

Original article

The rodents from the Late Miocene *Oreopithecus*-bearing site of Fiume Santo (Sardinia, Italy)[☆]

Les rongeurs du site miocène supérieur à Oreopithecus de Fiume Santo (Sardaigne, Italie)

Isaac Casanovas-Vilar^{a,*}, Jan A. van Dam^{a,b}, Luciano Trebini^c, Lorenzo Rook^d

^a Institut Català de Paleontologia, Universitat Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain

^b Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, de Boelelaan 1086, 1081 HV Amsterdam, The Netherlands

^c Soprintendenza per i Beni Archeologici per le Province di Sassari e Nuoro, Piazza S. Agostino 3, 07100 Sassari, Italy

^d Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira, 4, 50121 Firenze, Italy

Received 7 May 2010; accepted 9 August 2010

Available online 16 February 2011

Abstract

The locality of Fiume Santo (Sardinia, Italy) represents the westernmost extension of endemic *Oreopithecus*-bearing faunas. Here we describe the rodent fauna recovered at this site, which only includes the murids *Huerzelerimys oreopithecii* and *Anthracomys lorenzi*, and the glirids *Anthracoglis engesseri* nov. sp. and *Anthracoglis* nov. sp. *I. A. engesseri* nov. sp. differs from *Anthracoglis marinoi*, the other species of this genus known so far, by its larger size, wider upper cheek teeth and more reduced accessory ridges, particularly in the upper cheek teeth. *Anthracoglis* nov. sp. I is only known by a single tooth and cannot be adequately characterized. The fauna seems to be a mixture of elements from the V-1, V-2 and V-3 local zones of the Baccinello-Cinigiano basin (Tuscany, Italy), with *H. oreopithecii* being characteristic from zone V-1 and *Anthracoglis lorenzi* from zone V-3. Nevertheless, a few remains of *A. lorenzi* have been also recovered from V-2 assemblages at Baccinello and *A. engesseri* nov. sp. is also recorded in Monte Bamboli, which is correlated to V-2 faunas. Accordingly, a correlation to V-2 zone of the Baccinello-Cinigiano basin is preferred. Finally, the structure and composition of the rodent assemblage is compared to those of the Tuscan sites. The Fiume Santo assemblage resembles the insular faunas of Tuscany by its low species richness, although it is more balanced. This may be related to slight chronological or environmental differences between the two areas or to the existence of a geographical barrier.

© 2011 Elsevier Masson SAS. All rights reserved.

Keywords: Insular faunas; Small mammals; Muridae; Gliridae; New species; Late Miocene; Hominoidea

Résumé

La localité de Fiume Santo (Sardaigne, Italie) représente l'extension la plus occidentale des faunes endémiques à *Oreopithecus*. Nous décrivons ici la faune de rongeurs de ce site, qui ne comprend que les muridés *Huerzelerimys oreopithecii* et *Anthracomys lorenzi*, ainsi que les gliridés *Anthracoglis engesseri* nov. sp. et *Anthracoglis* nov. sp. *I. A. engesseri* nov. sp. diffère de *Anthracoglis marinoi*, l'autre espèce de ce genre connue à ce jour, par sa plus grande taille, des dents jugales supérieures plus larges et des crêtes accessoires plus réduites, notamment sur les dents jugales supérieures. *Anthracoglis* nov. sp. I n'est connu que par une seule dent et ne peut être correctement caractérisé. La faune semble être un mélange d'éléments des zones locales V-1, V-2 et V-3 du bassin Baccinello-Cinigiano (Toscane, Italie), *H. oreopithecii* étant caractéristique de la zone V-1 et *Anthracoglis lorenzi* de la zone V-3. Néanmoins, quelques restes de *A. lorenzi* ont également été retrouvés dans des assemblages de la zone V-2 à Baccinello, et *A. engesseri* nov. sp. est également enregistré au Monte Bamboli, corrélé aux faunes de la zone V-2. De fait, une corrélation avec la zone V-2 du bassin Baccinello-Cinigiano est favorisée. Finalement, la structure et la composition de l'assemblage de rongeurs sont comparées à celles des sites toscans. L'assemblage de Fiume Santo ressemble aux faunes insulaires de Toscane par sa faible richesse spécifique, bien qu'il soit plus équilibré. Cela peut être relié à de légères différences chronologiques ou environnementales entre ces deux régions, ou bien à l'existence d'une barrière géographique.

© 2011 Elsevier Masson SAS. Tous droits réservés.

Mots clés : Faune insulaire ; Petits mammifères ; Muridae ; Gliridae ; Nouvelle espèce ; Miocène supérieur ; Hominoidea

[☆] Invited editor: Jordi Agustí.

* Corresponding author.

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

1. Introduction

The Late Miocene land mammal record of Italy includes just a few tens of localities, which evidence a complex palaeogeographic history. During most of the Miocene, Italy was an archipelago isolated from the European mainland. Up to three distinct bioprovinces can be recognized during this time span: the Abbruzzi-Apulia, Tusco-Sardinia and the Calabria-Sicily areas (Rook et al., 2006). The two former bioprovinces are characterized by highly endemic faunas and do not share a single taxon with each other. This suggests that they represent two distinct emerged areas with completely independent palaeobiogeographic histories, one on the Adriatic side of Italy (Abruzzi-Apulia) and the other on the Tyrrhenian side (Tusco-Sardinia). The Messinian faunas of the Calabria-Sicily area include non-endemic mammals related to North African and European taxa (Rook et al., 2006).

Most of what is known about the Tusco-Sardinian palaeobioprovince is documented by the faunas from the Baccinello-Cinigiano basin in southern Tuscany. The earliest fossil finds date back to the 19th century and were recovered from lignite mines (Savi, 1843; Gervais, 1872; Major, 1873). The Tuscan faunas have deserved considerable attention because of the recovery of a fossil great ape, *Oreopithecus bambolii*, in the Monte Bamboli coal mine, as well as in other mines in the region. *Oreopithecus* deserves the doubtful honour of being the fossil primate for which the greatest number of different phylogenetic hypotheses has been proposed. It has been considered as a cercopithecoid, a hominoid, a hominid and even a simian descendent from Eocene artiodactyls (for a review, see Delson, 1987). All these works have referred to *Oreopithecus* as a “bizarre” or “enigmatic” primate and the reconstructions of its postural and locomotor behaviour are as distinct as the reconstruction of its phylogenetic relationships. More recent studies have related this taxon to other European Miocene hominoids such as *Hispanopithecus* (Moyà-Solà and Köhler, 1997) and 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). The faunas of the Tusco-Sardinian palaeobioprovince are often referred to as *Oreopithecus* faunas and consist of an endemic and taxonomically poor assemblage without carnivores other than otters (*Tyrrhenolutra*, *Paludolutra*). Hürzeler and Engesser (1976) were the first to recognize the endemic insular character of these faunas and remarked that many mammals show typical specializations such as markedly hypsodont cheek teeth and continuously growing incisors (e.g., the bovid *Maremmia*; Hürzeler, 1983). The peculiar anatomical adaptations of *Oreopithecus* would also be a product of an insular evolution (Moyà-Solà and Köhler, 1997). The endemic rodents show a tendency to attain large sizes and to develop high-crowned cheek teeth (Hürzeler and Engesser, 1976). These include a giant dormouse known by a single molar (*Gliridae* nov. gen. et nov. sp. in Engesser, 1983), the much smaller dormouse *Anthracoglis marinoi* (Engesser, 1983), and the mice *Huerzelerimys oreopithecii*, *Anthracomys lorenzi* and *Anthracomys majori* (Engesser, 1989).

The dating of the *Oreopithecus* faunas has been problematic because of their endemism. The Baccinello-Cinigiano basin succession has been divided into four different biochronological units named V-0 to V-3 (Lorenz, 1968; Engesser, 1989; Rook et al., 1996). The V-1 and V-2 faunas are completely endemic but the V-0 and V-3 assemblages are not, allowing some constraints on the age of the *Oreopithecus* faunas. The occurrence of the non-endemic murid *Huerzelerimys vireti* in the V-0 assemblage allowed Engesser (1989) to propose a tentative correlation of this unit with Mein's Mammal Neogene (MN) Zones. This murid indicates a MN11 age for V-0, while the presence of *Apodemus*, *Celadensia* and *Hystrix* in the V-3 assemblage points towards an MN13 age (Engesser, 1989; Rook et al., 2000). Therefore, the *Oreopithecus* faunas were short lived, spanning less than 2 million years, from ~8.5 to ~6.5 Ma (approximate chronological boundaries for the MN zones following Agustí et al., 2001). The chronology of the endemic faunas has been further refined thanks to the radiometric dating of 7.5 ± 0.03 Ma for a volcanic layer within the Baccinello succession, placed between units V-1 and V-2 (Rook et al., 2000).

In the early 1990s a new *Oreopithecus*-bearing site, named Fiume Santo, was discovered in north-western Sardinia during the construction of a parking area near a thermo-electric power station (Cordy and Ginesu, 1994; Cordy et al., 1995; Rook et al., 2006a). This finding allowed the expansion of the geographical range of the endemic *Oreopithecus*-bearing faunas in the northern Tyrrhenian area from Tuscany to Sardinia. Furthermore, the fossils recovered at Fiume Santo do not show the extensive deformation and distortion present in the specimens recovered in the lignite mines of Tuscany. The Fiume Santo site has been intensively sampled and has delivered a rich fauna that includes both macro- and microvertebrates. The macrovertebrates were described by Abbazzi et al. (2008) and include many other endemic taxa shared with the Tuscan sites besides *Oreopithecus* (*Maremmia*, *Umbrotherium*, *Tyrrhenotragus*, *Eumaiocoerus*). On the basis of the macromammal assemblage Abbazzi et al. (2008) correlated Fiume Santo to the V-2 unit of the Baccinello-Cinigiano basin. Regarding the small mammals, Cordy et al. (1995) listed the murid *Valerimys* aff. *turoliensis* (sic) and a large-sized glirid. Thanks to the continuous works carried out at the Fiume Santo site by the team of the University of Florence, a rich microvertebrate sample that includes ~200 rodent cheek teeth is now available. In this work we describe these rodent remains and we provide further data on the chronology and palaeoecology of the Fiume Santo fauna.

