puente Minero (Spain)	–	0.96	136.66	2.09
<i>Occitanomys adroveri</i>	Los Mansuetos (Spain)	–	0.99	151.95	2.50
<i>Occitanomys alcalai</i>	Valdecebro 3 (Spain)	–	0.97	138.87	2.30
<i>Occitanomys sondaari</i>	Tortajada A (Spain)	–	0.96	142.04	2.33
<i>Parapodemus barbarae</i>	Los Mansuetos (Spain)	–	0.94	129.08	2.08
<i>Parapodemus lugdunensis</i>	Crebillente 2 (Spain), Lefkon (Greece)	–	0.89	131.72	1.92
<i>Progonomys cathalai</i>	Masía del Barbo 2B (Spain)	–	0.88	127.09	2.21
<i>Progonomys hispanicus</i>	Masía del Barbo 2B (Spain)	–	0.93	136.52	2.23
<i>Rhagapodemus frequens</i>	Tourkoubounia (Greece)	–	0.91	152.52	2.23
<i>Rhagapodemus hautimagnensis</i>	Capu Mannu (Sardinia, Italy)	–	0.84	149.07	1.92
<i>Stephanomys donnezani</i>	Layna (Spain)	–	1.04	144.41	2.66
<i>Stephanomys ramblensis</i>	Puente Minero (Spain)	–	0.99	140.36	2.42

<sup>a</sup> Indicates the species present at the Tusco-Sardinian palaeobioprovince.



**Figure 2.** Upper (top) and lower (below) molar rows of *Parapodemus* (a) and *Aethomys* (b) showing the morphometric variables considered in the analyses. Note that *Aethomys*, a murid that includes grasses in its diet, shows wider molars with straighter lamellae than *Parapodemus*. The distribution of the discriminant scores is summarized in (c). Four distinct dietary groups are considered: extant species that include grass in their diet (EGR), extant species that do not include grass in their diet (ENG), fossil species that are classified as GR by the discriminant analysis (FGR), and fossil species

central cusp, and the other at the same position in the next more posterior valley. The measure  $b$  is the maximum width perpendicular to  $a$ . (2)  $e/d$ , an index of relative width of the m2 where  $d$  is the antero-posterior length of the molar and  $e$  is the maximum width perpendicular to  $d$ . (3)  $2\delta$ , an angle indicating the curvature of the chevrons on the m2. It is estimated as  $\arctan(c/0.5e)$ , where  $c$  is the length of the posterior cusp along  $d$ . The mean values for each one of these indices were computed for each species (see Table 1) and used as variables for a Discriminant Analysis (DA).

For the DA, the extant species were divided into two groups: species that include grass in their diet (GR) and species that do not include grass in their diet (NG). The dietary preferences are taken from van Dam (1997), who used data from Kingdon (1974), Nowak (1991), and Corbet and Hill (1992).

The position of *Oenomys hypoxanthus* is controversial. According to the most recent compilation of Nowak (1999), *O. hypoxanthus* seems to favour moist areas with thick vegetation and feeds mostly on fresh green vegetation and insects. In his most recent guide, Kingdon (1997) mentioned their commonness in elephant grass and sedge beds, with a diet consisting of green leaves, stems, shoots, buds, green seeds, and also insects. Whether or not the green plant parts actually include the grass species themselves is not clear from these descriptions, but seems very likely. In accordance, we prefer assigning this species to the GR group, but given the uncertainty on their dietary habits, we have also repeated the analyses changing its placement to the NG group. In contrast to van Dam (1997), *Pseudomys hermannsburgensis* is assigned to the NG group. This species exclusively inhabits arid areas of Australia and is commonly found in or under hummocks of spinifex grass (Murray and Dickman, 1994; Nowak, 1999). The analysis of its stomach contents indicates that its diet changes significantly throughout the year but seeds and invertebrates are its major components (Murray and Dickman, 1994). Because the goal of DA is not only finding the function that maximizes the separation between the two groups but also assigning the fossil species to one of these groups, the fossil species were left ungrouped.

