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## PLIO-PLEISTOCENE FOSSIL VERTEBRATES OF MONTE TUTTAVISTA (OROSEI, EASTERN SARDINIA, ITALY), AN OVERVIEW

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**Abstract.** The preliminary results of the analysis of fossil vertebrate remains from 19 fissure fillings in the karst network at Monte Tuttavista (Orosei, Nuoro) are reported. About 80 taxa, among fishes, amphibians, reptiles, birds and mammals have been recognised.

These remains document the evolution of vertebrate assemblages in the Sardinian insular domain, during a time interval apparently spanning the Late Pliocene to Late Pleistocene or Holocene. A succession of at least four populating complexes has been identified which document the vertebrate colonisation phases from the Italian mainland and the following periods of insularity. Indeed, the occurrence of endemic taxa such as the murid *Rhagapodemus minor*, the primate *Macaca* cf. *M. majori* and the caprine *Nesogoral*, suggest some fissure fillings date to a phase close to the Plio/Pleistocene boundary since these taxa occur at the Sardinian locality Capo Figari I which has been dated to about 1.8 Ma. However, the presence of the "hunting-hyaena" *Chasmaporthetes*, never reported before in Sardinia, could suggest that the beginning of the vertebrate record of Monte Tuttavista is older, given that this carnivore is documented in European Middle Pliocene-Early Pleistocene localities.

The vertebrate assemblages that document the most recent migratory phases in the karst network of Monte Tuttavista are characterised by the occurrence of the endemic megalocerinid cervid *Praemegaceros cazioti* and the arvicolid *Tyrrhenicola henseli* which are comparable with those occurring in other Late Pleistocene and early Holocene Sardinian sites.

**Riassunto.** Nel presente lavoro sono riportati i risultati preliminari dello studio dei resti fossili di vertebrati rinvenuti nei riempimenti di 19 diverse fessure carsiche, localizzate nel Monte Tuttavista (Sardegna nord-orientale, Orosei, Nuoro).

I reperti fossili sono stati attribuiti a circa 80 taxa, appartenenti a pesci ossei, anfibi, rettili, uccelli e mammiferi. L'insieme di questi resti documenta l'evoluzione delle associazioni a vertebrati di ambiente insulare in un intervallo di tempo piuttosto lungo, in cui si sono succeduti almeno quattro complessi faunistici diversi, che testimoniano le fasi di collegamento ed isolamento che il territorio sardo ha subito rispetto alle aree continentali della penisola italiana, nel corso del Plio-Quaternario. Infatti, la presenza del muride *Rhagapodemus minor*, di un primate affine alla specie *Macaca majori*, e del caprino appartenente al genere *Nesogoral*, suggerisce di riferire alcuni dei riempimenti carsici ad una fase prossima alla transizione Plio/Pleistocene, visto che questi taxa caratterizzano l'associazione faunistica della località sarda Capo Figari I, datata a circa 1.8 Ma. Tuttavia la presenza dello ienide *Chasmaporthetes*, mai segnalato in precedenza nelle associazioni dell'isola, potrebbe essere indicativa di un livello cronologico più vecchio, visto che questo carnivoro è diffuso nelle località europee durante il Pliocene Medio-Pleistocene Inferiore.

Le associazioni di vertebrati che rappresentano le fasi più recenti nel sistema carsico del Monte Tuttavista, sono caratterizzate dalla presenza del cervide endemico *Praemegaceros cazioti* e dell'arvicolid endemico *Tyrrhenicola henseli* e sono pienamente confrontabili a quelle diffuse in altre località dell'isola durante il Pleistocene superiore e l'inizio dell'Olocene.

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## Introduction

In 1995, in the Eastern part of Sardinia, a wildlife expert, G. Mele, discovered some fossils in the area of Monte Tuttavista, within the stone quarries of Orosei (Ginesu & Cordy 1997; Sondaar 2000). This discovery provides a new huge amount of information on the faunal and biogeographic history of Sardinia to be added to the already well-documented Pleistocene faunas found in Corbeddu Cave (Oliena), and in Capo Figari (Golfo Aranci) (Dehaut 1911; Gliozzi & Malatesta 1982).

The exceptional value of these finds was a strong motivation to undertake an extensive collection of all the necessary data for estimating the areal extent of the deposits and for collecting a large assemblage of vertebrate fossils. The quarrying activity present in the area and its importance for Sardinian vertebrate palaeontology was also taken into consideration by the plan, which inevitably interacted with the economic reality. The *Soprintendenza per i Beni Archeologici* of the provinces of Sassari and Nuoro, responsible for the protection and development of archaeological and palaeontological heritage, has promoted a number of meetings with the public authorities and with the quarry operators aimed at an effective collection of these fossils. A successful collaboration with the local quarrying firms has been possible thanks to the careful involvement of local operators. The presence of fossils has in fact been presented as a positive factor capable of adding value and enhancing the tourism of the area, through a combination of natural and cultural attractions.

During 1998-2001, the Ministry of Culture (*Ministero per i Beni e le Attività Culturali*) sponsored an initial research project charged with the registration and classification of the palaeontological deposits of Monte Tuttavista. The assignment involved three main institutions: the *Istituto di Scienze Geologico Mineralogiche* of the Sassari University, the *Université de Liege* (Belgium; U.R. "E.V.E.H."), and the *Rotterdam NatuurMuseum* (The Netherlands).

Site excavation and the difficult process of collection and preparation of the finds for study and exhibition purposes have been carried out since 1996 by the experts of the *Soprintendenza per Beni Archeologici* (Operating Office of Nuoro), and thanks to their constant supervision of the quarrying activity a considerable number of fossiliferous cavities and fissures have been discovered. These palaeontological sites yielded a huge quantity of fossil remains (an up to date number of findings can be estimated to be about 80.000), which are of paramount interest because of the variety of present taxa, and for the excellent state of fossil preservation.

All the area where these paleontological deposits lie, has been declared of Considerable Palaeontological Interest in conformity with Italian Laws (D.L. n° 490 of 29/10/99), after being favourably judged by the Pal-



Fig. 1 - Location map of the Monte Tuttavista area.

aeontology Commission of the *Ministero per i Beni e le Attività Culturali*.

In 2002, the *Soprintendenza per i Beni Archeologici* appointed a new team of specialists from three Italian institutions (*Università degli Studi di Firenze*, *Università degli Studi di Roma "La Sapienza"*, *Università degli Studi "Roma Tre"*) to undertake a study of these fossils. We present here a preliminary report on fossils found at Monte Tuttavista from 1996 – 2003.

## Location and geological setting

The area of palaeontological interest extends for about 3 km<sup>2</sup>, to the southwest of Orosei (Fig. 1), on the eastern side of Monte Tuttavista, along the area of Canale Longu, Oroe and Santa Rughe (IGM topographic maps, scale 1:25.000, sheet n° 500, section I - Galtelli and sheet n° 501, section IV - Orosei).

This territory is part of an imposing massif, extending towards northeast/southwest and forming a line of mountains, of which Monte Tuttavista is the most prominent (836 m a.s.l.). These structural highs, formed by Mesozoic limestones (Dieni & Massari 1966; Dieni et al. 1966; Calvino et al. 1972) are characterised by surface karst formations such as karren, cavities, cracks and niches. Because of the high permeability of karst, due to intense fracturing and the karst phenomena, a proper surface river system is not possible, whereas small, random water streams are instead present and flow towards southeast.

This massive underground karst activity has created wide, vertically oriented fissures of different shapes and

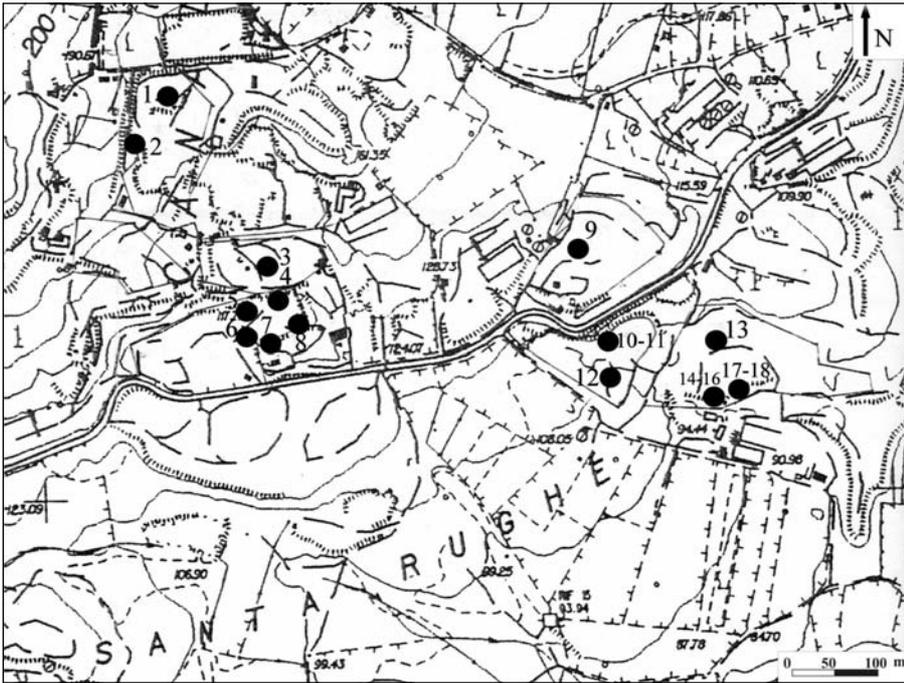


Fig. 2 - Location map of the fissures in the karst network of Monte Tuttavista. 1) IV 20; 2) IV 5 *Prolagus*; 3) VI banco 6; 4) VI 3; 5) VII 2; 6) VII blocco strada; 7) VII cervo; 8) VII mustelide; 9) IX *Prolagus*; 10) X uccelli; 11) X Mele; 12) X ghio; 13) XI 3; 14) XI dic.2001; 15) XI mar02; 16) XI rondone; 17) XI antilope; 18) XI canide.

sizes. The general shape and morphology of fissures (most are narrow and coincident with fracture lineaments) reveal a relatively young development of the karst network. In the area of Canale Longu, some fissures are filled by fluvial sediments derived from the erosion of the Palaeozoic crystalline basement. Presently, Monte Tuttavista is bordered by basalts, dated by K/Ar to  $2.32 \pm 0.09$  and  $2.75 \pm 0.11$  Ma respectively (Beccalupa & Macciotta 1983), from the main volcanic vents of Conca 'e Janas and Pirastru Mannu. No elements of volcanic rocks have been identified within the fissure fillings, but in fissure "IX *Prolagus*".

Fractures are often filled with detrital sediments of varying lithology and age, which come from the surrounding area and containing fossil remains. Nowadays, about twenty fossiliferous fissures characterised by the occurrence of abundant fossil vertebrate remains have been found inside this wide karst network (Fig. 2). The filling pattern of these fossiliferous fissures is not constant but with types of sedimentologic/lithologic settings ranging from fossil breccia made up by limestone elements to dark clays. Varying detrital sediments often fill the karst cavities as a result of various morphogenetic processes. In the wider fissures, which open into large cavities, the succession of lithotypes reveal different phases of deposition/erosion/deposition.

### Vertebrate palaeontology

The vertebrate fauna, along with their specific fissure provenances, are given in Tables 1-4. A synthetic overview of the identified taxa is offered here in systematic order.

All the fossil remains are kept in the Operating

Office of the Soprintendenza per Beni Archeologici in Nuoro, and in the Archaeological Museum of Nuoro.

### Fishes

We have identified 86 fish vertebrae and some pharyngeal bones. The state of preservation is not particularly good and several vertebrae reveal that they were rolled during transport when viewed under the microscope. The pharyngeal bones have been studied by means of direct comparison with recent specimens, vertebrae have been compared also by means of X-ray images.

The analysis of this sample has allowed us to recognize the occurrence of some shallow water marine and *Posidonia* grasslands fish species. The presence of some labrids is recognized and precisely of the brown wrasse (*Labrus merula*), ballan wrasse (*Labrus bergylta*) and rainbow wrasse (*Coris julis*). In addition to these three species, we have also identified the painted comber (*Serranus scriba*) and Gadidae indet.

Vertebral growth rings have been examined under an optical microscope and for a good number of the remains, the age and the season of death have been calculated. The more frequent season of death would appear to be spring (15 vertebrae) the remains of fishes that died in summer (two vertebrae) and in autumn (three vertebrae) are rarer, while vertebrae of fishes that died in winter are missing.