2. Material and methods

The material described in this paper is provisionally housed at the Earth Sciences Department of the University of Florence (collection numbers refer to as FS-#). Once the study of the site will be accomplished, the final repository of the entire Fiume Santo fossil collection will be in the archives of the *Soprintendenza per i Beni Archeologici per le Provincie di Sassari e Nuoro*. The classification of rodents used in this work follows McKenna and Bell (1997) while the terminology of the

dental features and the measurement method follow Daams (1981) and Van de Weerd (1976) for the Gliridae and the Muridae, respectively. Estimated measurements (due to minor damage or distortion) are given within parentheses. The measurements were taken using a Nikon Measuroscope 10 optic caliper connected to a digital monitor Nikon SC-112. When three or more specimens were measured, the mean measurements, as well as maximum (max.) and minimum (min.) values and the standard deviation (SD), are provided. The determination and measurements of all the studied specimens is given in Appendix A. The drawings of the specimens were performed using a Leica light camera mounted on a Leica MZ6 stereomicroscope while the photographs of the specimens were taken using a Leica IC3D camera mounted on a Leica MZ16 stereomicroscope. On the figures (except in Fig. 1), all teeth are figured as if they were from the left side, indicating those cases in which the original image has been reversed.

3. Taphonomical remarks

At the present the regional geological context of Fiume Santo is not satisfactorily known (Cordy et al., 1995) and an extensive geological survey of the area is in progress (Benvenuti and

Papini, ongoing work). The fossils were recovered from silts and sands from a single well-defined stratigraphic layer. The roughly similar state of preservation of all the recovered remains agrees with their provenance from a single level. In general the large mammal bones are not well preserved and appear “decorticated”, with the innermost part of cortical bone or even the trabecular bone being exposed. Concerning teeth, the enamel is well preserved but the dentine and roots are often chemically eroded or sometimes completely absent (Rook et al., 2006a; Abbazzi et al., 2008). The small mammal remains show a similar state of preservation with bone decortications that expose the trabecular bone in the epiphyses (Fig. 1(4, 5)). The dentine and roots are not preserved and the dental remains consist of just a fragile wall of enamel (Fig. 1(1, 2, 6)). This indicates that the remains were buried in a highly alkaline environment, since this kind of environments predominantly affects the most organic components of the skeleton (bones, roots and dentine), leaving the highly mineralized enamel intact (Fernández-Jalvo et al., 2002). Brief immersions of teeth in alkaline solutions result in a surface and mosaic cracking of the dentine (experiments by Fernández-Jalvo et al., 2002; see also Abbazzi et al., 2008). The dentine is preserved in just four *Anthracomys* molars (see Fig. 1(3)). Interestingly in these specimens the dentine is partly dissolved, but the enamel is more strongly affected and has even

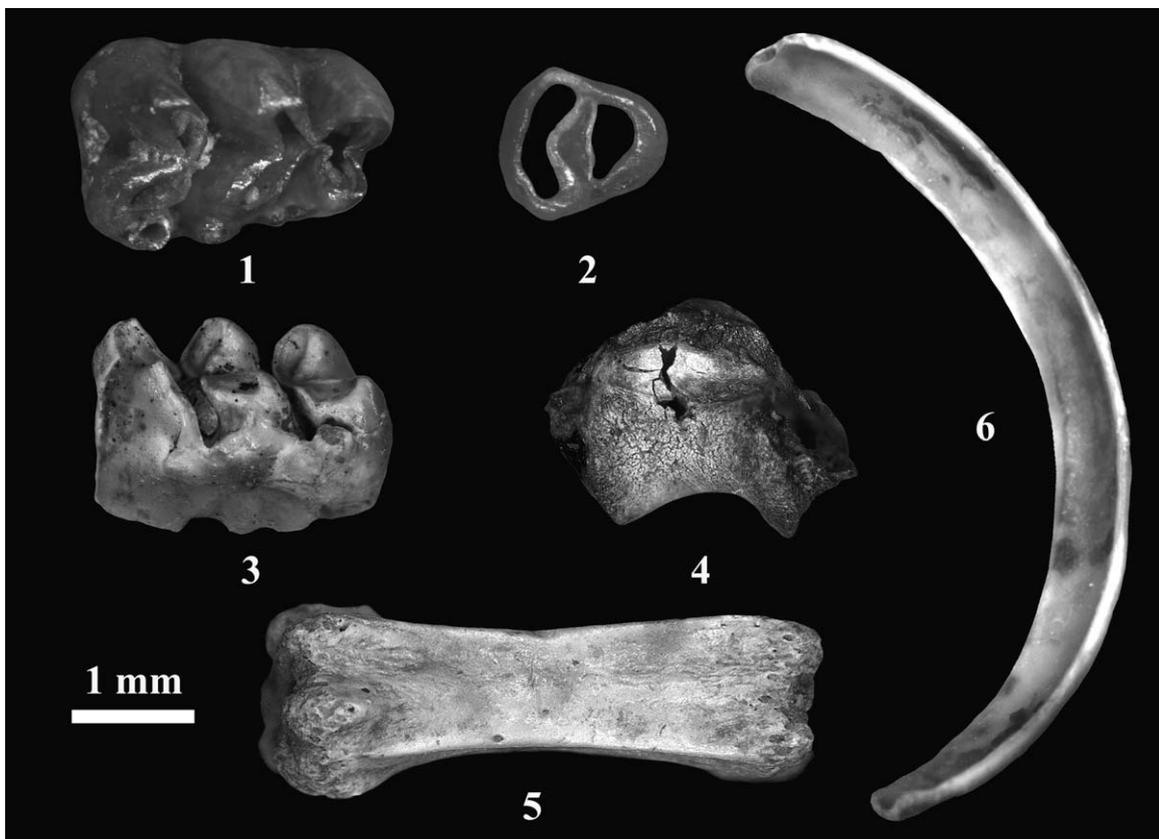


Fig. 1. Stereomicroscope photographs of micromammal remains from Fiume Santo showing distinct taphonomical features. **1.** Complete dissolution of dentine in a right m1 of *Anthracomys lorenzi* (unnumbered specimen). **2.** Complete dissolution of dentine in a highly worn left m3 of *Huerzelerimys oreopitheci* (FS-899). **3.** Heavily digested left m1 of *A. lorenzi* (FS-800). Unlike the condition in the rest of the dental material, the dentine and the base of the roots are preserved. The enamel in the antero-labial wall of the molar is completely dissolved, exposing the dentine. **4.** Broken distal epiphysis of a left humerus of a small mammal. Note the cracking of the bone surface and the exposition of trabecular bone on the edges of the epiphysis. **5.** Caudal vertebra of a small mammal. Note the exposed trabecular bone on the vertebral processes. **6.** Complete dissolution of dentine in a fragment of a lower incisor or rodent.

partially disappeared from the walls of some cusps. The dissolution of enamel is commonly related to the digestion of the remains by a predator. Quite surprisingly, the posterior burial of these remains did not lead to the disappearance of the dentine. Different grades of digestion can be recognized allowing the identification of the predator(s) involved in the accumulation (Andrews, 1990). The intensity of the alterations is related to the acidity of the stomach gastric juices, to the time of digestion and enzymatic activity (Denys et al., 1995). The high degree of digestion shown by these molars is comparable to that produced by mammalian carnivores and certain diurnal raptors (Andrews, 1990). Nocturnal owls, which produce very light digestion, can be excluded. We can also exclude crocodiles, which are present at Fiume Santo (Abbazzi et al., 2008; Delfino and Rook, 2008), since they strongly demineralise calcified tissues, leading to the complete disappearance of the enamel but leaving dentine intact (Fisher, 1981). Given that the evidence for predation is scarce our micro-mammal accumulation does not seem to be the product of the action of predators. However, predation by nocturnal owls cannot be excluded. These animals only produce light digestion of the dentine and bone (Andrews, 1990), but unfortunately the potential evidence has disappeared by burial in an alkaline environment.

4. Systematic palaeontology

Order RODENTIA Bowdich, 1821

Family GLIRIDAE Muirhead, 1819

Subfamily LEITHIINAE Lydekker, 1896

Genus *Anthracoglis* Engesser, 1983

Anthracoglis engesseri nov. sp.

Fig. 2(1–9)

Derivatio nominis: Dedicated to Dr. Burkart Engesser from the Naturhistorisches Museum of Basel, who pioneered the study of the rodent faunas of the Tusco-Sardinian palaeobio-province.

Holotype: A left isolated M2 from Fiume Santo (FS-739; Fig. 2(3)).

Paratypes: The other specimens of this taxon recovered at the type locality are designed as paratypes of *A. engesseri*.

Type locality: Fiume Santo, north-west Sardinia, Italy.

Age: Late Miocene, Turolian, local biozone V-2 from the Baccinello-Cinigiano basin (Tuscany).

Hypodigm: A single isolated M2 recovered at Monte Bamboli (Tuscany) and stored within the collections of the Naturhistorisches Museum of Basel (collection number Bb. 20) is also ascribed to *A. engesseri* sp. nov.

Material: 6 P4, 4 M1, 6 M2, 1 M3, 5 p4, 6 m1, 5 m2, 7 m3, 7 molar fragments.

Measurements: See Table 1, Fig. 3 and Appendix A.

Diagnosis: Large-sized *Anthracoglis* species with wide upper cheek teeth. The accessory ridges, especially in the upper cheek teeth, tend to be short and weak. In the M1 and M2 the anteroloph and the posteroloph are separated from the paracone and the metacone by a weak groove.

Differential diagnosis: Differs from *Anthracoglis marinoi* by: its larger size; wider upper cheek teeth; more reduced accessory ridges, particularly in the upper cheek teeth; the anteroloph and posteroloph separated from the paracone and metacone, respectively, in the M1 and the M2.