We present our DA results (Table 2) and a boxplot summarizing the distribution of discriminant scores for four groups (Fig. 2c): (1) extant species that eat grass (EGR); (2) extant species that do not eat grass (ENG); (3) fossil species that are classified as GR by the DA (FGR); and (4) fossil species that are classified as NG (FNG). The species from the genus *Anthracomys* and the genus *Huerzelerimys* (the only two murid genera present at the Tusco-Sardinian palaeobioprovince) are plotted next to the boxplots and their ecology is discussed in more detail in the text. Besides the boxplot of the discriminant scores we have also built similar diagrams for each one of the morphometric parameters, namely  $b/a$ ,  $e/d$ , and  $2\delta$  (see SOM, Fig. S1). All the boxplots as well as the DA were performed using SPSS 15.0.

## Results

Because the number of discriminant functions is always the number of groups minus one, a single discriminant function was obtained that correctly classifies 100% of the extant taxa (Table 2). After cross-validation 85.7% of the cases were correctly classified, the misclassified ones being *Lemniscomys striatus* and *O. hypoxanthus*, which are classified as NG. Most of the fossil species are

that are classified as NG (FNG). Each boxplot shows the mean value for each group, the interquartile range, and the maximum and minimum values as whiskers. The outliers are represented as discrete points outside the whiskers. The species within the genera *Huerzelerimys* and *Anthracomys* are plotted outside the groups (see text for details). (a) and (b) have been modified from van Dam (1997).

**Table 2**  
Main results of the discriminant analysis (see text for details). Extant species are indicated in bold. Extant species are classified into two dietary groups: species that include grass in their diet (GR) and those that do not (NG). The discriminant analysis assigns the fossil species to one of these two groups. Non-significant prediction probabilities as well as the misclassified extant taxa are indicated in bold. Note that all the species present at the Tusco-Sardinian palaeobioprovince are classified as GR with a high prediction probability.