There are no studies about the Pleistocene ichthyofauna in the area. Comparisons are possible only with some otoliths from the Early Pliocene site of Orosei (Dieni 1968). The assemblage from this site is however not comparable with the Monte Tuttavista one, since it

CAVE	X	XI	XI	VI
quarry	3 uccelli	3	rondone	Banco 6
<b>TAXA</b>				
<b>FISHES</b>				
Gadidae indet.	X			
<i>Serranus scriba</i>	X			
<i>Labrus bergylta</i>	X			
<i>Labrus merula</i>	X			
<i>Labrus</i> sp.	X			
<i>Coris julis</i>	X			
"Pisces" indet.	X	X	X	X

Tab. 1 - List of fish taxa from quarries of Monte Tuttavista. The sequence of fissures is according the hypothesized chronological succession.

is made up by taxa typical of bathial environment. The only common occurrence is that of the family Gadidae, a taxon with a wide environmental distribution.

The origin of these remains in the Monte Tuttavista fissure fillings may be supposed either as result of predation by birds nesting in the fissure area and/or by the reworking of Pliocene marine deposits which outcrop in the surroundings of Monte Tuttavista.

### Herpetofauna

Fossil remains of amphibians and reptiles are very abundant in the fissures of Monte Tuttavista. The preliminary analysis of 14.747 fossil remains referable to the herpetofauna resulted in the identification of 14 taxa (4 amphibians and 10 reptiles): *Speleomantes* sp., *Discoglossus sardus*, *Bufo viridis*, *Hyla* gr. *H. arborea*, *Testudo* cf.

*T. hermanni*, Gekkonidae indet., *Podarcis* sp., *Lacerta* sp., *Agama* (s.l.) sp., *Amphisbaenia* indet., *Colubrinae* indet., *Natrix* sp., *Vipera* sp., *Serpentes* indet. (Tab. 2).

### Amphibians

#### Order Caudata

We have identified several vertebrae belonging to *Speleomantes* sp., the only plethodontid genus inhabiting Europe. This taxon is identified based on the presence of an amphicoelous vertebral body, occasionally slightly longer than 3 mm, with intravertebral foramina for the exit of spinal nerves (Estes 1981).

These specimens, and the associated caudate remains, cannot be allocated to the specific level since the 4 modern species that have been described for Sardinia (Lanza et al. 1995) do not show characters allowing the specific identification of fossils (Delfino 2002).

#### Order Anura

The presence of the family Discoglossidae is documented by some ilia showing a distinct inter ilial groove. The fossil material has been referred to *Discoglossus sardus*, the only member of the family presently living in Sardinia (Societas Herpetologica Italica 1996).

Several sacral and presacral vertebrae clearly belong to *Bufo viridis* (Family Bufonidae), the only toad that presently inhabits Sardinia (Societas Herpetologica Italica 1996).

A few ilia show the typical morphology of the genus *Hyla* (family Hylidae). The material has been referred to the group of the Mediterranean tree frogs, *Hyla arborea* group, since the osteology of the Sardinian species, *Hyla sarda*, is not known in detail.

CAVE	VII	VII	VI	XI	IX	XI	XI	IV	VI	VII
quarry	bl. St.	mustelide	3	canide	<i>Prolagus</i>	Dic.2001	3	20	Banco 6	2
<b>TAXA</b>										
<b>AMPHIBIANS</b>										
<i>Speleomantes</i> sp.	X		X	X		X	X	X	X	X
<i>Discoglossus sardus</i>				X		X	X		X	
<i>Bufo viridis</i>						X			X	X
<i>Hyla</i> gr. <i>H. arborea</i>									X	
Anura indet.	X		X	X		X	X		X	X
<b>REPTILES</b>										
<i>Testudo</i> cf. <i>T. hermanni</i>		X								
Chelonii indet.										X
Gekkonidae indet.			X	X					X	
<i>Agama</i> (s.l.) sp.	X		X	X						
<i>Podarcis</i> sp.				X		X	X	X	X	X
<i>Lacerta</i> sp.	X		X	X	X	X	X		X	
Sauria indet.			X	X			X		X	X
<i>Amphisbaenia</i> indet.			X						X	
"Colubrinae" indet.	X		X	X		X	X		X	X
<i>Natrix</i> sp.				X		X	X		X	X
<i>Vipera</i> sp.			X							
Serpentes indet.			X	X		X	X		X	X

Tab. 3 - List of herpetofauna taxa from quarries of Monte Tuttavista.

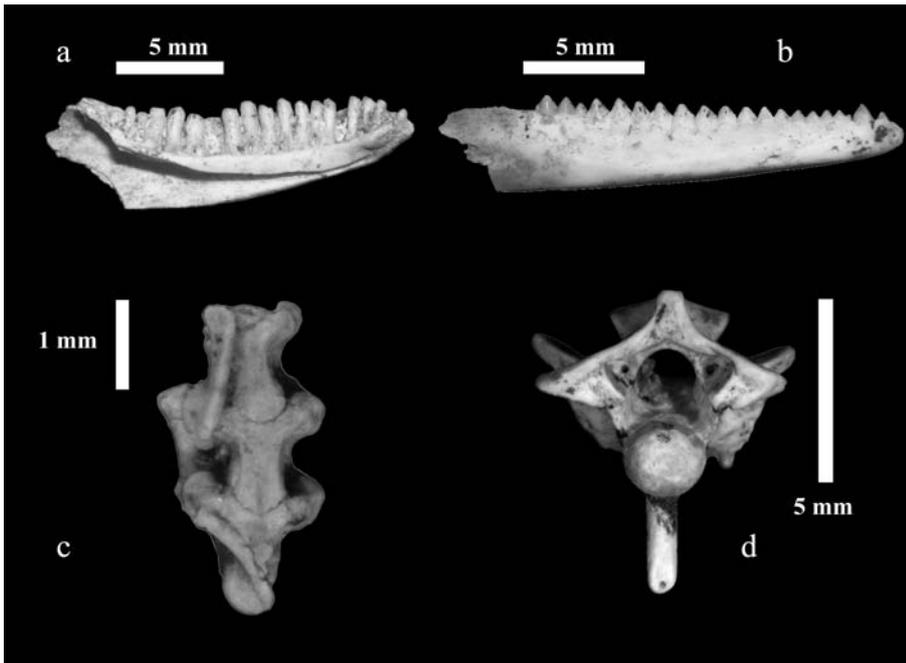


Fig. 3 - Reptilian remains from fissure fillings of Monte Tuttavista: a) *Lacerta* sp., left dentary in lingual view, La1/quarry "VI 3"; b) *Agama* (s.l.) sp., right dentary in labial view, Ag1/quarry "VI 3"; c) *Amphisbaenia* indet., trunk vertebrae in ventral view, Am1/quarry "VI banco 6"; d) *Vipera* sp., vertebra in caudal view, Vp1/quarry "VI 3".

## Reptiles

### Order Chelonii

Chelonians are represented by a fragmentary shell (partly included in rock), an isolated anterior lobe of a plastron, and a single humerus. It is possible to refer all the material to tortoises (family Testudinidae) of average size (the total length of the carapace is approximately 15 cm). The development of the epiplastral lips does not reach that of *Testudo graeca* and *T. marginata* being more similar to that of *T. hermanni* (cf. Amiranashvili 2000; Hervet 2000), the only tortoise that is considered autochthonous in Sardinia.

### Order Sauria

There are few small sized amphicoelous vertebrae and tooth-bearing bones with long conical, pleurodont teeth which are referable to Gekkonidae gen. and sp. indet.

Lacertidae remains of two sizes have been identified: the tooth-bearing bones of both show bicuspid pleurodont teeth nearly cylindrical in shape. Part of the material (*Lacerta* sp.) has a size comparable with that of a modern *Lacerta viridis* (Fig. 3a) while the rest is comparable to the genus *Podarcis* (*Podarcis* sp.). Several other skeletal elements have been tentatively referred to these two size classes.

A relevant number of tooth-bearing bones can be distinguished from the previous ones in having acrodont teeth triangular in shape (Estes 1983). Moreover, dentaries exhibit a Meckel's canal that is not as wide as in lacertids and relatively deep grooves developed on the external surface between adjacent teeth. Such a morphology (Fig. 3b) is typical of Agamidae and particularly of the

genus *Agama* s.l. (inclusive of at least the genera *Agama* and *Laudakia*, whose comparative osteology has never been investigated in detail).

### Order Amphisbaenia

Few tiny vertebrae, with ventrally flat vertebral bodies, are referable to the order Amphisbaenia (Fig. 3c). Since the vertebral morphology of amphisbaenians does not offer any taxonomic character below order level, the material has not been referred to any family.

### Order Serpentes

The family Colubridae is represented by two forms. To the operational taxon "Colubrines" have been referred all the precloacal vertebrae devoid of hypapophysis (bearing therefore a haemapophysis), that is to say the trunk vertebrae belonging to the non natricine colubrids (cf. Szyndlar 1991a). Some of them could belong to the genus *Hierophis*, but since all the diagnostic characters of this genus are not perceivable on one single vertebra, the remains have been referred to Colubrines. The bulk of the herpetological material coming from the Monte Tuttavista quarries can be referred to the genus *Natrix*. Precloacal vertebrae are characterised by sigmoid hypapophyses, long prezygapophyseal processes, and neural spines overhanging both anteriorly and posteriorly (Szyndlar 1991b). Some features, like the inclination of the prezygapophyses and the shape of the neural arches cast doubt on the occurrence of *N. natrix* that was previously identified by Delfino (2002).

Some vertebrae have been referred to the genus *Vipera* (Fig. 3d). The size and cranio-caudal compression of the vertebrae rule out the presence of members of the *Vipera berus* group.

CAVE	VII	VI	X	XI	XI	XI	VI	VII
Quarry	bl. St	3	3 uccelli	canide	dic.2001	3	Banco 6	2
<b>TAXA</b>								
<b>BIRDS</b>								
Anatidae indet.		X			X			
<i>Aquila</i> sp.		X					X	X
<i>Buteo</i> cf. <i>B. buteo</i>							X	
Accipitridae indet.		X		X			X	
<i>Coturnix coturnix</i>							X	X
Rallidae indet. sp. 1		X					X	
Rallidae indet. sp. 2		X				X		
<i>Columba livia</i>							X	
<i>Bubo</i> cf. <i>B. insularis</i>				X			X	X
<i>Athene</i> sp.		X			X		X	
Strigidae indet.	X			X			X	
<i>Alauda</i> cf. <i>A. arvensis</i>			X					
<i>Melanocorypha</i> cf. <i>M. calandra</i>			X					
Hirundinidae indet.						X	X	
<i>Pyrhacorax graculus</i>							X	
<i>Pyrhacorax</i> sp.				X	X		X	X
<i>Corvus</i> cf. <i>C. corone</i>							X	
Corvidae indet.							X	X
<i>Turdus</i> sp.					X		X	
<i>Muscicapa</i> sp.							X	
Sylviidae indet.							X	
<i>Sturnus</i> sp.							X	X
<i>Carduelis chloris</i>			X					X
<i>Emberiza</i> sp.					X			
Passeriformes indet.			X	X	X		X	X
Aves indet.		X		X	X		X	X

Tab. 2 - List of bird taxa from quarries of Monte Tuttavista.

Several vertebrae coming from the cervical, cloacal or caudal districts, along with vertebral fragments and ribs have been simply referred to the order (Serpentes indet.). Since *Natrix* is by far the most abundant snake in the assemblage, the bulk of the undetermined material likely belongs to this genus.

The palaeoherpetofauna includes some elements that are still members of the Sardinian herpetofauna and are known as fossils (Kotsakis 1980; Delfino 2002), but also others who do not; it is the case of *Lacerta* sp. (size comparable to that of *L. viridis*), *Agama* (s.l.) sp., *Amphisbaenia* indet. and *Vipera* sp. The medium-sized lizards have been recovered in Sardinia for the first time while amphisbaenians and vipers have been already quoted in the past (cf. literature in Delfino 2002). Agamids and amphisbaenians do not presently live in Italy (Societas Herpetologica Italica 1996).

### Birds

Among the rich vertebrate assemblage found in the Monte Tuttavista quarries, a large number of fossil bird remains have been collected, coming from different fissure fillings of different age (Tab. 3). The preliminary analysis of the bird fossil bones revealed the presence of at least 25 taxa, some of which are endemic. We have ordered these re-

mains by fissure in order to document inter-fissure population differences. We have identified the following avian taxa: Anatidae indet., *Aquila* sp., *Buteo* cf. *B. buteo*, Accipitridae indet., *Coturnix coturnix*, Rallidae indet. sp. 1, Rallidae indet. sp. 2, *Columba livia*, *Bubo* cf. *B. insularis*, *Athene* sp., Strigidae indet., *Alauda* cf. *A. arvensis*, *Melanocorypha* cf. *M. calandra*, Hirundinidae indet., *Turdus* sp., *Muscicapa* sp., Sylviidae indet., *Pyrhacorax graculus*, *Pyrhacorax* sp., *Corvus* cf. *C. corone*, Corvidae indet., *Sturnus* sp., *Carduelis chloris*, *Emberiza* sp., Passeriformes indet.