Description:

Upper dentition: the roots are not preserved because the dentine is dissolved. The upper cheek teeth are wider than long and the crown is relatively high for a glirid. The wear surface is

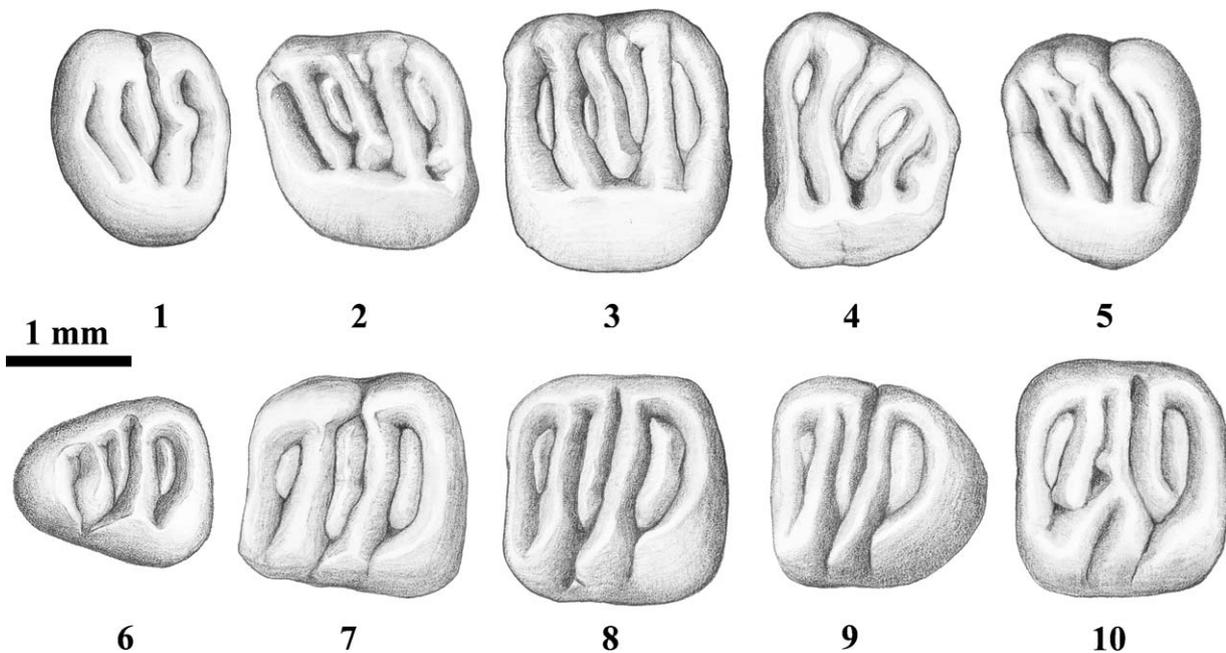


Fig. 2. Gliridae from Fiume Santo. 1–9. *Anthracoglis engesseri* nov. sp. from Fiume Santo. 1: Right P4 FS-732 (reversed); 2: Left M1 FS-734; 3: Left M2 FS-739, holotype; 4: Right M3 FS-744 (reversed); 5: Left P4 FS-728; 6: Right p4 FS-748 (reversed); 7: Left m1 FS-753; 8: Left m2 FS-760; 9: Left m3 FS-763. 10. *Anthracoglis* nov. sp. I. Right m2 FS-775 (reversed). Original artwork by Marta Palmero.

Table 1
Length and width synthetic measurements for the molars of *Anthracoqlis engesseri* nov. sp. from Fiume Santo.

	Length					Width				
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD
P4	4	1.53	1.66	1.78	0.12	5	1.82	1.94	2.03	0.10
M1	3	1.86	1.99	2.05	0.11	4	2.09	2.16	2.24	0.06
M2	4	1.92	2.03	2.11	0.09	5	2.32	2.39	2.48	0.07
M3	1	–	1.67	–	–	1	–	2.18	–	–
p4	3	1.74	1.84	1.93	0.10	3	1.51	1.63	1.70	0.11
m1	5	2.03	2.07	2.12	0.03	5	2.04	2.10	2.22	0.07
m2	5	1.99	2.07	2.17	0.08	5	2.07	2.20	2.38	0.12
m3	6	1.77	1.90	2.02	0.10	6	1.73	1.89	2.06	0.11

N: number of measured specimens; SD: standard-deviation.

concave and the lingual border is clearly higher than the labial one. The main ridges are wide.

Two different P4 morphotypes can be distinguished on the basis of the arrangement of the main ridges. In the first one (FS-728, FS-729; Fig. 2(5)) there are four main ridges that merge the endoloph: anteroloph, protoloph, anterior centroloph and posteroloph. The metaloph is somewhat narrower than the main ridges and does not join the endoloph, just extending to the midpoint of the molar. In the second morphotype (FS-730, FS-732, FS-733; Fig. 2(1)) there are also four main ridges that join the endoloph, being defined by the anteroloph, protoloph, metaloph and posteroloph. The metaloph is well developed whereas the anterior centroloph is narrower than the main ridges and does not reach the endoloph. In one specimen (FS-730) this ridge is clearly lower than the main ones and it is completely isolated. The main ridges tend to end in rather prominent buccal cusps. The development of accessory ridges is highly variable. However, when present, these ridges are always narrower than the main ones. FS-728 (Fig. 2(5)) shows two accessory ridges between the protoloph and the anterior centroloph. The most anterior one is weaker and shorter and is connected to the protoloph whereas the distal one weakly joins the anterior centroloph. An isolated accessory ridge is present between the protoloph and the anterior centroloph in FS-729. In FS-730 there is a tiny accessory ridge between the metaloph and the posteroloph which is placed towards the labial side. The accessory ridges are missing in the remaining P4.

The M1 shows four main ridges which are straight and markedly oblique to the antero-posterior axis of the molar: anteroloph, protoloph, metaloph and posteroloph. All these ridges merge the endoloph. There is always a long anterior centroloph generally as wide as the main ridges, which joins the endoloph in one specimen (FS-734; Fig. 2(2)). In all the other specimens this ridge ends free except in one (FS-735) where it joins the posterior centroloph. In all the specimens but this one the posterior centroloph is narrower, lower and shorter than the anterior one. The accessory ridges (when present) are only slightly narrower than the main ones. The specimens that are not damaged (FS-734, FS-736) show at least two accessory ridges: an isolated ridge between the protoloph and the anterior centroloph and another one in their last syncline. The latter one is present in all the studied M1. FS-736 also shows a third

accessory ridge between the anteroloph and the protoloph which is quite long and joins the anteroloph. This accessory ridge is also present in another specimen (FS-735) but it is isolated.

The M2 resembles the M1, however the main ridges cross the antero-posterior axis of the molar in a less acute angle than in the first molar. The anteroloph is separated from the paracone by a marked groove, whereas the posteroloph is separated from the metacone by a much weaker one. The anterior centroloph is always present and is as wide as the main ridges. In most molars this ridge is long and more oblique than the main ridges (FS-739; Fig. 2(3)), but in one (FS-738) it is shorter and parallel to the main ones while in another (FS-741) its lingual end merges with the metaloph. The posterior centroloph is present in all specimens but one (FS-738). This ridge is long, reaching the midpoint of the molar. It usually joins the metacone (FS-741, FS-742, FS-743), but in one specimen it is separated from this cusp by a weak groove (FS-739) and in a last one this ridge is somewhat less developed and it is completely isolated (FS-740). Most molars show three accessory ridges, which are slightly narrower than the main ones. These are placed in the first, second and fourth synclines. The second accessory ridge is the weaker one and it is missing in one specimen (FS-738). The last one is the best developed and it even contacts with the posteroloph in two cases (FS-738, FS-741).

The M3 is markedly wider than long and the distal part of the molar is reduced (FS-744; Fig. 2(4)). It shows four main ridges: anteroloph, protoloph, metaloph and posteroloph. The metaloph and the posteroloph are highly reduced and both ridges are connected labially. These two ridges have a sinuous course whereas the anteroloph and the protoloph are straight. The anteroloph ends in a marked labial cusp which is almost as high as the paracone. The protoloph is separated from the anteroloph in the labial side. The anterior centroloph is shorter than the posterior one and is completely isolated. The posterior centroloph is separated from the metacone by a weak groove. There are three short accessory ridges, which are almost as wide as the main ones: one between the anteroloph and the protoloph, one between the posterior centroloph and the metaloph, and a last one between the metaloph and the posteroloph which is partly fused to the posteroloph. The two more anterior accessory ridges are placed in the labial half of the molar.

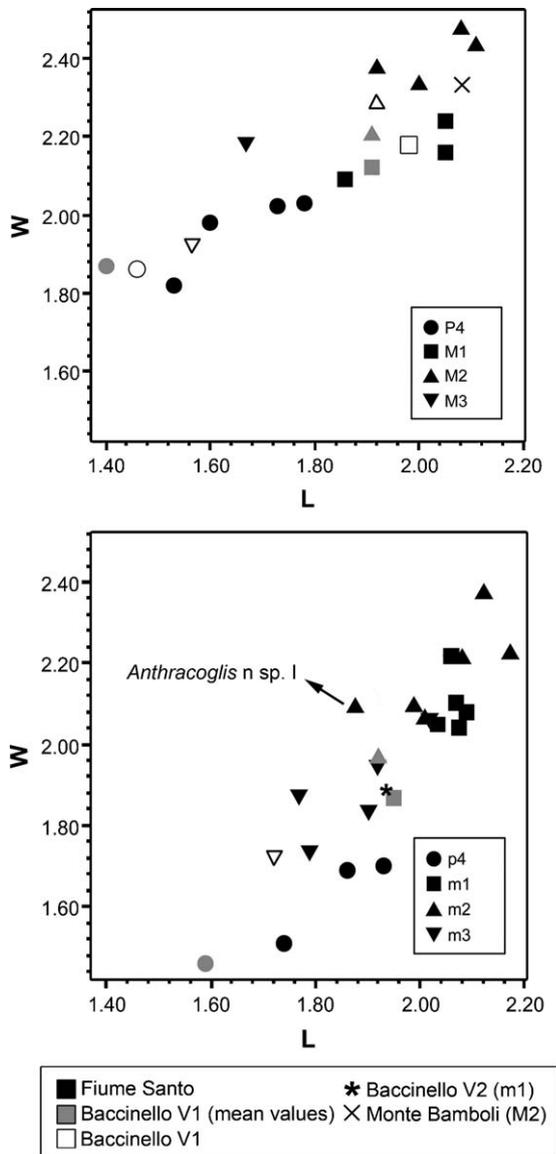


Fig. 3. Scatter diagrams for the length and width of the cheek teeth of *Anthracoglis engesseri* nov. sp. and *Anthracoglis* nov. sp. I from Fiume Santo. The measurements of the *Anthracoglis* material from the sites of Tuscany are included for the sake of comparison. It consists in *A. marinoi* from Baccinello V-1 and V-2 as well as *A. engesseri* nov. sp. from Monte Bamboli.