Species	Locality	Dietary group	Predicted group	Prediction probabilities	Predicted group (after cross-validation)	Discriminant score
<b><i>Aethomys kaiseri</i></b>	Wangereze Forest (Uganda)	GR	GR	0.99	GR	2.06
<b><i>Arvicanthis niloticus</i></b>	Nakuru (Kenya)	GR	GR	1.00	GR	2.63
<b><i>Dasymys incommisus</i></b>	Chaya (D.R. Congo)	GR	GR	1.00	GR	4.32
<b><i>Lemniscomys striatus</i></b>	Queen Elizabeth Park (Uganda)	GR	GR	<b>0.66</b>	<b>NG</b>	0.67
<b><i>Onomys hypoxanthus</i></b>	Namaganga Forest (Uganda)	GR	GR	<b>0.74</b>	<b>NG</b>	0.79
<b><i>Pseudomys hermannsburgensis</i></b>	Central Australia	NG	NG	1.00	NG	-2.22
<b><i>Apodemus mystacinus</i></b>	Scalita (Turkey)	NG	NG	1.00	NG	-1.47
<b><i>Apodemus sylvaticus</i></b>	Ethe (Belgium)	NG	NG	1.00	NG	-1.20
<b><i>Grammomys dolichurus</i></b>	Namaganga Forest (Uganda)	NG	NG	1.00	NG	-1.46
<b><i>Hybomys univittatus</i></b>	Wangereze Forest (Uganda)	NG	NG	<b>0.88</b>	NG	-0.14
<b><i>Lenothrix canus</i></b>	Kepong (Malaysia)	NG	NG	0.99	NG	-1.03
<b><i>Pseudomys higginsii</i></b>	Tasmania	NG	NG	0.95	NG	-0.47
<b><i>Thalpomys paeudulcus</i></b>	Stampriet (Namibia)	NG	NG	1.00	NG	-1.52
<b><i>Thammomys rutilans</i></b>	Western Ghana	NG	NG	0.99	NG	-0.96
<i>Anthracomys lorenzi</i> <sup>a</sup>	Fiume Santo (Sardinia, Italy)	—	GR	1.00	—	4.15
<i>Anthracomys majori</i> <sup>a</sup>	La Pavolona (Tuscany, Italy)	—	GR	1.00	—	4.12
<i>Apodemus gudrunae</i>	Valdecebro 3 (Spain)	—	NG	0.96	—	-0.54
<i>Huerzelerimys oreopitheci</i> <sup>a</sup>	Fiume Santo (Sardinia, Italy)	—	GR	1.00	—	3.01
<i>Huerzelerimys turolensis</i>	Concud 3 (Spain)	—	GR	<b>0.55</b>	—	0.52
<i>Huerzelerimys vireti</i> <sup>a</sup>	Puente Minero (Spain)	—	NG	0.98	—	-0.68
<i>Occitanomys adroveri</i>	Los Mansuetos (Spain)	—	GR	1.00	—	2.49
<i>Occitanomys alcalai</i>	Valdecebro 3 (Spain)	—	NG	<b>0.64</b>	—	0.29
<i>Occitanomys sondaari</i>	Tortajada A (Spain)	—	GR	<b>0.86</b>	—	1.02
<i>Parapodemus barbarae</i>	Los Mansuetos (Spain)	—	NG	1.00	—	-1.46
<i>Parapodemus lugdunensis</i>	Crevillente 2 (Spain), Lefkon (Greece)	—	NG	0.99	—	-0.91
<i>Progonomys cathalai</i>	Masía del Barbo 2B (Spain)	—	NG	<b>0.93</b>	—	-0.32
<i>Progonomys hispanicus</i>	Masía del Barbo 2B (Spain)	—	NG	<b>0.57</b>	—	0.38
<i>Rhagapodemus frequens</i>	Tourkoubounia (Greece)	—	GR	1.00	—	2.78
<i>Rhagapodemus hautimagnensis</i>	Capu Mannu (Sardinia, Italy)	—	GR	1.00	—	2.19
<i>Stephanomys donnezani</i>	Layna (Spain)	—	GR	0.94	—	1.34
<i>Stephanomys ramblensis</i>	Puente Minero (Spain)	—	GR	<b>0.61</b>	—	0.61

<sup>a</sup> Indicates the species present at the Tusco-Sardinian palaeobioprovince.

classified as GR except for species within the genera *Apodemus*, *Parapodemus*, and *Progonomys* as well as *Occitanomys alcalai* and *H. vireti*. Prediction probabilities are mostly significant except for the two misclassified extant species and the few fossil taxa classified as NG. DA results are in agreement with the results of the principal components analysis (PCA) carried out by van Dam (1997). If *O. hypoxanthus* is assigned to the NG group, the discriminant function correctly classifies 100% of the extant taxa and 85.7% after cross-validation (results not shown). The misclassified cases are *L. striatus* and *Aethomys kaiseri*. A few fossil taxa are then classified as NG, however, in both analyses the three murid species endemic to the Tusco-Sardinian province (*H. oreopitheci*, *A. lorenzi*, *A. majori*) are classified as GR and their discriminant scores stand out amongst the highest for this group (see Table 2 and Fig. 2c). The discriminant function is  $v = 1.38 \cdot 2\delta + 0.80 \cdot b/a - 1.10 \cdot e/d$  and GR show higher values of  $v$  than NG. Therefore, the murids that include a significant component of grasses in their diets are characterized by broad upper molars with straight lamellae (Fig. 2c).

The discriminant scores for the endemic murids of the Tusco-Sardinian palaeobioprovince are higher than those of other FGR, especially for *A. lorenzi* and *A. majori*, which can only be compared to the extant *Dasymys incommisus*. *D. incommisus* inhabits wet and grassy areas of Africa, south of the Sahara region, and feeds on grasses growing near water, as well as on tough parts of water plants such as stems (Hanney, 1965; Nowak, 1999). A similar diet, including a significant percent of grasses, can be inferred for both *Anthracomys* species. In contrast, *H. oreopitheci* shows a lower discriminant score, slightly higher than that of *Arvicanthis niloticus*.