The presence of *Aquila* sp. is documented by several bones; they are similar in size to the

modern *Aquila chrysaetos*, but a new endemic species of *Aquila* has recently been identified in some localities both in Sardinia and Corsica (Louchart 2002), so the Orosei material needs to be compared with this new form until a more precise determination is made. *Aquila* remains have been commonly reported in the Mediterranean islands with several species (Mourer-Chauviré et al. 2002).

Remains of *Coturnix coturnix* have been found in different fissure fillings. This species is the only member of the order Galliformes commonly reported in the Mediterranean islands (Alcover et al. 1992; Mourer-Chauviré et al. 2002); this fact is due to the migratory habit of *Coturnix coturnix* which crosses the Mediterranean Sea twice per year to go to the African winter quarters from the European breeding areas. The other members of the order Galliformes are particularly sedentary and do not cross any inlet; so the presence of Galliformes on islands is only due to human introductions, such as for *Alectoris barbara* commonly found today in Sardinia after a Roman age introduction, but never reported in Corsica, not even as vagrant visitor (Louchart 2002).

The family Rallidae is represented by several remains of two different size classes. The bigger ones, Rallidae indet. sp. 1, are to be referred to a medium-sized Rallidae, such as *Rallus aquaticus*, *Gallinula chloropus* or *Crex crex*, while the smaller ones, Rallidae indet. sp. 2, probably belong to a small species of the genus *Porzana*, such as *P. parva* or *P. pusilla*.



These taxa, commonly reported in Pleistocene island deposits (Mourer-Chauviré et al. 2002), are strictly related to open wetland and are very important for palaeoenvironmental reconstructions.

One of the most common bird taxa at Monte Tuttavista is *Bubo* cf. *B. insularis*. *Bubo insularis* is an extinct species endemic to Corsica and Sardinia (Mourer-Chauviré & Weesie 1986) commonly found in Pleistocene vertebrate deposits (Pavia 1999; Louchart 2002; Mourer-Chauviré et al. 2002). Initial results suggests that the Orosei material seems to be comparable to the type material from Rapaci Cave (Mourer-Chauviré & Weesie 1986) and with the rich material from Corsica (Louchart 2002), but we need to compare them directly to be sure of this referral. A single bone found in fissure filling named "VII blocco strada" shows the morphological characteristics of the genus *Bubo*, but it is clearly different from *Bubo insularis*; unfortunately the remain is too fragmentary to allow further considerations, and is determined as Strigidae indet..

Several bones have been determined as *Athene* sp.; they belong to a large species, somewhat similar to the extinct *Athene angelis*, described from the Middle Pleistocene of Corsica (Mourer-Chauviré et al. 1997), and regarded as endemic to northern Corsica. Since the initial discovery, no remains were found in the other Corsican and Sardinian localities analysed so far (Louchart 2002). The fossil bones from Orosei show similar proportions with *Athene angelis*, but they are slightly larger in every examined bone. The genus *Athene* is widespread in the Mediterranean islands during the Pleistocene with a number of endemic species (Pavia & Mourer-Chauviré 2002), so further analyses will clarify if the Monte Tuttavista *Athene* remains are referable to *Athene angelis*, or if they document the presence of a new extinct form of *Athene* in the Pleistocene of Sardinia.

The most abundant Monte Tuttavista taxa are the Corvidae of the genus *Pyrrhocorax* including two species: *Pyrrhocorax graculus* and *Pyrrhocorax* sp. The latter of these two species is less abundant and probably referable to *P. pyrrhocorax*. These species commonly occur and are often abundant in Corsican and Sardinian fossil localities (Louchart 2002; Mourer-Chauviré et al. 2002). Recently, Louchart (2002) emphasized the morphometric differences of the Pleistocene Corsican populations of both *P. pyrrhocorax* and *P. graculus* with respect to the mainland ones and described two new subspecies endemic to Corsica, *P. pyrrhocorax macrorhynchus* and *P. graculus castiglioneensis*. Further analyses will allow us to determine the systematic position of the Monte Tuttavista remains belonging to the genus *Pyrrhocorax*, and their relationships to the two endemic subspecies recently described.

Fossil birds often prove to be sensitive palaeoenvironmental indicators. Although preliminary, the analysis of the Monte Tuttavista bird associations, collected

in different fissure fillings of different age, suggests the presence of species typical of rocky habitats dominated by cliffs (e.g. *Aquila* sp., *Bubo* cf. *B. insularis*, *Athene* sp., *Pyrrhocorax graculus* and *Pyrrhocorax* sp.). Moreover, other taxa such as the Anatidae and the Rallidae, suggest the presence of marshlands not so far from Monte Tuttavista, while *Coturnix coturnix*, *Alauda* cf. *A. arvensis* and *Melanocorypha* cf. *M. calandra* indicate also the presence of important open dry area. The complete analysis of all the bird remains, separated in the different fissure fillings, will of course allow us to reconstruct the environmental evolution of the Orosei area, from the Pliocene to the Late Pleistocene.

## Mammals

Among large sized mammals, almost all of the orders known from the European Pleistocene are found with the exception of the Proboscidea and Perissodactyla (Tab. 4). Some taxa (e.g. cervids and bovids) are frequently represented by partially connected skeletons often characterized also by pre-diagenetic fractures, thus suggesting an accumulation by falling into fissures and sinkholes. This hypothesis is also supported by the occurrence of a large number of newborn and juvenile individuals. The micromammal record is also impressive: about 9.000 remains including cranial fragments, mandibles and teeth, have been identified and analysed. The small mammal fauna includes thirteen taxa (Tab. 4): one erinaceomorph (*Talpa tyrrhenica*), two soricomorphs (*Nesiotites* sp. 1, *Nesiotites* sp. 2), one bat (*Myotis* cfr. *M. bechsteini*), seven rodents (*Tyrrhenoglis* cf. *T. majori*, *T. cf. T. figariensis*, Gerbillidae indet., *Tyrrhenicola* n. sp., *Tyrrhenicola henseli*, *Rhagapodemus minor*, *Rhagamys orthodon*) and two lagomorphs (*Prolagus* cf. *P. sardus*, *Oryctolagus* aff. *O. lacosti*).

### Order Erinaceomorpha

A few remains of a mole (family Talpidae) have been discovered. They correspond in size and morphology to *Talpa tyrrhenica*, the endemic talpid of Sardinia (Bate 1945). This species, not very common (Gliozzi et al. 1984), has been recently reported for the first time also in Corsica (Pereira et al. 2001).

### Order Soricomorpha

Family Soricidae is represented by two species of *Nesiotites*, differing in size. *Nesiotites* is a genus erected by Bate (1944) for the endemic soricids of Mallorca, Menorca, Corsica and Sardinia.

The endemic *Nesiotites* of the Balearic Islands has been the object of many studies (Reumer 1980, 1982; Alcover et al. 1981 with bibliography), while specific analyses on the Sardinian soricid are nearly lacking. Bate (1944) reports the occurrence in Sardinia of *Nesiotites similis*, the

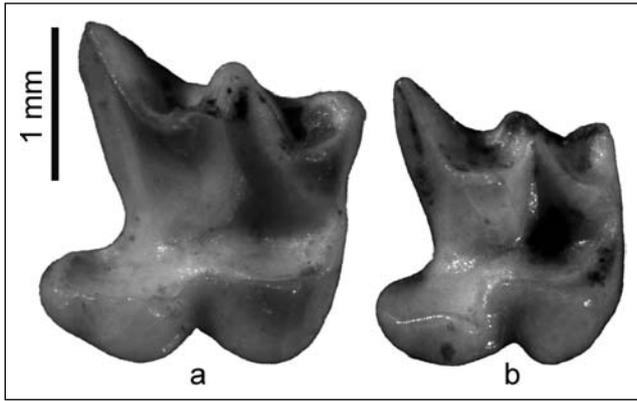


Fig. 4 - Insectivore remains from fissure fillings of Monte Tuttavista: a) *Nesiotites* sp. 1, M<sup>1</sup> dex., Nt9/quarry "XI 3"; b) *Nesiotites* sp. 2, M<sup>1</sup> dex., Nt5/quarry "X 3 uccelli".

smallest species of the genus. A bigger form, *Nesiotites corsicanus* is known from the Pleistocene of Corsica. The occurrence of this larger species in Sardinia is reported by Brandy (1978) and Fanfani (2000).

The big soricid of Orosei, *Nesiotites* sp. 1 (Fig. 4a), is morphologically similar but even larger than *N. corsicanus*. On the other hand the measurements reported by Hensel (1855) for the type specimen of *N. similis* seem to agree with the dimensions of our specimens of larger size. A contradiction exists between the dimensions of the type specimen and those of the specimens assigned by Bate to *N. similis*. Moreover, the attribution of the soricids of Sardinia and Corsica to the same genus of the soricid from the Balearic Islands has been questioned by Fanfani (2000), who believes these two forms are derived from different dispersal waves from the mainland.

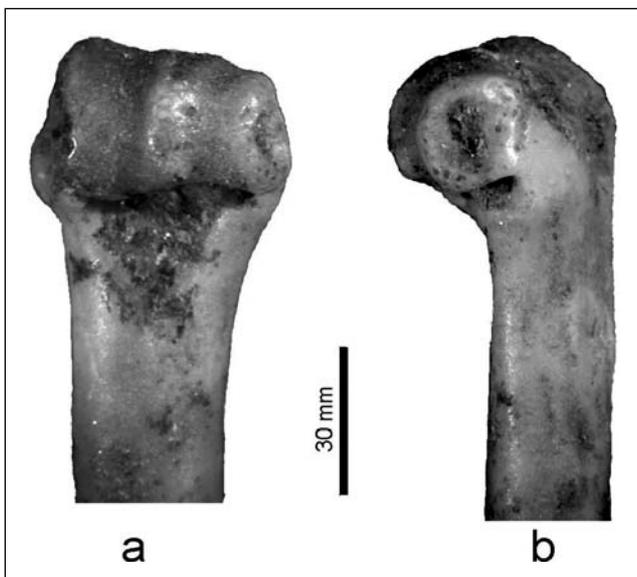


Fig. 5 - Distal part of right humerus of *Myotis* cf. *M. bechsteini* from fissure filling "XI dic.2001" of Monte Tuttavista (Orosei, Sardinia), Pi1/quarry "XI dic.2001": a) anterior view; b) lateral view.

Pending a general revision of the fossil material of Sardinia we prefer to classify our specimens only at the genus level.

The smaller form, *Nesiotites* sp. 2 (Fig. 4b), has been identified in quarries "X 3 uccelli" and "VI 3". It is a little smaller than the specimens described by Bate (1944) under the specific name *N. similis*. These fossils are similar to *Nesiotites* described as *N. similis* by Gliozzi et al. (1984), collected at Is Oreris in southwestern Sardinia. The morphological observations of the larger taxon essentially apply to this smaller form.

### Order Chiroptera

Only a single fossil among the thousands of specimens collected at Orosei belongs to a Vespertilionidae bat: the distal part of a right humerus (Fig. 5), referred to *Myotis* cf. *M. bechsteini* (cf. Felten et al. 1973). The species *M. bechsteini* does not live at present day in Sardinia (Lanza & Finotello 1985). On the other hand the remains of fossil bats of Pleistocene age collected in Sardinia are very few: *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros*, *Myotis capaccinii*, *Nyctalus* cf. *N. lasiopterus* and *Miniopterus schreibersi* picked in a fissure between Punta Padrebellu and Omo Morto (Alghero, Sassari), *Myotis myotis* of the Dragonara Quarry (Alghero, Sassari) (Kotsakis 1987), *Rhinolophus ferrumequinum* of the Corbeddu Cave (Oliena, Nuoro) (Sondaar et al. 1984) and *Eptesicus serotinus* and *Tadarida teniotis* from a bone breccia of Tavolara island (Comaschi Caria 1968). The later remains are perhaps Holocene in age.