Lower dentition: the lower cheek teeth are almost as long as wide. The crown is quite high and the wear surface is markedly concave. All the teeth show four wide main ridges that depart from the endolophid: anterolophid, metalophid, mesolophid and posterolophid.

The anterior margin of the p4 is clearly narrower than the posterior one. The main ridges end in small labial cuspids except for the anterolophid. The labial ends of the four main ridges tend to close the first and the last synclinids. However the first valley is closed in just one specimen (FS-750) and the last synclinid is closed in another one (FS-748; Fig. 2(6)). The centrolophid is as long and wide as the main ridges and it almost reaches the labial border of the molar in most specimens. The centrolophid usually joins the endolophid

and this ridge is interrupted behind it. In one specimen (FS-750) the centrolophid joins the endolophid with the mesolophid and the posterolophid and the endolophid is interrupted just in front of the centrolophid. The first and the last synclinids show an accessory ridge, which is highly reduced in the first synclinid and has even disappeared in one specimen (FS-748; Fig. 2(6)). The last accessory ridge is quite long in two specimens (FS-749, FS-750) and very short in two others (FS-751, FS-748; Fig. 2(6)).

The first synclinid is closed in all the m1 (Fig. 2(7)) but one (FS-756). The metalophid, mesolophid and posterolophid end labially in well-defined protoconid, mesoconid and hypoconid, respectively. The centrolophid is as strong as the main ridges and it is usually very long. In one specimen (FS-752), this ridge is especially long and its labial end joins the mesoconid while its lingual one merges with the endolophid. In the same molar the endolophid is interrupted between the centrolophid and the metalophid. In all the other specimens the centrolophid just contacts weakly with the endolophid or it is completely isolated. Therefore, the endolophid is interrupted between the metalophid and the mesolophid in most specimens. The first and the last synclinids show accessory ridges, though the last one is always more developed, being as long and wide as the main ones. Two molars show a third, more reduced accessory ridge between the metalophid and the centrolophid (FS-752, FS-755), which is vestigial in FS-752.

The m2 is very similar to the m1. The first synclinid is closed in all the specimens. The centrolophid joins the endolophid in all the specimens but one (FS-759), where it is separated from this ridge by a weak groove. The first and the last synclinids show an accessory ridge, though the anterior one is highly reduced in some molars (FS-759, FS-760; Fig. 2(8)).

The m3 is subtriangular, with the anterior border straight and wider than the posterior one, which is rounded. In some specimens the anterolophid may be somewhat narrower and relatively lower than the other main ridges (FS-768, FS-763; Fig. 2(9)). The main ridges end in well-defined labial cuspids (protoconid, mesoconid and hypoconid). However, in two specimens the anterolophid is separated from the protoconid by a weak groove (FS-766, FS-769). The first synclinid is closed in all the specimens but one (FS-767). The centrolophid is shorter than in the other molars and does not continue beyond the midpoint of the molar except in two specimens (FS-763, FS-765). This ridge is always fused with the endolophid. The first and the last synclinids show an accessory ridge. As in the other molars, the first one is usually highly reduced and even it is completely lacking in one specimen (FS-768).

Remarks: *A. engesseri* nov. sp. is very similar to *A. marinoi* but differs from this species by its larger size and relative proportions of the cheek teeth (Fig. 3). The upper cheek teeth are relatively wider than those of *A. marinoi*. A groove separates the anterolophid and the posterolophid of the M1 and the M2 from the paracone and the metacone, respectively. In contrast, in most *A. marinoi* these ridges join the labial cuspids. The accessory ridges are more reduced than in *A. marinoi* and are clearly shorter in the upper cheek teeth. In half of the P4 the accessory ridges are missing. In the lower cheek teeth, the

reduction of the accessory ridges is not so marked, except in the m3. The vestigial accessory ridges that are placed next to the centrolophid in some m1 and m2 of *A. marinoi* (Engesser, 1983: fig. 1) have mostly disappeared in *A. engesseri*. Furthermore, the first accessory ridge has disappeared in a few lower cheek teeth (FS-748, FS-768; Fig. 2(6)).

Engesser (1983: fig. 4a) described and figured a single M2 from Monte Bamboli. This author noted that this molar, the only glirid specimen recovered at Monte Bamboli, is conspicuously larger than *A. marinoi*. The posteroloph is separated from the metacone by a marked groove. The anterior accessory ridge is very long and well developed, reaching the labial margin of the molar. This implies that the proloph and the anteroloph are widely separated. The remaining accessory ridges are long and wide. The size and morphology of the Monte Bamboli specimen fits within the range of *A. engesseri* nov.sp., so we ascribe that M2 to the same species, thus extending its geographical range to Tuscany. In the same paper, Engesser (1983: fig. 4b) also described and figured a single m1 from La Pavolona (Baccinello zone V-2). This author ascribed the material to *A. cf. marinoi* noting that the molar fit within the dimensions of this species. That m1 is clearly smaller than the material from Fiume Santo, so we prefer to ascribe it to *A. marinoi* rather than to *A. engesseri* nov. sp.

Anthracoglis nov. sp. I

Material: 1 m2 (FS-775; Fig. 2(10)).

Measurements (L × W): 1.87 × 2.12 (Fig. 3).

Description: This molar is clearly distinguished from *A. marinoi* and *A. engesseri* nov. sp. by a bizarre morphology (Fig. 2(10)). Furthermore, it is clearly smaller than *A. engesseri* nov. sp. (Fig. 3). The molar has a square outline, a relatively high crown and a markedly concave wear surface as in *Anthracoglis*. There are four main ridges (anterolophid, metalophid, mesolophid and posterolophid), which are very wide and merge the endolophid. The centrolophid also fuses with the endolophid and is more developed than the main ridges. The endolophid is interrupted between the centrolophid and the mesolophid. The first as well as the last synclinids show an isolated accessory ridge, which is longer in the last one. All these morphological characters agree with the generic diagnosis of *Anthracoglis*, but the centrolophid has a peculiar development. This ridge is very long and splits into two ridges as it approaches to the labial side of the molar. One of these ridges merges the protoconid whereas the other one merges with the mesoconid. This bizarre structure of the centrolophid implies that the main ridges are shorter than usual. Furthermore, the labial end of the mesolophid does not join the mesoconid, whereas the labial end of the metalophid does not join the protoconid but contacts the anterior arm of the centrolophid.

Remarks: The overall morphology of this specimen fits within that of the genus *Anthracoglis* even though the particular structure of the centrolophid has not been described in any species of the genus. Nevertheless, we consider that there are no cogent arguments precluding its ascription to *Anthracoglis*. The scarce material recovered does not allow the adequate

characterization of this species, so for the moment it is left in open nomenclature until further material is recovered at Fiume Santo.

Family MURIDAE Illiger, 1811

Genus *Huerzelerimys* Mein, Martín Suárez and Agustí, 1993

Huerzelerimys oreopitheci (Engesser, 1989)

Fig. 4(1–5)

Material: 5 M1, 7 M2, 8 M3, 22 m1, 25 m2, 7 m3 and 1 fragment of m1 or m2.

Measurements: See Table 2, Fig. 6 and Appendix A.

Description:

Upper molars: relatively high-crowned molars (Fig. 5(3)). The main cusps are conspicuously inclined towards the posterior side of the teeth. As we have already mentioned, dentine has dissolved, so the roots are not preserved.

The M1 is relatively elongated. A well-developed t6 bends backwards and merges with the t9, which is slightly smaller than t6 (Fig. 4(1)). The t1 is placed more anteriorly than the t3; it is rounded in all the specimens but one in which it is comma-shaped (FS-834). In two specimens the base of the anterior wall of the t2 shows a small cingular terrace. The t3 does not contact the t6 but in two specimens the t3 shows a short spur pointing posteriorly (FS-830, FS-834). The t4 is approximately as large as the t6 but it is elongated in antero-posterior axis. The t7 is missing, the t4 and t8 being connected by a short and low ridge. A highly reduced t12 is present in all the M1.

The morphology of the M2 is analogous to that of the M1 except for the reduced t12, which is present in one single M2 only (FS-836; Fig. 4(2)).

The M3 are small and button-shaped except for their protruding t1. In all the M3 but two (FS-846, FS-847) the area comprised between the t5 and the t8 has collapsed so this region of the molar can only be described for these two specimens. The t1 is well developed and it can be rounded or comma-shaped. The t3 is absent in all the molars but one that shows a vestigial t3 fused to the antero-buccal wall of the t5 (FS-846).

Lower molars: relatively high-crowned molars with the buccal cuspids higher than the lingual ones.

The m1 has a subtriangular outline so its anterior margin is clearly narrower than the posterior one. The metaconid is the higher cuspid. The protoconid-metaconid pair are separated from the hypoconid-entoconid pair by a deep valley. The antero-lingual cuspid shows a weak posterior spur that merges the metaconid. This antero-lingual cuspid is just slightly larger than the antero-buccal one. Both cuspids are tightly fused and an antero-central cuspid may be present (in 11/21, e.g. in FS-851; Fig. 4(3)). The antero-central cuspid is small and becomes fused with the other anterior cuspids at moderate wear stages. There are always accessory cuspids on the buccal cingulid, which tend to become larger from the anterior to the posterior side of the tooth. At least two accessory cuspids are present: the posterior accessory cuspid plus another accessory cuspid placed just behind the protoconid. In 4 (FS-850, FS-855, FS-856 and FS-860) out of 19 m1 there are also two cuspids more besides the two posterior ones: one between the antero-buccal