This extant African murid mainly inhabits savannahs and grasslands of Southern and Eastern Africa and feeds mostly on grasses, although its diet includes other items such as seeds and leaves. Finally, the oldest murid present in the Tusco-Sardinian faunas, *H. vireti*, is assigned to the NG group and shows a value between that of *Pseudomys higginsii* and *Thammomys rutilans*. These two extant mice inhabit tropical to subtropical forest areas from Tasmania and western Africa, respectively (Nowak, 1999). They are omnivores, although green plant parts and fruits define the bulk of their diet. Accordingly, *H. vireti* may have been an omnivore as well.

## Discussion

### The "customary" explanation of dental adaptation and its contradiction with palaeobotanical evidence

The genus *Huerzelerimys* is restricted to the Early and Middle Turolian of the so-called Ibero-Occitanian province, an area comprising the whole Iberian Peninsula and southern France, and characterized by a very homogenous rodent fauna (Hartenberger et al., 1967). The only occurrence of this genus outside the Ibero-Occitanian province is that of *H. vireti* and the endemic *H. oreopitheci* in the faunas of the Tusco-Sardinian palaeobioprovince (Engesser, 1989; Casanovas-Vilar et al., 2011). *H. vireti* dispersed into the Tusco-Sardinian province by the Early Turolian (MN11, local zone V-0) where it gave rise to *H. oreopitheci* (from local zones V-1 and V-2), which, in turn, is the ancestor of the endemic genus *Anthracomys* (from local zones V-2 and V-3). Once we incorporate our

palaeodietary inferences into this phylogenetic scheme, an appealing evolutionary scenario emerges: *H. oreopithecus* evolves from the omnivore *H. vireti* and becomes adapted to a more herbivorous diet that also includes a significant percentage of grasses. This trend is taken further in *A. majori* and *A. lorenzi*, which, according to our results, were probably strictly herbivorous and included an even greater proportion of grasses in their diets. The occurrence of highly hypsodont bovids in the Tusco-Sardinian faunas, such as *Maremmia*, *Tyrrhenotragus*, and *Turritragus*, seems to be in agreement with the occurrence of open and dry environments as suggested by Bernor et al. (2001) and Abbazzi et al. (2008).

Paradoxically, all of this evidence is challenged by the palaeobotanical data from the Tuscan area. These comprise plant macrofossils mostly recovered from the fine clays and silts of Monte Bamboli (Gaudin and Strozzi, 1858) as well as several pollen samples from the same mammal-bearing succession of the Baccinello-Cinigiano basin (Harrison and Harrison, 1989; Benvenuti et al., 1994). The samples, which are unevenly spaced but cover all the series, indicate that during this whole time interval, the area seems to have been covered by a temperate mixed mesophytic forest with conifer forests occurring at upland areas. The high frequency (especially in the oldest samples from units V-0 and V-1) of taxa that commonly grow in wet lowland areas such as *Alnus*, *Salix*, and Taxodiaceae, suggests that the forests may have been interrupted by shallow pools and lakes, which is confirmed by the occurrence of aquatic angiosperms and algae. The forest understory included small trees, shrubs, and ferns, the latter ones being major components of the pollen samples. Mediterranean evergreen elements are very rare. However, the most remarkable fact is the paucity of herbaceous pollen, even though these become more abundant in the younger samples of zone V-3 (Benvenuti et al., 1994). The palaeobotanical evidence clearly contrasts with the interpretation based on mammal hypsodonty, which indicates an open environment with extensive grasslands. Because the same mammalian taxa recovered in the Tuscan localities have been found in Fiume Santo (Abbazzi et al., 2008; Casanovas-Vilar et al., 2011), it is logical to assume that similar environments existed in Sardinia.

The apparent contradiction between functional interpretations of mammalian dentition and palaeobotanical data either presupposes the consumption of tough food other than grass, or should be understood taking into account the special ecological conditions of island ecosystems. According to the first explanation, *Anthracomys* may have specialized in the consumption of hard parts of water plants, which were widely available in the low wetlands. Similar adaptations are seen in *D. incomtus*, the extant “shaggy swamp rat,” which feeds both on grasses as well as on stems and other tough parts of water plants.