### Order Primates

The first identification of a fossil primate (family Cercopithecidae) in Sardinia was made by Dehaut (1911). He erroneously associated a skull fragment of the owl *Bubo insularis* from Capo Figari with fragmentary mammalian postcrania (cf. Comaschi Caria 1968; Pavia 1999), and in a later paper (Dehaut 1914) with an M<sub>3</sub> of a fossil macaque. Between 1910 and 1914 Major recovered an abundant fossil assemblage from this locality through systematic excavation. Amongst these fossils was a rich collection of primate remains which were classified as belonging to the genus *Macaca* (Major 1913). Before the discovery of the Monte Tuttavista sites, only a second locality was known to have yielded *Macaca* remains in Sardinia, Is Oreris (Comaschi Caria 1970).

The first detailed study of the Capo Figari *Macaca* assemblage was carried out by Azzaroli (1946) who analysed the collection kept in the University of Florence Museum and erected the new species *M. majori*. Since Azzaroli's paper, no specific study has dealt with this species. Some authors have however dealt with these remains in the context of wider reviews maintaining it as a separate species of the genus *Macaca*. Gentili et al. (1998) considered *Macaca majori* to be related to the Plio-Pleis-

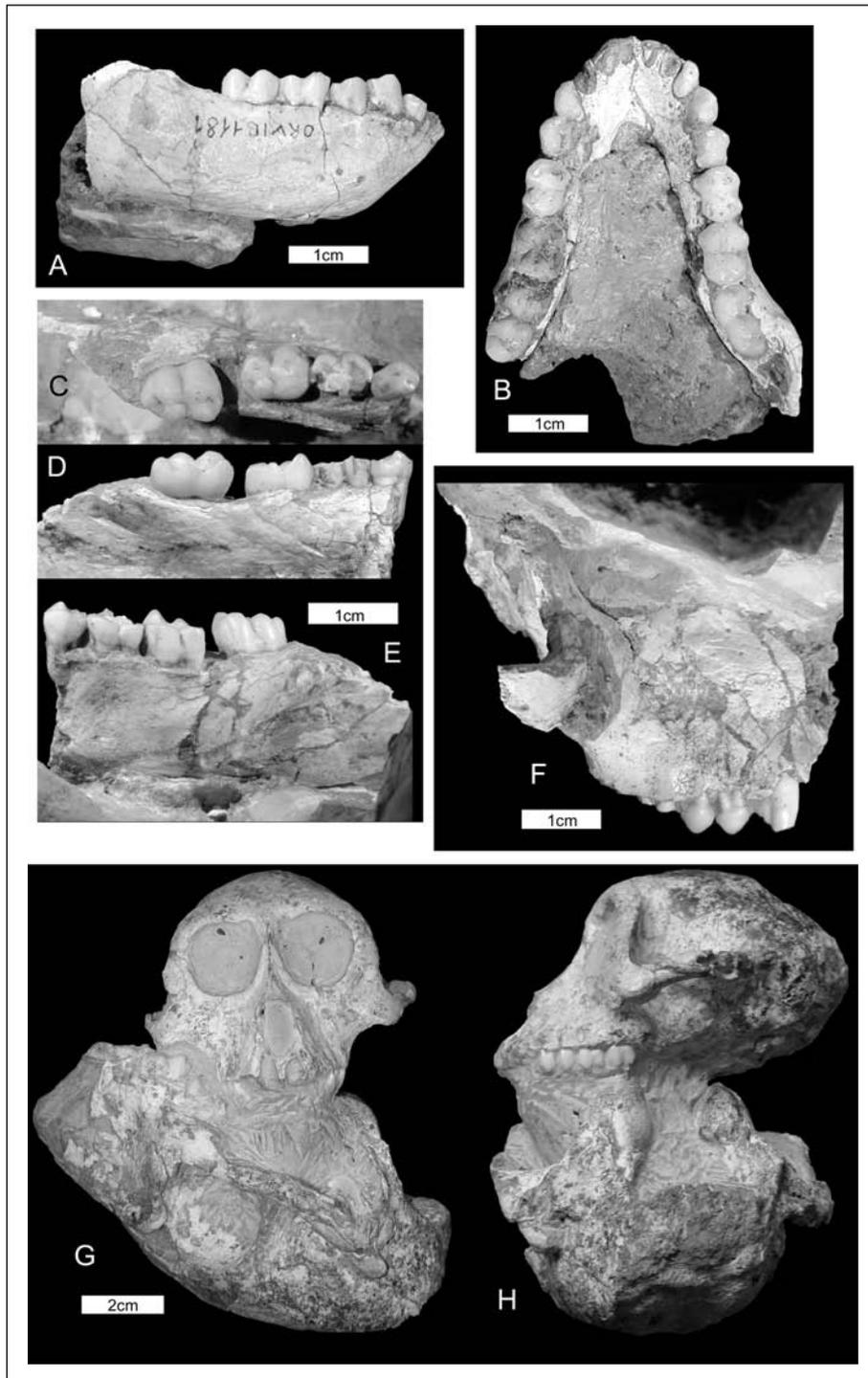


Fig. 6 - *Macaca* cf. *M. majori* from Monte Tuttavista (quarry "VI 3"). A-B) fragmentary mandible VI-3-1181 in right lateral (A) and occlusal (B) views; C-E) fragmentary left mandibular ramus VI-3-1185 in occlusal (C), lingual (D) and labial (E) views; F) fragmentary skull VI-3-1185 still embedded in the bone-breccia in right lateral view; G-H) complete *Macaca* skull VI-3-2183 in anterior (G) and left lateral (H) views; note the *Sus* cf. *S. sondaari* skull in upside-down right lateral view (G) and occipital (H) views still united to the macaque specimen.

the fossil record beyond Middle Pleistocene faunal assemblages seems to indicate it became extinct locally then.

While fossil primates are usually rare in a fossil assemblage, the Monte Tuttavista macaque is abundant like at Capo Figari. The large amount of remains and the good preservation status (Fig. 6) will allow us, in addition to the taxonomic analysis, to deal also with palaeoecologic and taphonomic aspects responsible for the formation of such a sample. Like in Capo Figari, one of the characteristics of Mt. Tuttavista macaque sample is the high percentage of juvenile (and infantile) individuals. Zanaga (1998), studying the *Macaca majori* sam-

plage from Capo Figari, suggested a selective accumulation by large birds of prey, given some similarities between the Capo Figari sample and the sample from Taung as studied by Berger & Clarke (1995). The same could actually be also for Mt. Tuttavista.

A preliminary study of the Mt. Tuttavista macaque suggests that it is the same taxon that occurs at Capo Figari, *Macaca majori*. In size, both samples are smaller than extant *Macaca sylvana* and the related Plio-Pleistocene fossil forms *Macaca florentina*, that some authors include as a subspecies of the living form thus, *Macaca*

tocene European macaques, relatively abundant in fossil sites in Italy and around Europe. Some authors (Szalay & Delson 1979; Jablonski 2002) have cast doubts on the supposed insular dwarfism of this Sardinian macaque, and consider this form a subspecies of the extant macaque *M. sylvanus* (*Macaca sylvanus majori*).

*Macaca majori* is comparable in size with the smallest extant macaque species of insular and peninsular areas of south-eastern Asia, and is characterized by reduced cranial dimensions, relative to the body size. The timing of *M. majori* extinction is questioned. Its absence in

plage from Capo Figari, suggested a selective accumulation by large birds of prey, given some similarities between the Capo Figari sample and the sample from Taung as studied by Berger & Clarke (1995). The same could actually be also for Mt. Tuttavista.

A preliminary study of the Mt. Tuttavista macaque suggests that it is the same taxon that occurs at Capo Figari, *Macaca majori*. In size, both samples are smaller than extant *Macaca sylvana* and the related Plio-Pleistocene fossil forms *Macaca florentina*, that some authors include as a subspecies of the living form thus, *Macaca*

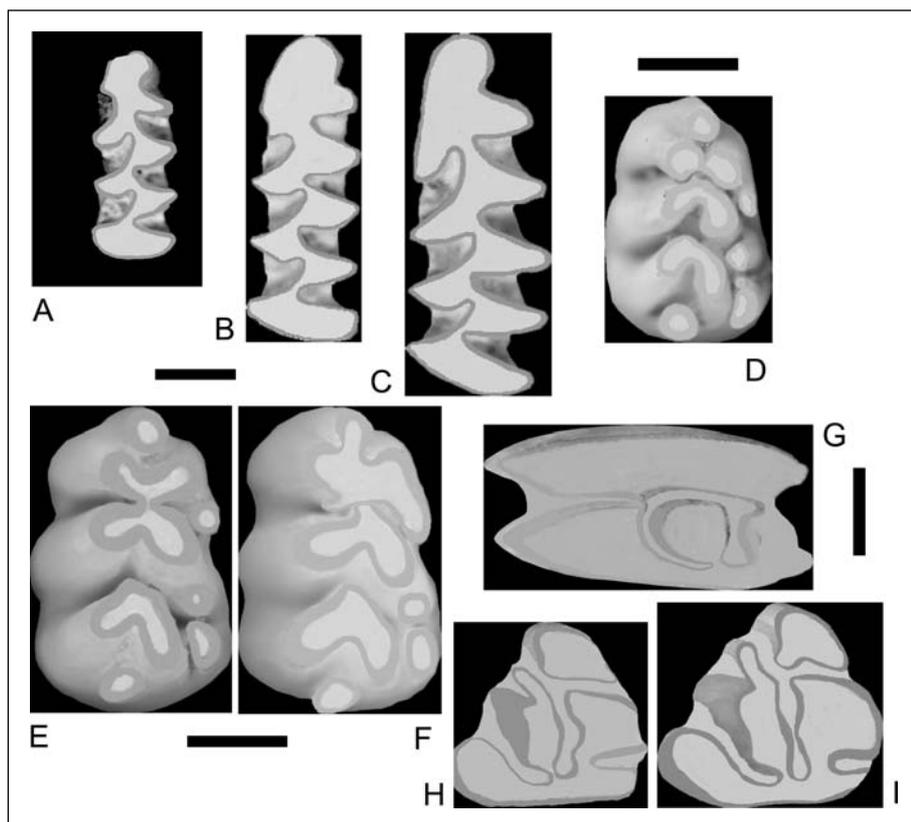


Fig. 7 - Rodents and lagomorphs from fissure fillings of Monte Tuttavista. *Tyrrhenicola* n. sp.: a)  $M_1$  dex., Ty105/quarry "X 3 uccelli", refl.; *Tyrrhenicola henseli*: b)  $M_1$  sin., morphotype 1, Ty107/quarry "XI canide"; c)  $M_1$  sin., morphotype 4, Ty104/quarry "VI banco 6"; *Rhagapodemus minor*: d)  $M_1$  dex., Rh20/quarry "X 3 uccelli"; *Rhagamys orthodon*: e)  $M_1$  dex., Rh11/quarry "IV 20"; f)  $M_1$  dex., Rh60/quarry "VI banco 6". *Prolagus* cf. *P. sardus*: g)  $P^3$  sin., Pr14(III)/quarry "XI canide"; h)  $P_3$  sin., PrMand5/quarry "IV 20"; i)  $P_3$  dex., Pr14/quarry "VI banco 6" (refl.). Scale bar = 1 mm.

*sylvana florentina* (see Rook et al. 2001a for a discussion). Like *Macaca majori*, the Mt. Tuttavista sample is characterized by molars with a peculiar morphology: the crown is in fact slightly inflated just above the neck giving the tooth a "puffy" aspect (Szalay & Delson 1979). Although very close to *M. majori*, we are still cautious in the specific attribution of the Mt. Tuttavista remains. In fact, some traits of the facial morphology observable in the maxillary VI-3-1185 (Fig. 6f) and especially in the skull VI-3-2183 (Fig. 6g,h), seem to differ qualitatively from the peculiar morphology reported for the Capo Figari sample (O'Higgins et al. 2001; Rook & O'Higgins in press). We provisionally refer the Mt. Tuttavista remains to *Macaca* cf. *M. majori*.

## Order Rodentia

### Gliridae

A single mandible of a glirid without teeth has been collected in quarry "X ghiro". The dimensions are a little larger than those of *Tyrrhenoglis majori*, type species of the endemic Sardinian genus *Tyrrhenoglis*, collected from Capo Figari (Engesser 1976). In Sardinia another large fossil glirid has been collected from the Middle Pliocene aged deposits Nuraghe Su Casteddu (Dorgali, Nuoro), and referred to *Hypnomys* sp. (Esu & Kotsakis 1980). Besides strong similarities with this endemic Balearic Islands genus (Mein 1983), an attribution to the genus *Tyrrhenoglis* is more probable (Kotsakis 2003).