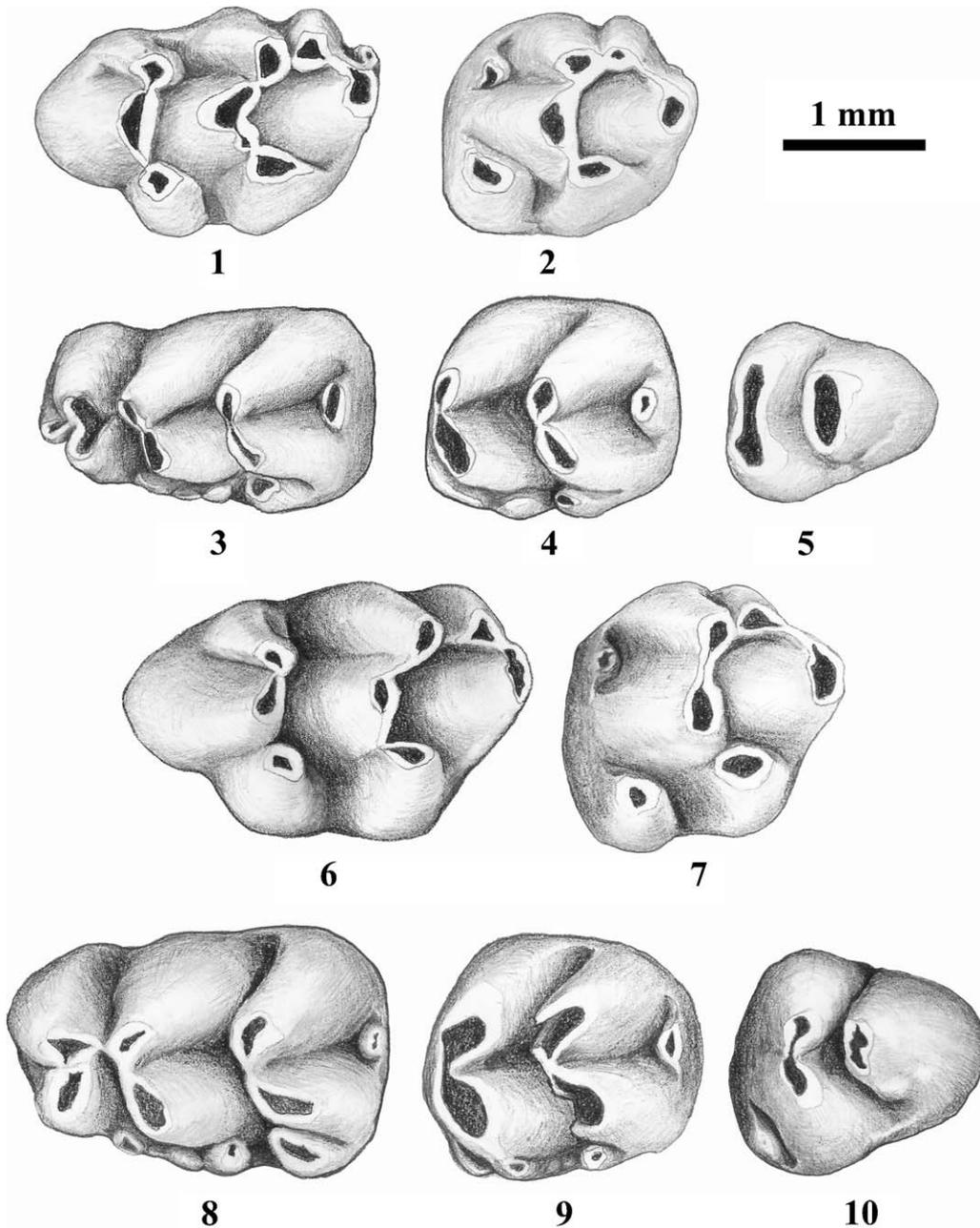


Fig. 4. Muridae from Fiume Santo. 1–5. *Huerzelerimys oreopithecii*. 1: Left M1 FS-831; 2: Left M2 FS-836; 3: Left m1 FS-851; 4: Left m2 FS-872; 5: Left m3 FS-897. 6–10. *Anthracomys lorenzi*. 6: Right M1 FS-779 (reversed); 7: Right M2 FS-784 (reversed); 8: Right m1 FS-792 (reversed); 9: Left m2 FS-803; 10: Right m3 FS-822 (reversed). Original artwork by Marta Palmero.

cuspid and the protoconid; and a more reduced cuspid between these and the cuspid placed just behind the protoconid. These two cuspids may commonly develop into a cingulid that merges the cuspids placed just behind them (in 7/19 m1, e.g. in FS-851; Fig. 4(3)). The terminal heel is well developed and usually elongated in bucco-lingual direction. It merges with the hypoconid and the entoconid by the means of two very low ridges.

Morphologically the m2 resemble the m1, and the most important differences between the two molars are related to the development of the accessory cuspids on the buccal cingulid. The m2 always show two accessory cuspids: the posterior

accessory cuspid and a crescent-shaped antero-labial cuspid. A smaller cuspid placed between these two accessory cuspids is also present in 7 out of 13 m2 (such as in FS-872; Fig. 4(4)).

The m3 is subtriangular, with the distal margin markedly narrower than the anterior one. This molar only shows the three main cuspids (Fig. 4(5)).

Remarks: The material from Fiume Santo is very similar in size and morphology to the material of Baccinello assemblage V-1 (Fig. 6), the other locality with *H. oreopithecii* known so far (Engesser, 1989). Cordy et al. (1995) listed the murid *Valerimys* aff. *turoliensis* (sic) and a large-sized glirid from Fiume Santo. Since the material on which these authors based their

Table 2
Length and width synthetic measurements for the molars of *Huerzelerimys oreopitheci* from Fiume Santo.

	Length					Width				
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD
M1	5	2.51	2.67	2.85	0.13	5	1.57	1.69	1.94	0.15
M2	6	1.65	1.80	1.89	0.08	7	1.48	1.59	1.68	0.07
M3	8	1.13	1.33	1.54	0.13	8	1.20	1.34	1.50	0.11
m1	18	2.15	2.28	2.40	0.08	17	1.34	1.46	1.61	0.08
m2	19	1.55	1.65	1.78	0.06	21	1.40	1.51	1.63	0.07
m3	7	1.35	1.41	1.52	0.06	7	1.25	1.31	1.41	0.06

N: number of measured specimens; SD: standard-deviation.

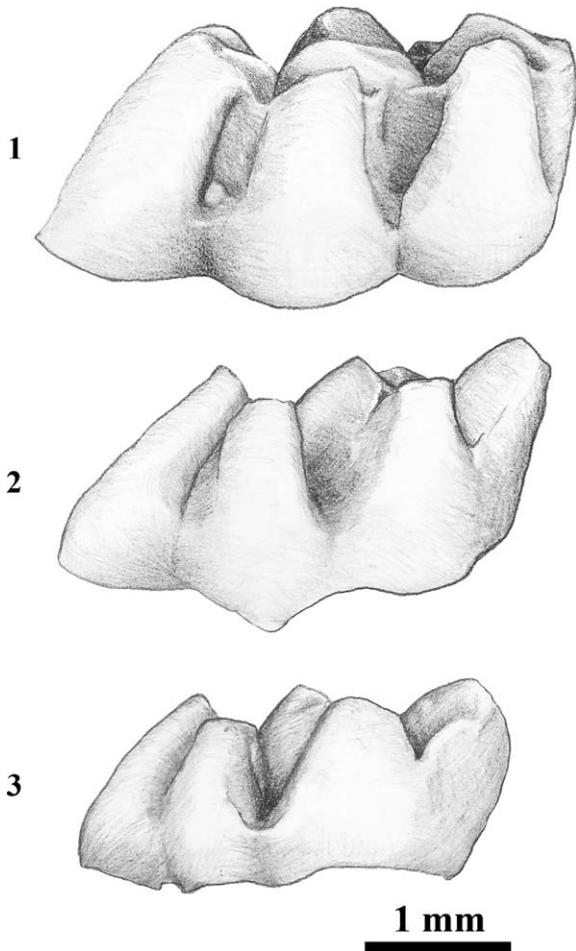


Fig. 5. Lingual view of the M1 of the murid species endemic to the Tusco-Sardinian palaeobioprovince. 1. *Anthracomys majori* from Monte Bamboli (B5). 2. *Anthracomys lorenzi* from Fiume Santo (FS-779, reversed). 3. *Huerzelerimys oreopitheci* from Fiume Santo (FS-831). Original artwork by Marta Palmero.

determination is no longer available (cf. Abbazzi et al., 2008), we presume that the glirid likely represents *A. engesseri* nov. sp., while *H. oreopitheci* was most probably confused with *V. aff. turoliensis*. *Huerzelerimys turoliensis* is larger than *H. oreopitheci* and commonly shows connections between t1 and t5 and between t3 and t5 in the M1 (e.g., Van de Weerd, 1976; Van Dam, 1997). This species does not seem to be related to *H. oreopitheci*, a putative insular offshoot of *H. vireti*, which is recorded in the so-called V-0 faunas (Engesser, 1989).

Engesser (1989) proposed that *H. oreopitheci* is the ancestor of both *Anthracomys lorenzi* and *A. majori*. *Anthracomys* differs from *Huerzelerimys* by its larger and more hypsodont molars and by a simplification of the molar pattern, evidenced by the disappearance of the t12 in the M1 and the M2, of the antero-central cusp in the m1, and by the reduction of the accessory cusps in the m2 and the m3. It is hard to tell if *H. oreopitheci* of Fiume Santo is more derived than those of Baccinello V-1. The reduction of the t12 in M1 and M2 and of the accessory cusps in the m3 is stronger in the Fiume Santo material, although some other plesiomorphic characters are more common in the specimens of the Sardinian locality than in the Tuscan material – presence of the antero-central cuspid in the m1 and of more well-developed accessory cusps in the m2.

Genus *Anthracomys* Schaub, 1938

Anthracomys lorenzi Engesser, 1989

Fig. 4(6–10)

Material: 8 M1, 3 M2, 1 M3, 15 m1, 13 m2, 16 m3 and 1 fragment of m1 or m2.

Measurements: See Table 3, Fig. 7 and Appendix A.

Description:

Upper molars: high-crowned molars with the main cusps markedly inclined backwards (Fig. 5(2)). The central cusp row is clearly higher than the buccal and the lingual ones. The roots are not preserved.

The M1 is wide and stout. The t4 is always larger than the t6 and the former cusp weakly joins the t8 (Fig. 4(6)). The t6 is not connected to the t9. The former cusp tends to be smaller than the latter one, which is situated very posteriorly. The t3 is somewhat smaller than the t1 and shows a small posteriorly-directed spur in two specimens (FS-776, FS-779). In one of these (FS-776), this spur joins the t6. In two specimens (FS-781, FS-918) the t1 shows a very short spur that points towards the t4 without reaching it. Two molars (FS-780, FS-781) show a vestigial cingulum-like t1bis placed at the end of the antero-lingual valley, close to the base of the crown. A vestigial t12 is present in only two M1 (FS-776, FS-777).