#### *An alternative explanation based on the ecology of insular systems*

While our first hypothesis would account for the evolution of such dental adaptations in the murids, it is unlikely that most of the herbivorous mammals present in the area fed on hard parts of water plants. Alternatively, the evolution of dental adaptations that promote functional durability and efficiency of the dentition may have arisen because of the unique ecological conditions of insular ecosystems (Köhler, 2010). Endemic insular mammals differ from their mainland relatives in sharing a series of unique traits irrespective of phylogeny or geological age (Sondaar, 1977; Grant, 1998). The unusual adaptations that characterize insular vertebrates such as gigantism and dwarfism are commonly explained in the context of island ecology (Sondaar, 1977, 1991; Case, 1978; Heaney, 1978; Grant, 1998). These include the limitation of space and, even more importantly, of trophic resources. Because species diversity is positively related to island size (MacArthur and Wilson,

1967), small- or medium-sized islands are generally characterized by low diversity with an absence or reduction of predation because of its position at the top of the trophic pyramid. The lack of control of population growth rates through predation leads to an increase in population density and, concomitantly, to an increase in inter- and intraspecific competition for limited food resources (e.g., MacArthur and Wilson, 1967; Sondaar, 1977, 1991; Grant, 1998). This will periodically lead to times of overpopulation, resulting in overconsumption of resources and subsequent episodes of mass starvation (Sondaar, 1977, 1991; Alcover et al., 1981). This process has been reconstructed on the basis of several island fossil sites, where the existence of a starvation period is clear through evidence of malnutrition and disease (Sondaar, 1977, 1991; Köhler, 2010). The mass starvation episodes are highly selective moments, increasing even more the competition between individuals for the scarce and probably low-quality remaining food resources. Under this regime, density-dependent selection is expected to favour an increase in efficiency coupled with a decrease in productivity (MacArthur and Wilson, 1967; Boyce, 1984). Many insular mammals, from elephants to rodents, have evolved towards greater feeding efficiency and durability of dentition, in order to obtain and to process low-quality food resources. In insular ruminants, this usually implies the development of adaptations that resemble those of grazers, such as high-crowned cheek teeth, which are proportionally broader in the upper series as compared to the lower one (van der Geer, 2005; van der Geer et al., 2010). However, some adaptations of insular mammals to provide increased durability and efficiency of the dentition are not present in extant or fossil non-insular grazers. These include the development of ever-growing lower incisors, which have evolved in at least two unrelated insular bovids: *Myotragus* from the Balearic Islands (Alcover et al., 1981) and *Maremmia* from the Tusco-Sardinian palaeobioprovince (Hürzeler, 1983). Furthermore, *Myotragus* has lost some premolars and has markedly increased the size of its posterior molars (Alcover et al., 1981). Finally, an increase in enamel thickness is also common in insular mammals, for example in some suids (*Sus nanus* from the Plio-Pleistocene of Sardinia, and *Eumaiiochoerus etruscus* from the Late Miocene Tusco-Sardinian palaeobioprovince; van der Made, 1988, 1999, respectively) as well as in the hominoid *Oreopithecus* (Olejniczak et al., 2007; Zanolli et al., 2009).

In the case of *Myotragus*, it has been suggested that these unusual dental adaptations evolved in response to increased individual life expectancy (Köhler and Moyà-Solà, 2009) by extending the lifetime of the feeding apparatus (Köhler, 2010). Molars worn down to their roots are frequent in *Myotragus* samples but very rare in continental settings because predation selectively affects juvenile and old age classes. Therefore, in a predator-free environment these changes in tooth morphology would be the main constraint on longevity, since they would allow for the exploitation of dietary items otherwise not available to a “normal” bovid dentition (Köhler and Moyà-Solà, 2004; Köhler, 2010). An alternative hypothesis, proposed by Raia et al. (2003) in their study of the Sicilian pygmy elephant (*Elephas falconeri*), suggests that hypsodonty evolved as a response to increased food intake, which is in line with the observation of an increased metabolic rate in dwarf forms as compared to their continental ancestors. The increased amount of food would result in rapid tooth wear, which would require a higher hypsodonty. However, this alternative explanation is contrary to the predictions of the equilibrium model of insular biogeography (MacArthur and Wilson, 1967) and presupposes favourable environmental conditions with abundant and high quality food supply, which is not apparent from the fossil record given the evidence of malnutrition seen in many fossil insular mammal samples (Sondaar, 1977, 1991; Köhler, 2010).