Very few teeth collected in quarry "VI 3" belong to a smaller glirid. Both morphology and dimensions of these fossils agree well with the type population of *Tyrrhenoglis figariensis*, the smaller member of the genus. This species is present in two fissure fills of Capo Figari associated with murids belonging to different stages of the *Rhagapodemus minor*-*Rhagamys orthodon* lineage (Zammit Maempel & de Bruijn 1982). A more primitive species, not yet formally erected, presumably the ancestor of *T. figariensis*, is present at Mandriola (Sinis Peninsula, Western Sardinia), in an assemblage of latest Ruscinian age (Zammit Maempel & de Bruijn 1982; Angelone & Kotsakis 2001).

### Gerbillidae

A single  $M^2$  of a gerbillid has been collected in the quarry "VI banco 6".

Gerbillidae is a living family of African and Asian rodents but some species have been reported from Miocene and Pliocene deposits of both Central-Eastern Europe and Iberian peninsula. In Italy, gerbillids are reported from Ciabòt Cagna (Piedmont), an assemblage of Late Turolian age (Cavallo et al. 1993), and from uppermost Miocene-lower Pliocene deposits in Tuscany (Rook et al. 2001b).

Since the fossil assemblage from fissure "VI banco 6" is one of the most recent because of the evolutionary stage of several mammals, it is thus probable that the gerbillid as well as the single fragment assigned to the agamid

lizard (a taxon associated in a few fissures of Monte Tuttavista with more primitive assemblages of mammals) are “exotic” elements reworked from an older assemblage.

#### Arvicolidae

*Tyrrhenicola henseli* is an endemic fossil vole widespread in Sardinia and Corsica during Middle and Late Pleistocene and Holocene. In recent papers, *Tyrrhenicola* has been considered to be a subgenus of *Microtus*.

Voies are often used as reliable biochronological indicators. However, very little biochronological informations are available for *Tyrrhenicola henseli*, due to the lack of a detailed biochronological framework for Sardinian faunas. The systematic position and phylogenetic relationships of *Tyrrhenicola* are also controversial. Brunet-Lecomte & Chaline (1990), on the basis of the typical pitemyan rhombus shown by *Tyrrhenicola*, suggest that *T. henseli* may represent an archaic branch of the same group that produced the Malta species *Terricola melitensis*, this is, the Mediterranean group of *Terricola* which the authors believe was derived from *Allophaiomys chalinei*. Other authors, on the contrary, believe the similarities with *Terricola* are only a parallelism and propose an evolution from *Allophaiomys pliocaenicus* as well as an immigration to Sardinia during the early Pleistocene (Van der Meulen 1973; Gliozzi et al. 1984). Mezzabotta et al. (1995) further suggest the evolution from the *Allophaiomys ruffoi*-*A. burgondiae* lineage, and an immigration to Sardinia within late Early Pleistocene to early Middle Pleistocene.

Since all the *Tyrrhenicola* populations recovered from Sardinia or Corsica are so highly derived, they are of no help for correlations with the European mainland. The population recovered in quarry “X 3 uccelli”, though only preliminarily studied, will probably add a deeper insight on this subject. As a matter of fact, quarry “X 3 uccelli” seems to be a very ancient fissure with a *Tyrrhenicola* showing relatively archaic features and small size, and these remains belong certainly to a new species, *Tyrrhenicola* n. sp. (Fig. 7a). The occurrence of a primitive new species of this arvicolid in Sardinia has been already reported by Brandy (1978), Cordy (1997) and Sondaar (2000).

The samples from other quarries (Fig. 7b,c) present different evolutionary degrees, showing a general trend towards an increase in the complexity of the anteroconid, with a progressive development of T7 and sometimes the presence of incipient T6 and T9 (teeth nomenclature follows Van der Meulen 1973).

Mezzabotta et al. (1995) define four main morphotypes (1 to 4, increasing with evolutionary degree) useful to distinguish *Tyrrhenicola* evolutionary stages. Samples from the Monte Tuttavista fissures have been attributed to these morphotypes. It has been therefore possible to show differences in evolutionary degrees among the studied samples. These have been used for reconstructing a

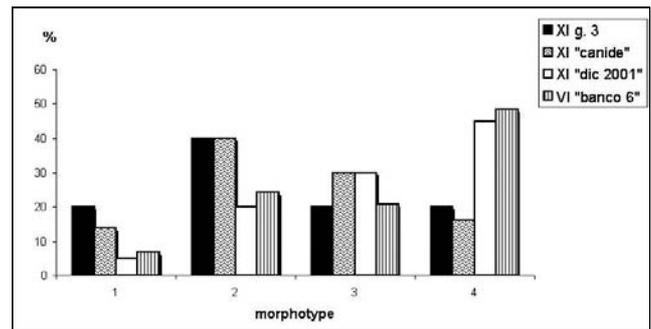


Fig. 8 - Histogram representing morphotypes distribution of  $M_{1s}$  of *Tyrrhenicola henseli* within quarries of Monte Tuttavista.

biochronologic succession of the different fissures. Population from quarry “IV” seems to be the less evolved, although the small specimen number. Populations from quarries “XI 3” and “XI canide” mainly belong to morphotypes 1 and 2 while those from quarries “XI dic. 2001” and “VI banco 6” seem to be the most evolved, with prevailing morphotype 4, and high percentage of morphotype 3 (Fig. 8).

#### Muridae

Only one of the fissures of the Monte Tuttavista area, “X 3 uccelli”, contains abundant fossil remains of *Rhagapodemus minor* an Early/Middle Pleistocene endemic Sardinian species (Brandy 1978). This species is also present, with a few specimens, at quarries “VI 3”, “VII mustelide” and “X ghiro” (Fig. 7d). *Rhagapodemus minor* is supposed to be an intermediate element of an anagenetic lineage whose continental ancestor is *Rhagapodemus ballesioi* (MN14 - basal MN15; Mein & Michaux 1970). Very likely *R. ballesioi* arrived in the Corso-Sardinian region during the Late Ruscinian: its descendant *R. azzarolii* (Mandriola, Sinis Peninsula, Western Sardinia; late MN15 – basal MN16?) (Angelone & Kotsakis 2001) still bears recognizable features of *R. ballesioi*, but shows evident incipient dental modifications, that prelude to *Rhagapodemus minor*. *Rhagamys orthodon* is an advanced form derived from *Rhagapodemus minor* and the last element of the evolutionary lineage.

Compared to *Rhagamys orthodon*, *Rhagapodemus minor* is still rather brachyodont and smaller; other differential features between the two species are the fusion of T2-T3 on  $M^1$  and the lack of T3 on  $M^2$  in *Rhagamys orthodon* (see Brandy 1978). Specimens from quarry “X 3 uccelli” show a more advanced evolutionary degree if compared to *Rhagapodemus minor* from the type locality (Capo Figari): T2 and T3 on  $M^1$  show different degrees of fusion, T3 on  $M^2$  is often still present, but extremely reduced. *Rhagapodemus minor* was formerly assigned to the genus *Rhagamys* by Brandy (1978); later systematic/nomenclatorial revisions (Martín Suárez & Mein 1998)

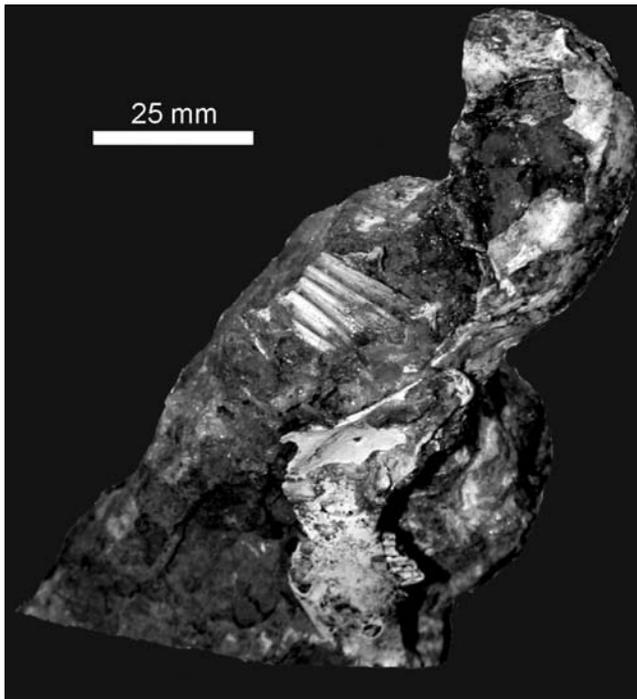


Fig. 9 - Fragment of skull and left mandibular ramus of *Oryctolagus* aff. *O. lacosti*, Monte Tuttavista, Or1/quarry "VII blocco strada".

suggest its attribution to the genus *Rhagapodemus*, while maintaining the generic name *Rhagamys* for the species *R. orthodon*.

A larger murid is a common element in other quarries ("IV 5 *Prolagus*", "IV 20", "VII 2", "XI 3", "XI canide", "XI dic. 2001", "VI banco 6"). This form shows also an extreme hypsodonty degree and tubercles arrangement, which made possible their classification as *Rhagamys orthodon* (Fig. 7e,f), an endemic insular form living in Sardinia and Corsica from Middle Pleistocene to Holocene (Vigne 1987). Nonetheless, some important morphometric differences exist between specimens collected in different quarries. Such differences allow us to recognize different evolutionary degrees and to give a chronological order to the various fissures. The most evident are the increase in size and hypsodonty, and the appearance of accessory roots. Other progressive trends have been observed, mainly in the first molars. During the last year *R. minor* has been collected also in Corsica (Pereira et al. 2003).

### Order Lagomorpha

#### Ochotonidae

The ochotonid has been identified as *Prolagus* cf. *P. sardus* (Fig. 7g-i). The general features of the nearly one thousand examined dental elements are very similar to those of *Prolagus sardus*, but some specimens show a mix of characters of both *P. sardus* and *P. figaro*, the two endemic Corso-Sardinian forms.

At a preliminary glance it appeared that, in spite to the great interspecific variability of *Prolagus* and its extreme bradytely, different morphotypes of the various dental elements could be clearly recognized within the quarries.

Following the approach described in Mazza (1986), we ordered the *Prolagus* morphotypes in a chronological cline, obtaining the following sequence of the richest fissure fillings (from the more primitive): quarries "IV 5", "IV 20", "VII 2", "XI 3", "XI canide", "XI dic. 2001", "VI banco 6". In addition to a general size increase, the main dental variations can be observed on  $P_3$  morphology (Fig. 7h,i). This tooth is characterized by progressive modification and deformation of the anteroconid (nomenclature follows López Martínez & Thaler 1975), a feature typical of endemic forms, observed in other insular *Prolagus* species (López Martínez 1978). The triangular shape of the metaconid observed in the most ancient forms shifts towards a rectangular shape. In the recentmost morphotypes the metaconid is very enlarged and tends to close the external side of the mesoflexid. Moreover, the percentage of the specimens with an enamel hiatus on the entoconid increases in the most advanced forms. As for the upper cheek teeth, even on  $P^2$  and  $P^3$  a slight but progressive deformation in the internal enamel folds can be noticed. Moreover, the general shape of the second premolar, from a predominant trapezoidal morphotype shifts towards an oval contour.

Very interesting is the morphologic trend observed in  $P^4$ s, a very conservative dental element: paraflexus and mesoflexus tend to join in the precone area, making the connecting precone-lagicone isthmus increasingly thinner; in the most advanced populations a new morphotype with a complete isolation of the lagicone occurs (Fig. 7g).

On the basis of metrical and morphological overlap among different morphotypes there is no reason to raise the *Prolagus* morphotypes to specific rank. Even some statistical tests (Student's "T" test and CV test; cfr. Esteban Aenlle & López Martínez 1987; Bachelet et al. 1991) tend to exclude the presence of different species. Further studies may clarify the continental specific affinities of *Prolagus sardus*, solve the problem of the time of its arrival on Sardinia and Corsica, as well as its taxonomic status.

#### Leporidae

In contrast to the great abundance of *Prolagus* in the Monte Tuttavista karst fissure fillings, the genus *Oryctolagus* is present only with a few elements in quarries "VI 3", "X 3 uccelli", "VII blocco strada", "X ghiro" and "XI antilope", which contain the most primitive faunal assemblages. The specimens, although larger in size, show morphological affinities with *Oryctolagus lacosti* (Fig. 9), a widespread Plio-Pleistocene Western European species (López Martínez 1989; Nocchi & Sala 1997).