The M2 is also very wide and morphologically resembles the M1. The t1 is very developed and it may be rounded (FS-784; Fig. 4(7)) or comma-shaped (FS-783, FS-919). The more reduced t3 is rounded and pointed. Both cusps join the well-developed t5 by means of a low ridge. The t6 is clearly smaller than the t9. All the M2 lack the t12.

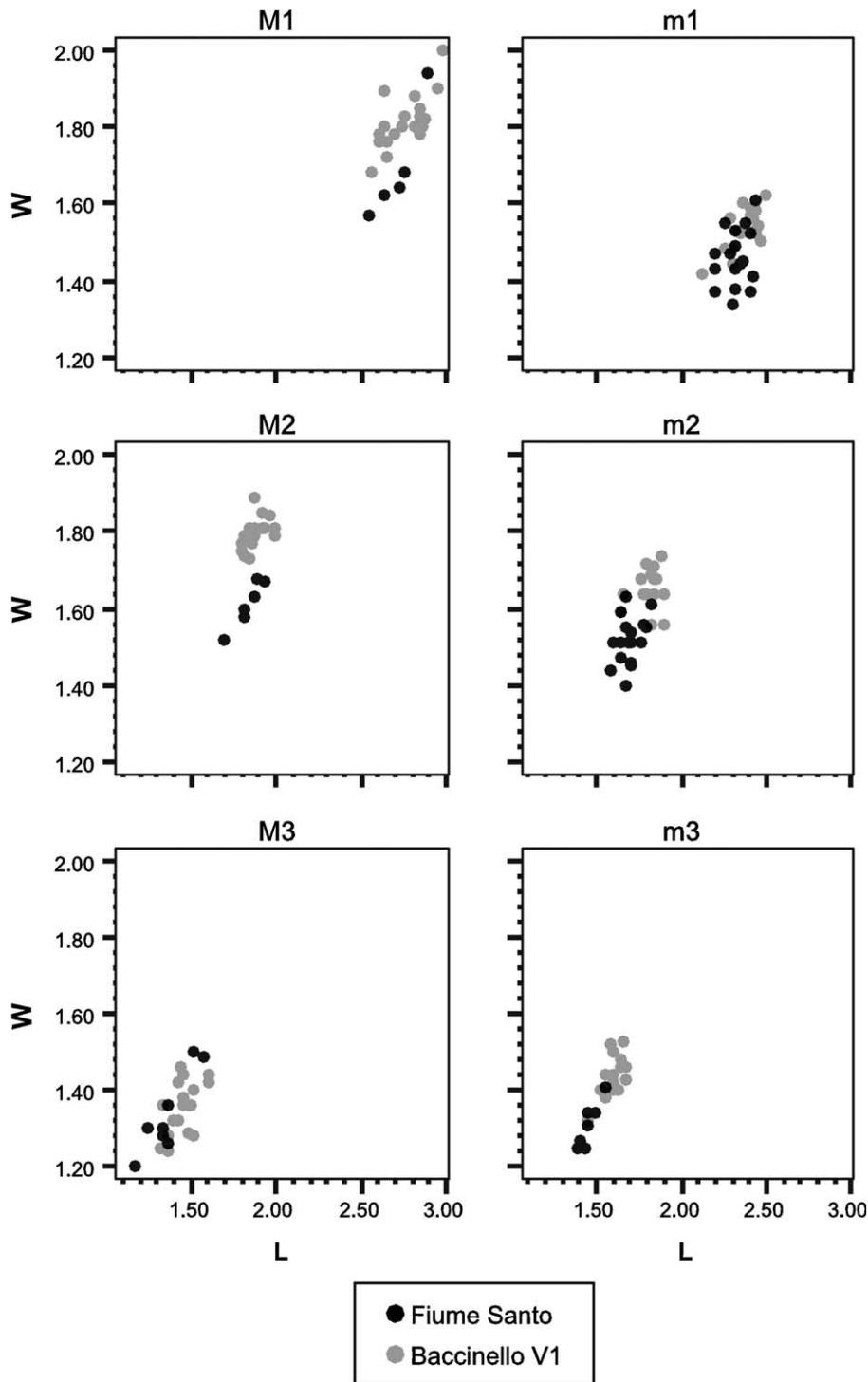


Fig. 6. Scatter diagrams for the length and width of the *Huerzelerimys oreopitheci* molars from Fiume Santo as compared to those of Baccinello V-1.

The only recovered M3 has a rounded outline. The area comprised between the t5 and the t8 has collapsed. The t4 joins the t8 and a small t6 is present. The t1 is large and rounded while the t3 is lacking.

Lower molars: high-crowned molars. The lingual cuspids are slightly higher than the buccal ones and the maximum high of the crown is reached at the metaconid. The molars are relatively wide.

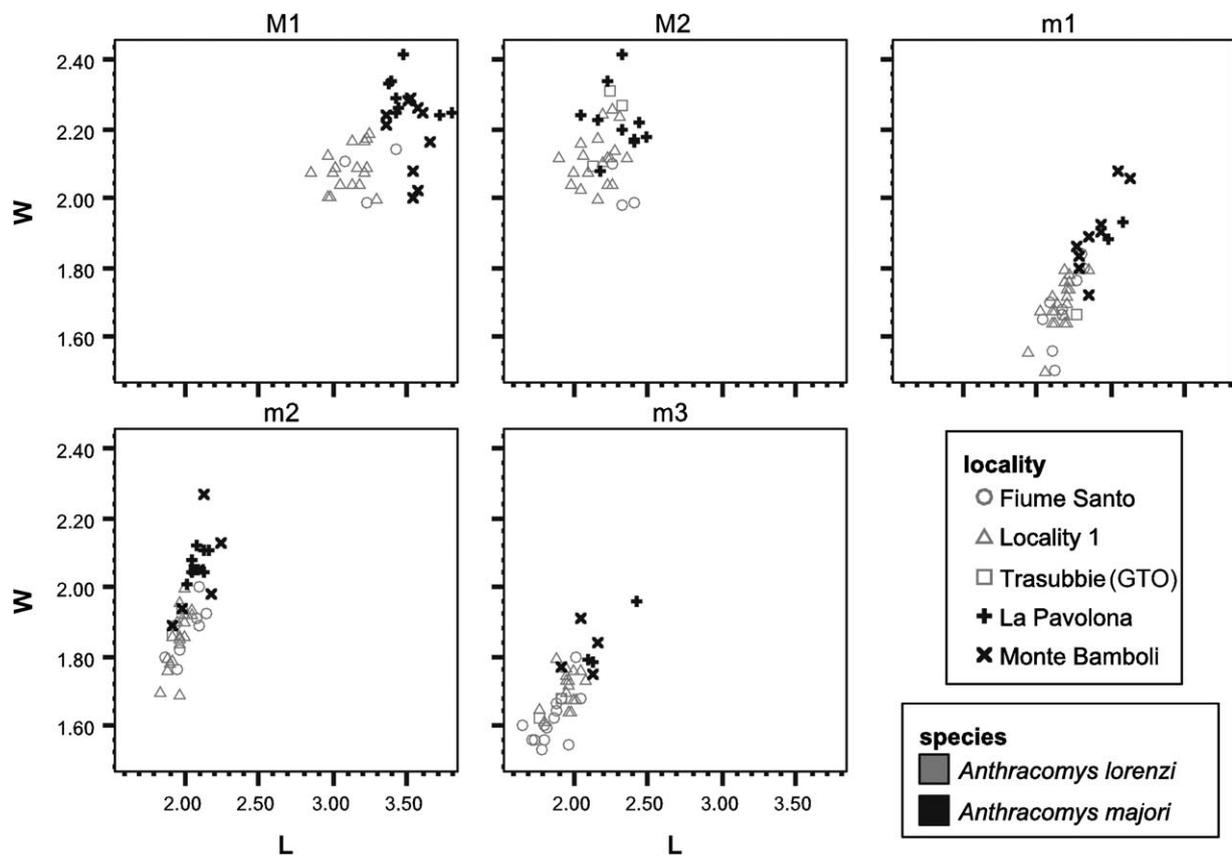
The m1 has an approximately rectangular outline because its anterior margin is only slightly narrower than the posterior one. The protoconid-metaconid pair is separated from the hypoconid-entoconid one without a trace of longitudinal spur. Most of the m1 (nine out of 10) show at least three accessory cusps on the buccal cingulid: a first one between the protoconid and the antero-buccal cuspid; a second one just behind the protoconid; and a last posterior accessory cuspid next to the hypoconid (e.g.

Table 3

Length and width synthetic measurements for the molars of *Anthracomys lorenzi* from Fiume Santo.

	Length					Width				
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD
M1	4	3.04	3.23	3.37	0.15	4	1.93	2.04	2.14	0.10
M2	3	2.22	2.29	2.37	0.08	3	1.98	2.02	2.10	0.07
M3	(1)		(1.61)			1		1.54		
m1	10	2.50	2.63	2.77	0.09	14	1.50	1.70	1.84	0.09
m2	9	1.83	1.97	2.10	0.09	9	1.76	1.88	2.00	0.08
m3	14	1.62	1.81	2.01	0.11	14	1.53	1.62	1.80	0.07

N: number of measured specimens; SD: standard-deviation.

Fig. 7. Scatter diagrams for the length and width of the molars of *Anthracomys majori* and *Anthracomys lorenzi* from Fiume Santo and the localities from Tuscany.

FS-788, FS-790, FS-791). Four out of these nine m1 also show a fourth accessory cuspid between the first and the second ones attached to the base of the protoconid (FS-792, FS-794, FS-796, FS-920, FS-792; Fig. 4(8)). In the specimens with four accessory cuspids, the two more anterior ones are rounded and of comparable size whereas the third one is somewhat larger. The posterior accessory cuspid, which is oval and relatively higher, is the largest one in all the specimens. In one m1 there are only two accessory cuspids: the posterior accessory cuspid and the one placed behind the protoconid (FS-787). The terminal heel is small and rounded; it joins occasionally the hypoconid-entoconid pair by means of a very low ridge.

The m2 resembles the m1, most of the differences being related to the development of the accessory cuspids on the

buccal cingulid. The m2 always show three accessory cuspids: a cingulid-like antero-buccal cuspid; a tiny accessory cuspid placed at the base of the protoconid; and a rounded posterior accessory cuspid, which is smaller and lower than the one of the m1 (Fig. 4(9)). The cingulid-like antero-buccal cuspid may fuse to the second accessory cuspid.