Island faunas have been considered “laboratories” of evolution since Darwin’s early observations on the Galápagos Islands. As such, they can reveal evolutionary responses that can have very distinct implications for ecomorphological inferences. If biotic interactions drive the evolutionary process (the “Red Queen” hypothesis) rather than environmental change (the “Court Jester” hypothesis) (Barnosky, 2001), palaeoenvironmental inferences on the basis of dentition may not reflect the response to environmental change but to competition. As exposed above, continuous evolutionary change of the masticatory complex is expected when isolated taxa are under a density-dependent selective regime fuelled by strong and continuously acting competition. This would explain why the murids of the Tusco-Sardinian palaeobioprovince, as well as other herbivores, show high-crowned teeth coupled with other adaptations that promote increased durability and efficiency of the dentition, even though the palaeobotanical evidence clearly shows that grasses should have been minor components of the vegetation.

## Conclusions

All the endemic murid species of the Tusco-Sardinian palaeobioprovince are characterized by high-crowned, broad upper molars with straight lamellae. An ecomorphological analysis of the dentitions of extant and fossil murids shows that these features are characteristic of predominantly herbivorous murids that include a significant proportion of grasses in their diets and that tend to inhabit open habitats. Nevertheless, this result is incongruent with the palaeobotanical evidence that clearly shows that grasses were not major components of the vegetation in the Tusco-Sardinian palaeobioprovince. Therefore, the common evolution of adaptations that provide increased functional durability and efficiency of the dentition (such as hypsodonty) in the mammals of this isolated area may not be primarily related to the existence of dry and open habitats. As seen in extant murids, they could arise from an adaptation to a special diet (e.g., including stems of water plants). On the other hand, an alternative explanation for the evolution of such adaptations can be proposed considering the special ecological conditions of island ecosystems, in particular absence or reduction of predation and high competition. This emphasizes the role of biotic interactions, which may be more important than environmental changes for insular mammals. On islands, these ecological factors shape a density-dependent selective regime stimulated by strong and continuously acting inter- and intraspecific competition, which would favour the selection of dental adaptations to increase feeding efficiency and durability. Obviously, this hypothesis needs further testing in other insular mammals taking into account other approaches such as paleohistology.

## Acknowledgements

This study has been possible thanks to the support of the Spanish Ministerio de Ciencia e Innovación (CGL2010-21672/BTE, CGL2008-00325/BTE and JCI-2010-08241 contract to I. C.-V.) and the Generalitat de Catalunya (Grup de Recerca Consolidat 2009 SGR 754 of the AGAUR). Palaeontological research at Fiume Santo is carried out under an agreement between the “Soprintendenza per i Beni Archeologici per le Province di Sassari e Nuoro” and the Earth Sciences Department of the University of Florence (responsible LR). For the continuous support during fieldwork at Fiume Santo, LR thanks the personnel of the Paleontology Section within the local office of the Soprintendenza archeologica (L.Trebini, N. Tuveri, and M. Arca), as well as the precious collaboration by M. Delfino, G. Gallai, and L. Abbazzi. Fieldwork at Fiume Santo was made possible thanks to the support of the National Geographic Society

(grant #7484-03 to LR), the RHOI program at the University of Berkeley (project NSF-BCS-0321893), and the logistic and economic support of ENDESA Italia. We sincerely acknowledge the comments and suggestions by the editors and two anonymous reviewers, which surely improved the final result.

## Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2011.01.003.

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