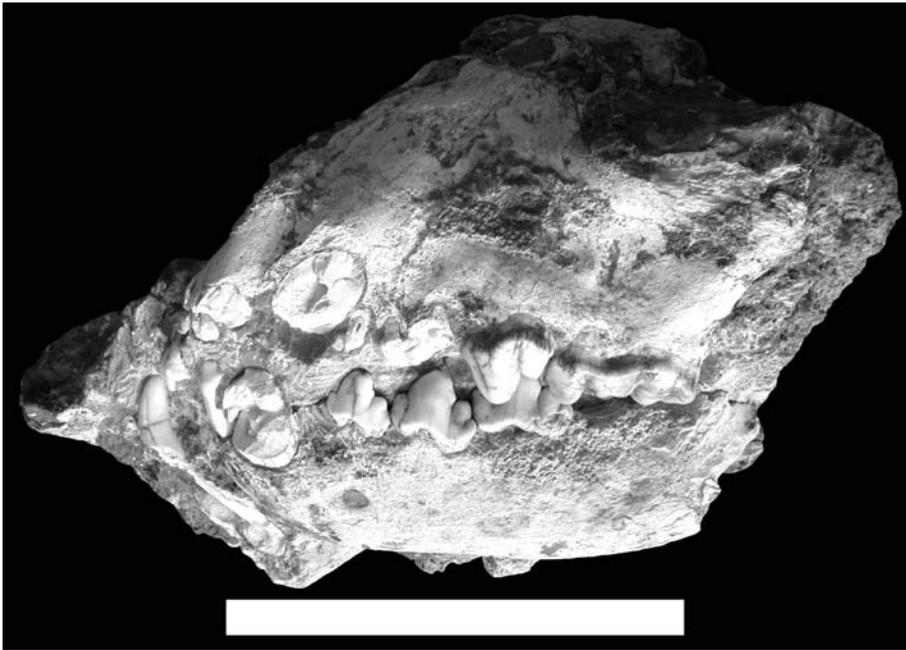


Fig. 10 - *Chasmaporthetes* n. sp., skull still embedded in the bone breccia block. Bar scale is 10 cm.

## Order Carnivora

### Hyaenidae

The Monte Tuttavista hyaena is represented by a rostrum with associated mandible still in occlusion (Fig. 10). This specimen is one of the first finding in the Monte Tuttavista quarry area (Ginesu & Cordy 1997). The occurrence of large carnivores in island ecosystems is an exception, especially if such a taxon maintains its behavior and a strictly carnivorous diet. Island endemic faunal assemblages are typically impoverished and ecologically unbalanced (cf. MacArthur & Wilson 1963; Sondaar 1977). The identification of a large-sized hyaenid at Mt. Tuttavista faunal assemblages forces us to reexamine the evolutionary history, including palaeoecology and biogeography, of the Plio-Pleistocene Sardinian mammal assemblages.

Although the left side of the specimen is still embedded in the covering rock matrix, the right is completely exposed and shows all the anatomical details that allow the taxonomic attribution to the genus *Chasmaporthetes* (Rook et al. 2004). Morphology of maxillary bone, nasals and frontals, canines stout and large cheek teeth are typical for a representative of the family Hyaenidae. Tooth morphology, and especially the symmetrical “architecture” of the P<sub>4</sub>, suggest a referral to *Chasmaporthetes*, the “hunting-hyaena”, widespread in the Old World from Late Miocene to the earliest Pleistocene. The taxonomic attribution is strengthened by the preliminary analysis of the pattern of Hunter-Schreger bands (HSB) in the enamel structure. Like modern and fossil hyaenids, *Chasmaporthetes* shows a typical complex zig-zag HSB pattern, although less pronounced than in true bone-breakers (Ferretti 1999); the Monte Tuttavista sample definitely fits the *Chasmaporthetes* HSB pattern.

Although definitely smaller, the Mt. Tuttavista specimen is morphologically comparable with *Chasmaporthetes lunensis*, the hunting-hyaena of the European Plio-Pleistocene (Ficcarelli & Torre 1967a; Galiano & Frailey 1977; Kurtén & Werdelin 1988). We maintain that such marked reduction in size could represent the result of an adaptation to the Sardinian insular ecosystem.

### Mustelidae

Three mustelids have been identified within the carnivore sample at Mt. Tuttavista: *Pannonictis*, *Enhydriactis* and cf. *Mustela*.

Before the discovery of the Mt. Tuttavista faunal assemblage, the only non lutrine mustelid known in the Sardinian fossil record was the genus *Enhydriactis* defined on material from Monte San Giovanni, a Late Pleistocene site (*E. galictoides*; Ficcarelli & Torre 1967b).

The status of this genus has been debated by several authors, and often it has been suggested a synonymy between this genus and another large mustelid widespread in the Plio-Pleistocene of the Eurasia *Pannonictis*. Kormos (1931) described a large mustelid from Villany and Beremend (Hungary) as *Pannonictis pliocenica* and few years later Kormos (1933) separated the smallest form in the sample as a separate species, *Pannonictis pilgrimi*. Viret (1954) included under the name *Enhydriactis ardea* the fossils from Saint Vallier (*Mustela ardea* Bravard) and the small Hungarian *Pannonictis pilgrimi*. The synonymy between *Enhydriactis* and *Pannonictis* is not supported on anatomical evidence (Ficcarelli & Torre 1967b; Rook 1995). While *Enhydriactis* is relatively rare in the fossil record of Eurasia, *Pannonictis* has a relatively wide distribution. This latter genus possibly occurs in China since the Late Miocene (Mustelide gen. indet. in Zdansky 1927)

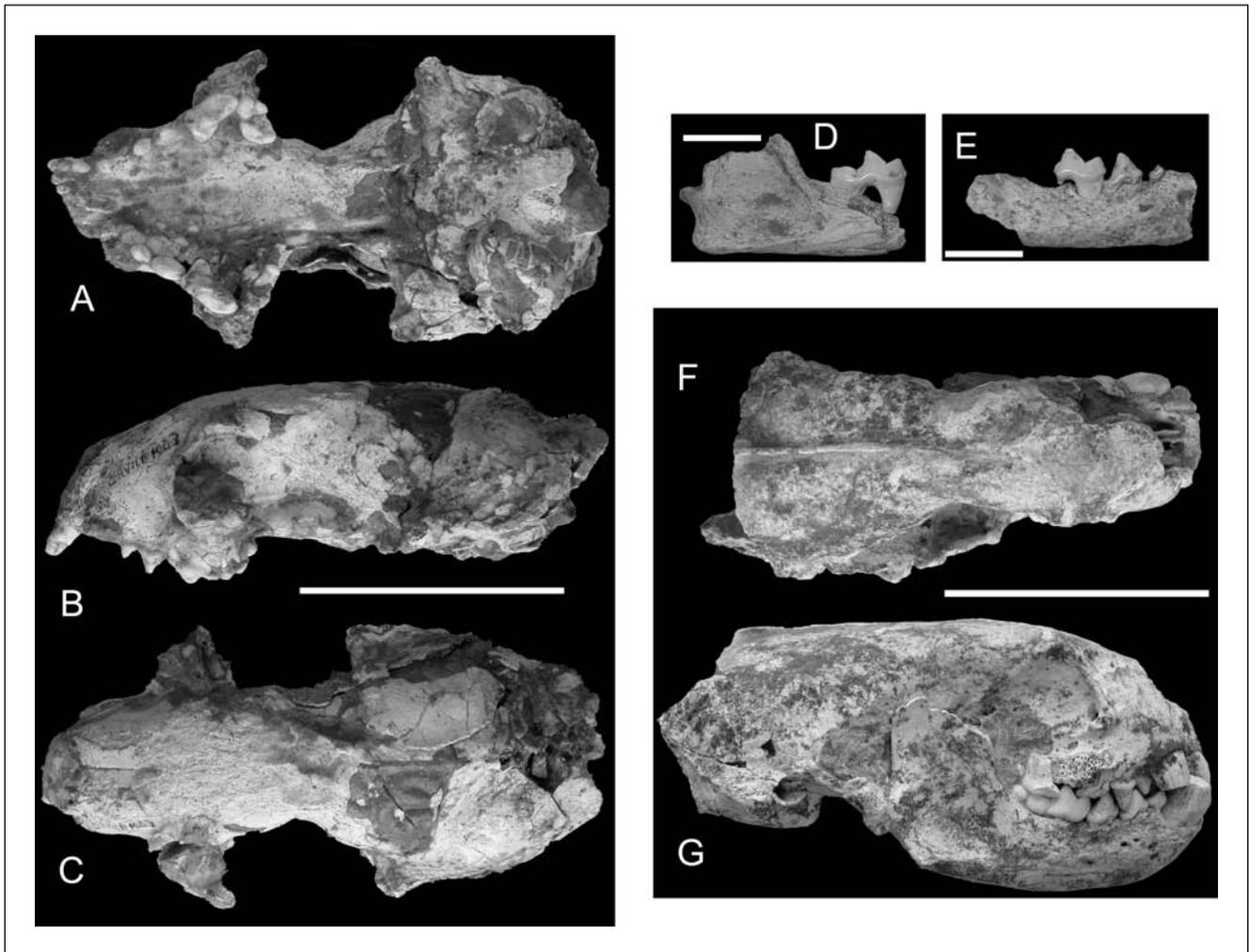


Fig. 11 - Mustelidae from Monte Tuttavista. A-C) Skull of *Pannonictis* sp. (VII-Mustelide-1003) in inferior (A), left lateral (B) and superior (C) views. D-E) cf. *Mustela putorius* from quarry "VI 3". (D) right fragmentary ramus (VI-3-1012) in labial view; (E) right fragmentary ramus (VI-3-1013) in labial view. F-G) Fragmentary skull (with articulated mandible) of *Pannonictis* sp. (VII-erratico) in superior (F) and right lateral (G) views. Bar scale is 5 cm for A-C and F-G and 1 cm for D-E.

where there is a good record during the Plio-Pleistocene (Teilhard de Chardin & Pivetau 1930; Teilhard de Chardin & Leroy 1945; Sotnikova 1980). In Europe *Pannonictis* is characteristic of the late Villafranchian. When it occurs in Italy, it is well documented as the species *Pannonictis nestii* (Ficcarelli & Torre 1967b; Rook 1995). Phylogenetic relationships among *Enhydrictis*, *Pannonictis* and the North American early Pleistocene genus *Trigonictis* still remain unclear (Repenning 1967; Thenius 1972; Rook 1995).

The taxonomy of these forms has been debated for a long time and still there is no agreement among different researchers. Pilgrim (1933) first regarded them as taxa representative of the living south American Grisoninae, and this view was followed by Reig (1957) who erected the name Galictinae, replacing and expanding the Grisoninae of Pocock (1921). The use of this subfamily name has been followed by several authors but there is no agreement however on its taxonomical as-

essment, some researchers (Wozencraft 1989a,b; Wol-san 1993) do not accept the taxonomic distinction of the Galictinae and include them within Mustelinae (cf. Rook 1995 for an exhaustive discussion). Together with the hyaenid skull, one of the first discoveries at Mt. Tuttavista has been a skull (with mandible in occlusion) of another, smaller carnivore (specimen VII-erratico) (Fig. 11f,g). The same large mustelid has been identified in other fissure fillings ("VI 3", "VII Mustelide" and "X 3 uccelli"), represented by a skull (Fig. 11a-c), fragmentary mandibles, isolated teeth and postcranial bones. Being of comparable size, the first comparisons of these remains were made with the known Sardinian fossil mustelid *Enhydrictis galictoides*. The comparative analysis revealed great differences that prevented the possibility to attribute this Mt. Tuttavista large mustelid to the genus *Enhydrictis*, the endemic Late Pleistocene *Enhydrictis galictoides* and the presumed Plio-Pleistocene ancestor