Most of the m3 only show a poorly developed antero-buccal cuspid, which is also cingulid-like. In one specimen a tiny, rounded and isolated antero-buccal cuspid is present (FS-822; Fig. 4(10)). Finally, three m3 do not have an antero-buccal cuspid (FS-819, FS-827, FS-828).

Remarks: *A. lorenzi* is known from Locality 1 within the Baccinello faunal assemblage V-3 and from a single mandible (IGF 9319 V) recovered from an outcrop on the right bank of

the Trasubbie River (Great Trasubbie Outcrop = GTO) that is correlated to the V-2 faunal assemblage (Rook, 1991). The specimens from Fiume Santo overlap in size with those from both Locality 1 and the GTO (Fig. 7). The described molars only show minor morphological differences with those from the Tuscan localities. The most remarkable discrepancies refer to the development of the accessory cusps on the buccal cingulid of the m1. The molars from Locality 1 and the single m1 from GTO show three accessory cusps, whereas 4 out of 10 m1 from Fiume Santo show a fourth accessory cuspid. The m3 from Fiume Santo show a cingulid-like antero-buccal cuspid, which is also a common feature in *A. majori* but mostly absent in *A. lorenzi*. It is also worth noting that two M1 show a vestigial t12, while this cusp has completely disappeared in *A. lorenzi* from Locality 1 and in *A. majori*. Finally, some of the M1 from Locality 1 show a t1-t5 connection, while this is absent in most of the specimens from Fiume Santo.

Engesser (1989) cogently stated that even though *A. lorenzi* was known from younger localities (V-3) than *A. majori* (V-2), the former species could not be derived from the latter one because it is clearly smaller and more brachyodont. The increase in size and hypsodonty from *H. oreopitheci* to *A. lorenzi* and to *A. majori* immediately suggests that these insular murids define a single anagenetic lineage (Fig. 5). However, this straightforward interpretation is challenged by the retention of certain plesiomorphic characters in *A. majori* that have disappeared in *A. lorenzi*: the terminal heel of m1 and m2 in *A. majori* is better developed than in *A. lorenzi* (compare Fig. 4(8, 9) with Engesser, 1989: 237, fig. 9); the t9 of M2 is less developed in *A. lorenzi* than in *A. majori* (but this seems to be a quite variable feature, since many M2 of Fiume Santo show a well developed t9). Furthermore, *A. lorenzi* shows a number of autapomorphic traits that are neither observed in *A. majori* nor in *H. oreopitheci*, and that are mostly related to the position and orientation of the cusps of the upper molars. On the M1 the t9 is situated much posteriorly than in *A. majori* and *H. oreopitheci* (compare Fig. 4(6) with Engesser, 1989: 234–235, figs. 7b, 8b). Additionally the tops of all cups and especially those of the t5, t8 and t9 bend markedly backwards in both the M1 and the M2. This is clearly evident in lateral view of the molars and is not present in *H. oreopitheci*, while in *A. majori* the cusps bend backwards but not so strongly. An additional difference with the latter taxon is the presence of a t1-t5 and sometimes also a t3-t6 connection in *A. majori* (Engesser, 1989: 234, fig. 7b). These connections are present in some *A. lorenzi* specimens from Locality 1 but they are weaker, the posterior spurs of the t1 and/or the t3 do not merge with the posterior cusps but just reach them (Engesser, 1989: 234, fig. 7a). In the Fiume Santo material these spurs are mostly lacking, nonetheless a posterior spur of the t3 is present in two specimens (FS-776, FS-779), reaching the t6 in one (FS-776) while in two others the t1 shows a very short spur that never reaches the t5 (FS-781, FS-919). All these morphological differences support Engesser's (1989) interpretation of an independent origin of the two *Anthracomys* species. The last common ancestor of

A. lorenzi and *A. majori* may be a yet unknown third *Anthracomys* species or *H. oreopitheci*. In case the second option would be correct, *Anthracomys* would be paraphyletic.

5. Biochronology

Abbazzi et al. (2008) suggested a correlation of Fiume Santo to faunal zone V-2 of the Baccinello-Cinigiano basin on the basis of the composition of the macromammal assemblage that includes the suid *Eumaiocoerus* cf. *etruscus* and the bovid *Maremmia* cf. *lorenzi*. These authors also noted the presence of slightly derived features in these taxa that they interpreted to be the result of either environmental or slight chronological differences as compared to the V-2 assemblages. The rodent assemblage from Fiume Santo does not give conclusive arguments on the age of this site since it seems to include a mixture of elements characteristic of different local zones of the *Oreopitheci*-bearing faunas of Tuscany. Regarding the murids, the *Anthracomys* species present at Fiume Santo is *A. lorenzi*, while *A. majori* is characteristic of the V-2 faunal assemblages such as Monte Bamboli. Even more surprising is that the most common murid in Fiume Santo is *H. oreopitheci*, the putative ancestor of *A. lorenzi* that is only known from the V-1 assemblages from the Baccinello-Cinigiano basin. The large-sized glirid from Fiume Santo is here described as a new species, *A. engesseri*, to which we also ascribe the material from Monte Bamboli (assigned to *Anthracoglis* sp. by Engesser, 1983). Apparently only the presence of *A. engesseri* nov. sp. is fully consistent with a correlation of Fiume Santo to the V-2 biozone. Nevertheless, Rook (1991) reported the presence of *A. lorenzi* from an outcrop on the right bank of the Trasubbie River that is correlated to the V-2 faunal assemblage. However, this species is better known from the V-3 fauna of Locality 1 (Engesser, 1989) and is the only endemic rodent to have survived in the area once a connection with the European mainland was established. The presence of *A. lorenzi* and *A. engesseri* nov. sp. seems to support a correlation to the V-2 faunal assemblages, which would be in agreement with the data provided by the macromammals. However, the occurrence of *H. oreopitheci* may indicate a somewhat older age. To sum up, a correlation to the V-2 faunal assemblage is preferred, although this may be somewhat controversial given the composition of the rodent assemblage.

6. Comparison with the faunas from Tuscany

We have compared the composition and structure of the Fiume Santo rodent assemblage to those of Tuscany. In order to do so, we have compiled the number of cheek teeth per rodent taxon in each locality (Table 4). For the sake of simplicity we have considered all the localities from the Baccinello basin, which belong to the same local biozone as a single rodent assemblage (namely the V-0, V-1, V-2 and V-3 assemblages). V0 rodent faunas were recovered at a single locality, Fosso della Fittaia. The V-1 faunas come from the lignite of the mine of Baccinello locality. In contrast, V-2 and V-3 faunas come

from different localities. V-2 rodent faunas were mainly recovered at the site of La Pavolona but a few remains were found at Podere la Crocina (*A. majori*; Engesser, 1989) and the Great Trasubbie Outcrop (*A. lorenzi*; Engesser, 1989; Rook, 1991). Concerning the V-3 faunas, most of them were recovered at Locality 1, however, a few molars of two undetermined murids were recovered at the Arcille site (Engesser, 1989) and a single mandible of the cricetid *Celadensia grossetana* was recovered at the Caprarecce site (Rook and Torre, 1995). For the location of the different sites of the Baccinello-Cinigiano basin see Lorenz (1968).

The rodent faunas from the Tusco-Sardinian palaeobioprovince are poor in species, with one species usually being dominant (Table 4). This pattern is typical for insular mammal communities (e.g., MacArthur and Wilson, 1967). In the faunas from Baccinello V-0 to V-2 as well as in Monte Bamboli a single murid species (either from the genus *Huerzelerimys* or *Anthracomys*) always represents more than 80% of the recovered cheek teeth. The remaining taxa represent just a minor portion of the assemblage, except for the V-1 faunas where *A. marinoi* accounts for about 15% of the recovered rodent cheek teeth. The V-3 faunas from Baccinello do not correspond to an insular community, and therefore species richness is higher and the mammal assemblage is more balanced. Although it is clearly dominated by *A. lorenzi*, *Apodemus etruscus* and *Kowalskia nestori* are major components as well. The Fiume Santo rodent assemblage includes just four different species: *A. engesseri* (about 20%), *Anthracoglis* nov. sp. I (less than 1%), *H. oreopitheci* (about 40%) and *A. lorenzi* (close to 35%). Species richness is comparable to that of the Tuscan sites and very similar to those of V-2 zone but the rodent assemblage of Fiume Santo is clearly more balanced. Abbazzi et al. (2008) remarked the high similarity of the macromammal assemblage of Fiume Santo to the V-2 faunas of Tuscany. In both Fiume Santo and the V-2 faunas of the Baccinello-Cinigiano basin the hypsodont bovid *Maremmia*

and the giraffid *Umbrotherium* are the most abundant large mammal remains, while the suid *Eumaiocoerus* and the primate *Oreopithecus* are very rare. In Monte Bamboli (a locality which is correlated to the V-2 zone as well) the latter two taxa are abundant while the hypsodont bovids *Maremmia* and *Tyrrhenotragus* are rare. Abbazzi et al. (2008) relate these differences to differences in the local palaeoenvironment associated to these sites: while Fiume Santo and the Baccinello localities are located in clays, sands and gravels of fluvio-lacustrine origin, the Monte Bamboli lignites correspond to a swampy and marshy lacustrine environment. Such highly local differences in environmental conditions may account for the differences in the composition and structure of the rodent assemblages from Fiume Santo and Monte Bamboli, but not for the differences with the Baccinello localities. The reasons for these differences are unclear and could be related to:

- slight chronological differences between the Tuscan and Sardinian sites;
- the occurrence of slightly different environments in both areas;
- the existence of a geographical barrier between both areas because these represented different islands during the studied time span.

The latter scenario is highly probable, since the northern Tyrrhenian sea was starting its intense tectonic opening and widening during this time (Sartori, 2001).

7. Conclusions

The rodent fauna from Fiume Santo consists of only four species: the glirids *A. engesseri* nov. sp. and *Anthracoglis* nov. sp. I, and the murids *H. oreopitheci* and *A. lorenzi*. Faunistically, the assemblage is a mixture of elements of zones V-1, V-2 and V-3 of the Baccinello-Cinigiano basin since

Table 4
Number of cheek teeth for the different rodent taxa present at Fiume Santo and the Tuscany endemic faunas.