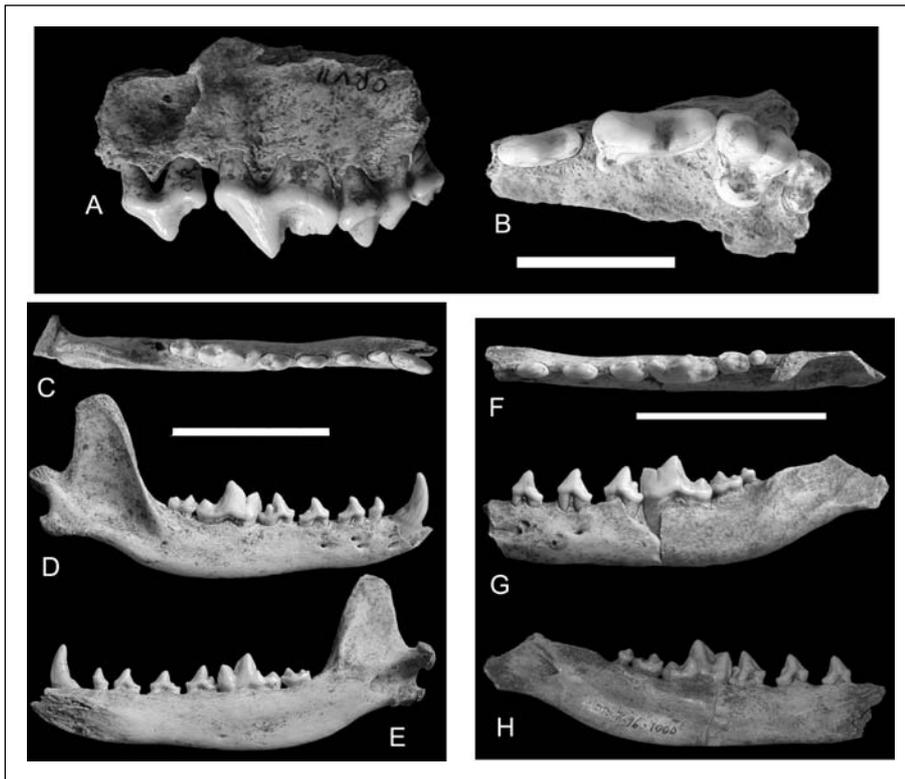


Fig. 12 - *Cynotherium sardous* and *Cynotherium* sp. from Monte Tuttavista. A-B) fragmentary left maxillary bone (VII-2-5275) in labial (A) and occlusal (B) views. C-E) Right mandibular ramus (VI-B6-991) in occlusal (C), labial (D) and lingual (E) views. F-H) Left fragmentary mandibular ramus (VII-2-1000) in occlusal (F), labial (G) and lingual (H) views. Bar scale is 2 cm for A-B and 5 cm for C-H.

from continental Europe, *Enhydriactis ardea*. The morphological traits marking the difference between the Mt. Tuttavista mustelid and *Enhydriactis* - the Orosei form has a less marked postorbital constriction, a cranial vault with a “rounded” profile in posterior view, a mandibular branch stout and robust, large postcranial skeleton - are the basic evidences for attributing them to the genus *Pannonictis*. Although the main similarities are shared with the large-sized species *Pannonictis pliocenica*, we prefer to remain cautious in the specific attribution of these remains, labelling them as *Pannonictis* sp.. As it has been the case for the occurrence of a large hyaenid, the occurrence of a large mustelid with no apparently endemic trait is one of the intriguing characteristics of this “insular” assemblage.

One of the fossiliferous fissure fillings identified most recently at Mt. Tuttavista (“IX *Prologus*”) yielded few remains (cranial and postcranial) of a large mustelid not attributable to *Pannonictis*.

Morphologically, the anterior portion of a skull (IX-*Prologus*-1) is fully comparable with *Enhydriactis galictoides* from Monte San Giovanni (Ficcarelli & Torre 1967b), showing a strongly marked postorbital constriction and the typical profile of cranial vault-frontals-nasals. The sample from this filling includes also several postcranial bones. In comparison with the large *Pannonictis* from quarry “VII Mustelide” these are relatively smaller and more gracile. Again the best comparison is with the postcranial remains of *Enhydriactis* from Monte San Giovanni.

Few remains from fissure filling “VI 3” (two fragmentary mandibular rami, few isolated teeth and postcranial fragments) attest to the occurrence of a very small mustelid (Fig. 11d,e). The profile of the angular process and of the basis of ascending ramus show the typical morphology of the small *Mustela putorius*. Size of the isolated teeth and postcranial remains also falls in the range of variation for this species. These features are however not conclusive for a referral of the material to this species and therefore we refer it to cf. *M. putorius*. If further finds confirm the presence of this small carnivore in the Sardinian Pleistocene then it will be an extremely interesting novelty since *Mustela putorius* is nowadays widespread in Europe and Italian peninsula, but is not known in the Mediterranean islands (cfr. Toschi & Lanza 1965).

#### Canidae

*Cynotherium sardous*, described by Studiati (1857) on the material from Monreale di Bonaria (Cagliari), is one of the best known species in the Sardinian endemic assemblages, in particular in the Late Pleistocene ones, as Dragonara (Malatesta 1970) and Corbeddu Cave (Eisenmann 1990; Eisenmann & Van der Geer 1999). Nevertheless, though this species is documented by a good fossil record, its evolutionary relationships with the continental representatives of the family Canidae have not yet been established. Since earlier works (e.g. Major 1877) and even in later ones (Malatesta 1970), *Cynotherium* has been referred to *Cuon* on the grounds of dental morphology, namely the unicuspidate talonid in  $M_1$ . Eisenmann (1990) and Eisenmann &

Van der Geer (1999) stressed that even though some morphological parameters of dentitions, as  $P^4-M^2$  length, are close to those characterising *Cuon*, other cranial characters (e.g. shorter palatal fissures) do not confirm this affinity. The same authors and Bonifay (1994) suggested that the ancestor of this canid could be searched among the Early Pleistocene representatives of lycaons, *Xenocyon*, at present widespread in the sub-Saharan Africa. The problem of the systematic position of *Cynotherium* is therefore an open topic, and the peculiar proportions checked in the skull must be considered as the result of a marked endemic evolution. The problem of the origin of this canid will not be taken into consideration here, but it will be the object of another work. It is important to stress that the unicuspidate talonid is not a taxonomic character since it is well known how such a morphology represents a case of "iterative evolution" among canids (Van Valkenburgh 1991).

*Cynotherium* is documented in the deposits of the Monte Tuttavista by abundant fossil remains (Fig. 12), especially postcranial bones and isolated teeth, which are unfortunately often not in a very good state of preservation. The comparative analysis of these remains suggests that biometrical and morphological differences exist among the fossil samples found in various fissures. These differences are likely due to the different age of accumulation of cave infillings and therefore fossil assemblages may document subsequent populating phases. The Monte Tuttavista *Cynotherium* has been compared with *C. sardous* from Dragonara (data from Malatesta 1970) which is the best reference of this species allowing the morphological and dimensional intraspecific range to be reconstructed. Material from fissure "VII 2" is comparable in size and morphology with the Dragonara sample, suggesting a conspecificity between *Cynotherium* from these sites. The remains from quarries "XI dic. 2001" and "XI canide" are significantly larger, while that from fissure "VI banco 6" is intermediate in size between Dragonara and "VII 2" site and "XI dic. 2001" and "XI canide". The larger size shown by the remains from quarries "XI dic. 2001" and "XI canide" could be indicative of an older age than that documented by "VII 2" and Dragonara sites. In this regard, the lesser developed trigonid in the  $M_1$ s from "XI dic. 2001" fissure could be a further confirmation of the more primitive condition of this sample. These remains are for the moment cautiously referred to *Cynotherium* sp..

A second phalanx of a young individual documents the occurrence of a canid, perhaps referable to *Cynotherium* (?*Cynotherium* sp.; see also Sondaar 2000) in the fissure "X 3 ucelli". This specimen is particularly interesting as it has been recovered from the same sediments from which *Macaca* cf. *M. majori* and *Pannonictis* sp. are derived. This specimen therefore seems to represent one of the oldest records of a canid in Sardinia, and it is worth mentioning that the occurrence of a canid significantly larger in size than *C. sardous* has also been recognized at Capo Figari (Van der Made 1999).

## Order Artiodactyla

### Suidae

In Sardinia an endemic suid, *Sus sondaari*, has been reported from the bone breccia of Capo Figari (Van der Made 1988, 1999) and, possibly, from the palaeosols at the bottom of the Capo Mannu Formation (Carboni & Lecca 1995). This endemic taxon is characterized by small size, simplified molar structure, especially the talon of  $M_3$ , and lack of  $P_1$ , as well as by the shortening of the anterior part of mandible. In Van der Made's (1999) opinion, the ancestor of the endemic suid (*Sus arvernensis*) reached the island during the Messinian Salinity Crisis.

At Monte Tuttavista, suids are represented by about 60 specimens and occur only in fissure "VI 3". Among these, a skull belonging to a young individual is characterized by inflated parietal bones and by a neurocranium more developed than in the suids of about the same age, belonging to continental taxa, i.e. *Sus scrofa*. The first molar shows a very smooth and simple enamel surface, the diastema between first milk tooth and canine is short. On this evidence we cannot rule out the hypothesis that this specimen belongs to the endemic Sardinian species *Sus sondaari*.

A larger sized suid, represented by a hemimandible with a  $P_1$  and erupting third molar, also occurs here (Fig. 13). In addition to the larger size, this specimen differs from *Sus sondaari* because of the retention of the  $P_1$  (according to specific diagnosis; Van der Made, 1988). On the other side, the specimen shows simple and smooth enamel as well as a very short diastema, like *Sus sondaari* and may reflect population variability. Pending further data, this hemimandible is referred to *Sus* sp.

Thus, we cannot exclude the hypothesis that two different suids, differing in size, both characterized by a relatively simple canine and cheek tooth morphology, occurred in the quarry "VI 3".

### Cervidae

In the Pleistocene of Sardinia, cervid remains are relatively common, especially in eolianites or in cave deposits, mostly attributed to the Late Pleistocene. The first reports date back to the second half of the 19<sup>th</sup> century (e.g. Studiati 1857; Dehaut 1911); however, it was only in 1935 that Tobien ascribed cervid remains from the Alghero area to the species "*Cervus*" *cazioti*, erected by Depéret in 1897 on the cervid remains found at Nonza (Corsica). In more recent times, the knowledge of the morphological and biometric characteristics of this species has been improved by the detailed studies carried out by Caloi and Malatesta (1974), Klein Hofmeijer (1997) and Pereira & Bonifay (1998), respectively based on the large cervid samples coming from the Late Pleistocene deposits of Dragonara and Corbeddu Caves (Sardinia), as well as those in Coscia Cave (Corsica). Other reports from Sardinia and Corsica, refer for the most part to

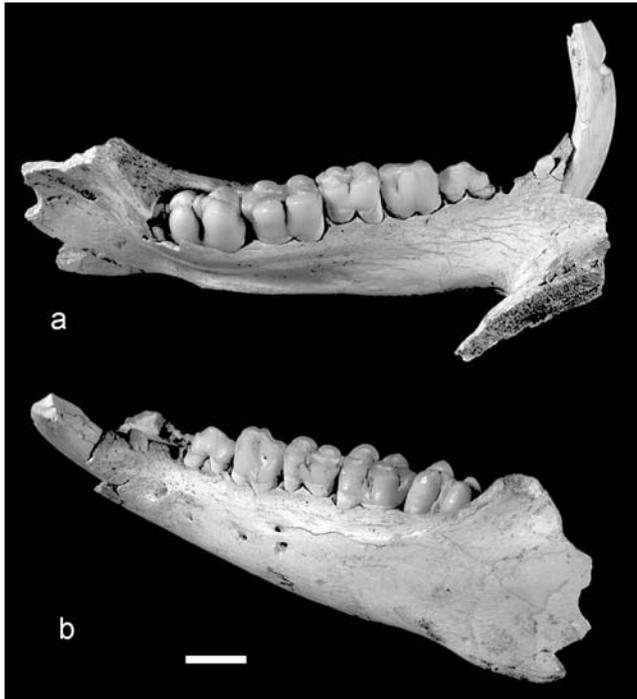


Fig. 13 - *Sus* sp. quarry "VI 3", SI-2232, incomplete left emimandible in lingual (a) and buccal (b) view. Bar scale is about 1 cm.

sporadic isolated remains (Dehaut 1911; Comaschi Caria 1955, 1956; Sigogneau 1960; Azzaroli 1961; Cordy & Ozer 1973; Caloi et al. 1981; Melis et al. in press) or samples not yet analysed.

Accordingly, the Sardinia and Corsica endemic cervid is quite a well-known species, but in spite of the many studies carried out, specialists still do not agree on the taxonomy and phylogenetic relationships of this taxon. The hypothesis of its derivation from megalocerines belonging to the so called "verticornis group" has been widely accepted, and we agree with it. For this group of large sized deer different authors use different names as *Praemegaceros*, *Megaceroides* or *Megaloceros*. Taking into account that the name *Megaceroides* cannot be used for Eurasian species (see Abbazzi in press for a discussion), we provisionally employ the generic name *Praemegaceros*, because widely utilised also in the recent literature, though there is a lot of discussion about its actual validity.