Species	Locality/faunal horizon					
	Baccinello V-3	Monte Bamboli	Baccinello V-2	Baccinello V-1	Baccinello V-0	Fiume Santo
<i>Anthracoglis marinoi</i>	0	0	0	26	0	0
<i>Anthracoglis engesseri</i>	0	1	1	0	0	48
<i>Anthracoglis</i> nov. sp.	0	0	0	0	0	1
<i>Muscardinus</i> aff. <i>vireti</i>	14	0	0	0	0	0
Gliridae nov. gen et. sp.	0	0	0	1	0	0
<i>Huerzelerimys vireti</i>	0	0	0	0	26	0
<i>Huerzelerimys oreopitheci</i>	0	0	0	117	0	76
<i>Anthracomys majori</i>	0	58	54	0	0	0
<i>Anthracomys lorenzi</i>	132	0	3	0	0	62
<i>Parapodemus</i> sp. 1	0	0	1	0	0	0
<i>Parapodemus</i> sp. 2	0	0	0	5	0	0
<i>Apodemus etruscus</i>	57	0	0	0	0	0
Muridae indet. 1	1	0	0	0	0	0
Muridae indet. 2	1	0	0	0	0	0
Muridae indet. 3	1	0	0	0	0	0
<i>Kowalskia nestori</i>	44	0	0	0	0	0
<i>Celadensia grossetana</i>	2	0	0	0	0	0

H. oreopithecii is characteristic of zone V-1 and *A. lorenzi* is characteristic from zone V-3. Nevertheless, a few remains of *A. lorenzi* have been also recovered from V-2 assemblages at Baccinello and *A. engesseri* is also recorded in Monte Bamboli, which is correlated to V-2 faunas. Accordingly, a correlation to V-2 zone of the Baccinello-Cinigiano basin is preferred. Both the Fiume Santo and Tuscan faunas are species-poor although the former one is even more. This may be related to slight chronological or environmental differences between the two areas or to geographical separation by sea.

Acknowledgements

We will be always indebted to Pierre Mein for his outstanding works, his interesting and useful comments and discussions and his charming company. He is still a great source of inspiration and encouragement to all of us and we consider it a great honour to contribute to a volume dedicated to him. We thank our colleague S. Moyà-Solà (Institut Català de Paleontologia, Cerdanyola del Vallès) for the critical revision of some sections of the text and for his useful comments, as well as Marta Palmero (Institut Català de Paleontologia, Cerdanyola del Vallès) for the excellent drawings of the studied material. We also thank the organizers and attendants to the “Neogene Mammalian successions and dispersals: Homage to Pierre Mein” special session within the 13th RCMNS Congress held in Naples on September 2009. We are indebted to the editors (Drs G. Escarguel and J. Agustí) and reviewers (Drs R. Minwer-Barakat and P. Mein) of this manuscript for their constructive comments and suggestions which surely improved the final result. This study has been possible thanks to the support of the Spanish Ministerio de Ciencia e Innovación (CGL2010-21672/BTE) and 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). Field work at Fiume Santo was made possible thanks to the support of the National Geographic Society (grant #7484-03 to LR), the RHOI program at University of Berkeley (project NSF-BCS-0321893), and the logistic and economic support of ENDESA Italia.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.geobios.2010.08.002](https://doi.org/10.1016/j.geobios.2010.08.002).

References

Abbazzi, L., Delfino, M., Gallai, G., Trebbini, L., Rook, L., 2008. New data on the vertebrate assemblage of Fiume Santo (North-West Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinian palaeobioprovince. *Paleontology* 51, 425–451.

- Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. *State of the art. Earth-Science Reviews* 52, 247–260.
- Andrews, P., 1990. *Owls, caves and fossils*. Natural History Museum Publications, London.
- Cordy, J.M., Ginesu, S., 1994. Fiume Santo (Sassari, Sardegna, Italie) : un nouveau gisement à Oréopithèque (Oreopithecidae, Primates Mammalia). *Comptes Rendus de l'Académie des Sciences de Paris (2)* 318, 679–704.
- Cordy, J.M., Ozer, A., Sias, S., 1995. Geomorphological and palaeoecological characteristics of the *Oreopithecus* sites of Fiume Santo (Sassari, northern Sardinia, Italy). *Geografia Fisica e Dinamica Quaternaria* 18, 7–16.
- Daams, R., 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridyromys*. *Utrecht Micropaleontological Bulletins Special Publication* 3, 1–115.
- Delfino, M., Rook, L., 2008. African crocodylians in the Late Neogene of Europe: a revision of *Crocodylus bambolii* Ristori, 1890. *Journal of Paleontology* 82, 336–343.
- Delson, E., 1987. An anthropoid enigma: Historical introduction to the study of *Oreopithecus bambolii*. *Journal of Human Evolution* 15, 523–531.
- Denys, C., Fernández-Jalvo, Y., Dauphin, Y., 1995. Experimental taphonomy preliminary results of the digestion of micromammal bones in the laboratory. *Comptes Rendus de l'Académie des Sciences de Paris (2)* 321, 803–809.
- Engesser, B., 1983. Die jungtertiären Klinsäuger des Gebietes der Maremma (Toskana, Italien. 1.Teil: Gliridae (Rodentia, Mammalia). *Eclogae Geologicae Helvetiae* 76, 763–780.
- Engesser, B., 1989. The Late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part: Muridae and Cricetidae (Rodentia, Mammalia). *Bolletino della Società Paleontologica Italiana* 28, 227–252.
- Fernández-Jalvo, Y., Sánchez-Chillón, B., Andrews, P., Fernández-López, S., Alcalá Martínez, L., 2002. Morphological taphonomic transformations of fossil bones in continental environments, and repercussions on their chemical composition. *Archaeometry* 44, 353–361.
- Fisher, D.C., 1981. Crocodylian scatology, microvertebrate concentrations, and enamelless teeth. *Paleobiology* 7, 262–275.
- Gervais, P., 1872. Sur un singe fossile, d'espèce non encore décrite, qui a été découvert au Monte Bamboli. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris* 74, 1217–1223.
- Hürzeler, J., 1983. Un alcéphaliné aberrant (Bovidae: Mammalia) des « Lignites de Grosseto » en Toscane. *Comptes Rendus de l'Académie des Sciences de Paris (2)* 295, 697–701.
- Hürzeler, J., Engesser, B., 1976. Les faunes de mammifères néogènes du Bassin de Baccinello (Grosseto, Italie). *Comptes Rendus de l'Académie des Sciences de Paris (2)* 283, 333–336.
- Köhler, M., Moyà-Solà, S., 1997. Ape-like or hominid-like? The positional behaviour of *Oreopithecus* reconsidered. *Proceedings of the National Academy of Sciences of the USA* 94, 11747–11750.
- Lorenz, H.G., 1968. Stratigraphisches und mikropaläontologisches Untersuchungen des Braunkohlengebietes von Baccinello (Grosseto, Italien). *Rivista Italiana di Paleontologia e Stratigrafia* 74, 147–270.
- MacArthur, R.H., Wilson, E.O., 1967. *The theory of island biogeography*. Princeton University Press, Princeton.
- Major, C.I.F., 1873. La faune des vertébrés de Monte Bamboli (Maremmes de la Toscane). *Atti della Società Italiana di Scienze Naturali* 15, 290–303.
- McKenna, M.C., Bell, S.K., 1997. *Classification of mammals above the species level*. Columbia University Press, New York.
- Mein, P., 1975. Résultats du Groupe de Travail des Vertébrés. Report on Activity of the RCMNS Working Groups (1971-1975). IUGS regional committee on Mediterranean Neogene stratigraphy. Bratislava 1975, 78–81.
- Moyà-Solà, S., Köhler, M., 1997. The phylogenetic relationships of *Oreopithecus bambolii* Gervais, 1872. *Comptes Rendus de l'Académie des Sciences de Paris* 324, 141–148.
- Moyà-Solà, S., Köhler, M., Rook, L., 1999. Evidence of hominid-like precision grip capabilities in the hand of the European Miocene ape *Oreopithecus*. *Proceedings of the National Academy of Sciences USA* 96, 313–317.
- Rook, L., 1991. The genus *Anthracomys*, a murid (Rodentia, Mammalia) endemic to the Baccinello region (Tuscany, Italy). *Bolletino della Società Paleontologica Italiana* 30, 235–238.

- Rook, L., Abbazzi, L., Delfino, M., Gallai, G., Trebini, L., 2006a. Il giacimento paleontologico di Fiume Santo. Stato delle ricerche e prospettive a dieci anni dalla scoperta. *Sardinia Corsica et Baleares Antiquae – International Journal* 4, 9–17.
- Rook, L., Bondioli, L., Köhler, M., Moyà-Solà, S., Macchiarelli, R., 1999. *Oreopithecus* was a bipedal ape after all: evidence from the iliac cancellous architecture. *Proceedings of the National Academy of Sciences of the USA* 96, 8759–8799.
- Rook, L., Gallai, G., Torre, D., 2006. Lands and endemic mammals in the Late Miocene of Italy: constraints for palaeogeographic outlines of Tyrrhenian area. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 263–269.
- Rook, L., Harrison, T., Engesser, B., 1996. The taxonomic status and biochronological implications of new finds of *Oreopithecus* from Baccinello (Tuscany, Italy). *Journal of Human Evolution* 30, 3–27.
- Rook, L., Renne, P., Benvenuti, M., Papini, M., 2000. Geochronology of *Oreopithecus*-bearing succession at Baccinello (Italy) and the extinction pattern of European Miocene hominoids. *Journal of Human Evolution* 39, 577–582.
- Rook, L., Torre, D., 1995. *Celadensia grossetana* nov. sp. (Cricetidae, Rodentia) from the Late Turolian Baccinello-Cinigiano basin (Italy). *Geobios* 28, 379–382.
- Sartori, R., 2001. Corsica-Sardinia block and the Tyrrhenian sea. In: Vai, G.B., Martini, I.P. (Eds.), *Anatomy of an Orogen: the Apennines and adjacent Mediterranean basins*. Kluwer academic Publisher, Dordrecht, pp. 367–374.
- Savi, P., 1843. *Sopra i carboni fossili dei terreni miocenice delle Maremme Toscane*. Tipografia Nistri, Pisa.
- Van Dam, J.A., 1997. The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): paleobiology and palaeoclimatic reconstructions. *Geologica Ultraiectiona* 156, 1–204.
- Van de Weerd, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins Special Publication* 2, 1–185.