Sondaar (personal communication) has argued that Sardinian cervids would have been phylogenetically related to the genus *Dama*. On the other hand, Van der Made (1999) believes they may have originated from the latest Early Pleistocene species *Eucladoceros giulii*. In any case, despite the different views about the phylogenetic relationships of this cervid, it is now commonly believed that only one lineage was present in Sardinia, perhaps represented by more than one chronosubspecies, while in Corsica, in addition to the megalocerines, deer closely related to red deer would also have occurred (Pereira 2001).

In Sardinia, megalocerine are absent in the *Rbagapodemus minor* fauna coming from Capo Figari-1 karst fissure, whose age has been hypothesised at 1.807.500 +/- 20% Ma (ESR on a *Nesogoral* molar, Van der Made 1999), whereas they are present, at the same locality, together with *Tyrrhenicola* sp. (archaic form) (Brandy 1978; Van der Made 1999) and become quite common in the typical Middle/Late Pleistocene faunas characterised by the occurrence of *Nesiotites similis*, *Rbagamys orthodon*, *Tyrrhenicola henseli*, *Prolagus sardus* and *Cynotherium sardous*.

Recently, megalocerine specimens have been discovered at Su Fossu de Cannas Cave (Sadali); after the preliminary morphological and biometrical analyses, this cervid displays peculiar features, suggesting its attribution to a new species, cogenetic with the endemic species *Praemegaceros cazioti*, of which it might be the direct ancestor (Palombo et al. 2003; Palombo & Melis in press).

The cervid remains from the fissure fillings of Monte Tuttavista show affinity to those referred to the endemic species *Praemegaceros cazioti*. In details the remains from fissure "VII 2" are fully comparable to the Late Pleistocene *P. cazioti* from both Corsica and Sardinia (e.g. Dragonara, Caloi & Malatesta 1974; Corbeddu Cave, Klein Hofmeijer 1997), while in particular those from fissures "XI canide" and "XI mar. 2002" document the occurrence of a larger sized and more robust form. The fully comparable cervids from fissure "VII 2" and from Late Pleistocene localities suggests that this quarry represent one of the youngest infillings in the karst network of Monte Tuttavista.

However, it is worth underlining that in spite of the large number of the recovered cervid remains, the greater part of them belongs to very young and/or female specimens (Fig. 14), while adult males are documented by few fossils in a bad state of preservation. The possibility of biometric comparison is therefore restricted to a very low number of specimens.

#### Bovidae

In Sardinia, bovids belonging to an endemic taxon were recognised since the last century, when in 1911 Dehaut established the new species "*Antilope (Nemorhaedus?) melonii*", on an incomplete skull found in a bone-breccia filling a karstic fissure at Capo Figari (North-Eastern Sardinia). During the XXth century, Forsyth Major and Miss Bate collected other bovid specimens at Capo Figari, but is doubtful whether such bones came from the same pocket which yielded the holotype or not. More recently, Gliozzi & Malatesta (1982) studied newly collected specimens and revised the material belonging to the Bate and Major's collections. The Italian palaeontologists established the genus *Nesogoral*, described as a small nemorhedine (sensu Gliozzi & Malatesta 1982), «[...]with almost straight horn-cores, extending backward on the same plane as the frontals, and



Fig. 14 - *Praemegaceros* sp. from Monte Tuttavista. Skull of female from quarry "XI canide". Bar scale is 5 cm.

very little diverging; dental formula 0I 0C 3P 3M upper and ?I ?C 3P 3M lower teeth; without lacrimal fossae; with transversely arched palatine vault, steep maxillaries, high mandibles; not notably shortened metapodials[...]. According to Van der Made (1999), in bone breccias filling the karstic fissure called Capo Figari I, *Nesogoral* sp. was present together with archaic micromammals, such as *T. figariensis* and *P. figaro*.

Bovoid remains were also reported from deposits outcropping at the top of the Mandriola Formation (Capo Mannu, Western-Central Sardinia, late MN15 – basal MN16?; Pecorini et al. 1974; Angelone & Kotsakis 2001) and in the paleosols interbedded within the dune complex outcropping at Capo Mannu (Carboni & Lecca 1995; Van der Made 1999).

More than 1500 bovid specimens have been collected from 6 fissures at Monte Tuttavista. Well preserved, complete bones are almost rare, while the occurrence of articulated bones, as well as of synsedimentary breakages and fractures is frequent. Consequently, in this preliminary analysis, only cranial specimens will be taken into consideration because their features can be considered the most important from a taxonomic point of view.

The specimens, with possibly the exception of morphotypes C (see below), can be ascribed to the Subfamily Caprinae based on their horn core and dental morphology (e.g. presence of frontal and horn core sinus, upper molars with additional small cavities near the lingual edge of the occlusal surface, lacking basal pillars between the lobes, M<sup>3</sup> metastyle in form of a large flange, occurrence of a transverse fold on the anterior part of lower molars). The features of the Monte Tuttavista skulls (12 specimens, belonging to adult individuals) enable us to recognise three different morphotypes. They can be defined on the basis of the following characters: 1) shape and position of

horn-cores, 2) morphology of frontal bone, 3) extension of pterygo-palatine fossae, 4) palatal width, 5) cheek teeth morphology, 6) development and shape of the palatine and pre-maxillary bones anterior to the P<sup>2</sup>, 7) position of the orbit and zygomatic arch. The original description provided by Dehaut (1911) for "*Antilope (Nemorhaedus?) melonii*" sounds: «l'Antilope fossile... était une espèce de moyenne taille... Les noyeux osseux des cornes... étaient droits au moins sur une longueur assez considérable... les cornes étaient fort inclinés en arrière... ne divergèrent que peu l'une de l'autre... prenaient naissance sensiblement en arrière des orbites... la section... paraît presque circulaire». On the basis of such description, two of the Mt. Tuttavista morphotypes must be ascribed to as many species within the genus *Nesogoral*.

- **The morphotype A, *Nesogoral* sp. 1 aff. *N. melonii*** (Fig. 15a) is the most closely related to the specimens previously ascribed to "*Nemorhaedus melonii*". They share: 1) the shape of the horn-cores (straight, extending backwards and slightly lateral and forming an angle of about 180° with the frontal), 2) the basal structure of the palate area (transversely arched and wide), 3) development of the pterygo-palatine fossae (reaching the second lobe of M<sup>3</sup>) and 4) the extension of the palatine bones behind M<sup>3</sup>. The Monte Tuttavista specimens differ from those of Capo Figari by their more gracile horn-cores and relatively inflated maxillae.

- **The morphotype B, *Nesogoral* sp. 2** (Fig. 15b) differs from the morphotype A in: 1) the ventral shape of the muzzle, 2) the position of the pterygo-palatine fossae (reaching only the first lobe of M<sup>3</sup>) and 3) lack of the extension of palatine bones behind M<sup>3</sup>. Besides, nasal bones seem to be larger, orbital sockets more protruding and turned forward. Instead, the maxillary bones are steep, a feature that seems to characterise also the specimen from Capo Figari (kept in the Rome Palaeontologi-

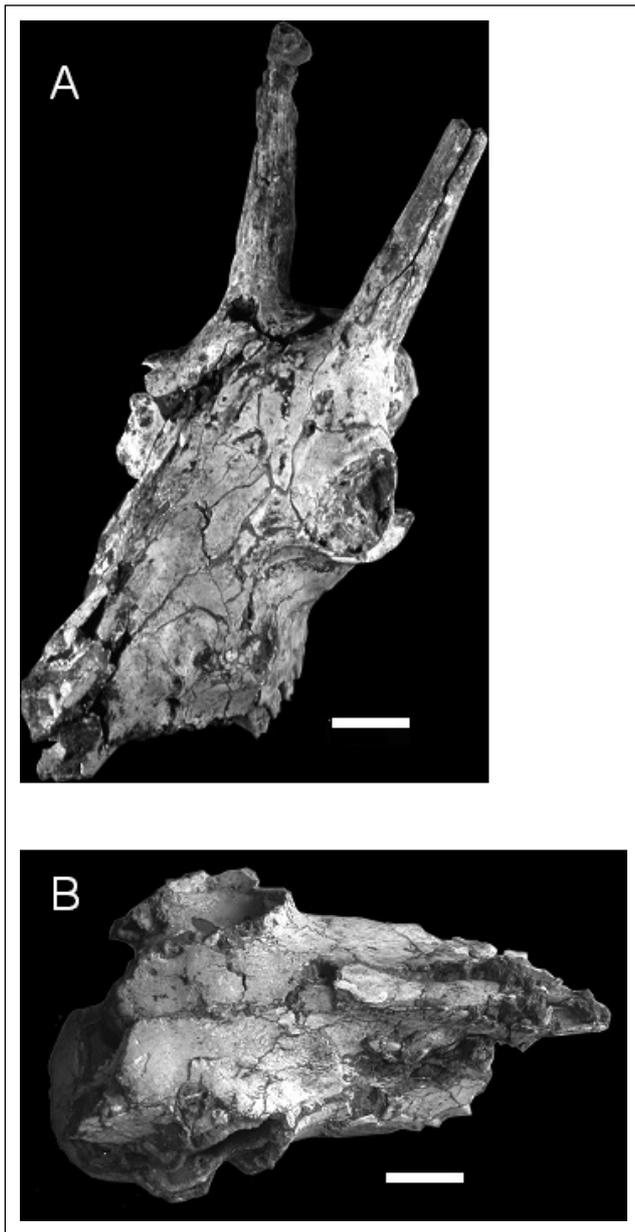


Fig. 15 - A) *Nesogoral* sp. 1 aff. *Nesogoral melonii*, quarry "XI anti-lope", M.Arc.Nuoro 1; B) *Nesogoral* sp. 2, quarry "VI 3", SI-11180, in dorsal view. Bar scale is 2 cm.

cal Museum), ascribed by Gliozzi & Malatesta (1982) to *Nesogoral melonii*.

• **The morphotype C, Bovinae (?Caprinae) gen. et sp. nov.** includes only one specimen, probably belonging to a new genus, characterised by small size, stout horn-cores markedly rejected backwards and jointed medially at their bases. The relatively long horn-cores medially nearly joined at their bases would suggest allocating such a taxon into the subfamily of Caprinae, although, so far, the presence of sinuses inside the horn-cores (Gentry 1992) has not been verified. Moreover, the peculiar morphology of this specimen makes it distinct from all the

Plio-Pleistocenic species belonging to Caprinae, already known in the Western Mediterranean.

In addition to the above identified three morphotypes, scanty remains belonging to a fourth taxon (a middle sized caprine: Caprinae gen. et sp. indet.), have been recognized among the material from quarry "X 3 ucelli".

Our preliminary analysis of the bovids suggests that more than a single taxon occurs at Monte Tuttavista. Moreover, the specimens from Capo Figari actually might belong to different taxa. Accordingly, the diagnosis given for *Nesogoral melonii* have to be reconsidered after the revision of all the Sardinian samples previously ascribed to *Nesogoral* genus.

#### Discussion and conclusions

The Monte Tuttavista fissure network represents one of the most important localities for Neogene-Quaternary fossil vertebrates in Sardinia. Indeed, the richness of the fissures makes Monte Tuttavista an emerging late Neogene - Holocene reference locality where faunal evolution and palaeoecology will be actively studied for decades to come.

Although preliminary, the present study allows some considerations on different general aspects such as biochronology, palaeoecology and biogeography.

First attempts at chronological sequence of Mt. Tuttavista fissure infillings have been made in Ginesu & Cordy (1997), Sondaar (2000) and Sondaar & Van der Geer (2002). The hypothesized chronological succession resulting from our study (Fig. 16) provides an updated synthesis combining the whole evidences from all taxa. The picture which emerges is quite consistent, with minor contradictions concerning a few number of fissures.

The entire quarries documentation can be subdivided in four successive complexes (Fig. 16):

The most primitive quarries are characterised by the occurrence of *Rhagapodemus minor*, *Tyrrhenoglis* cf. *T. figarensis*, *Nesogoral* sp., *Macaca* cf. *M. majori*, *Pannonictis* sp. and, possibly, *Chasmaporthetes* n. sp.. This assemblage belongs to the so-called "*Nesogoral* complex" (Sondaar 2000) and is probably attributable to the Early Pleistocene, although an older age (late Pliocene?) cannot be ruled out. This faunal complex is the assemblage identified at Capo Figari, with the new occurrences of the carnivores *Pannonictis* and *Chasmaporthetes*. However, since *Chasmaporthetes* is not associated with a faunal assemblage, but it has found as an erratic element, we cannot rule out it could represent an even older unrecognized complex.

Fissure "X 3 ucelli" assemblage can be considered as a new faunal complex, representing a peopling phase close to the colonisation of Sardinia by ancestors of the the following characterizing taxa : "*Praemegaceros-Tyr-*

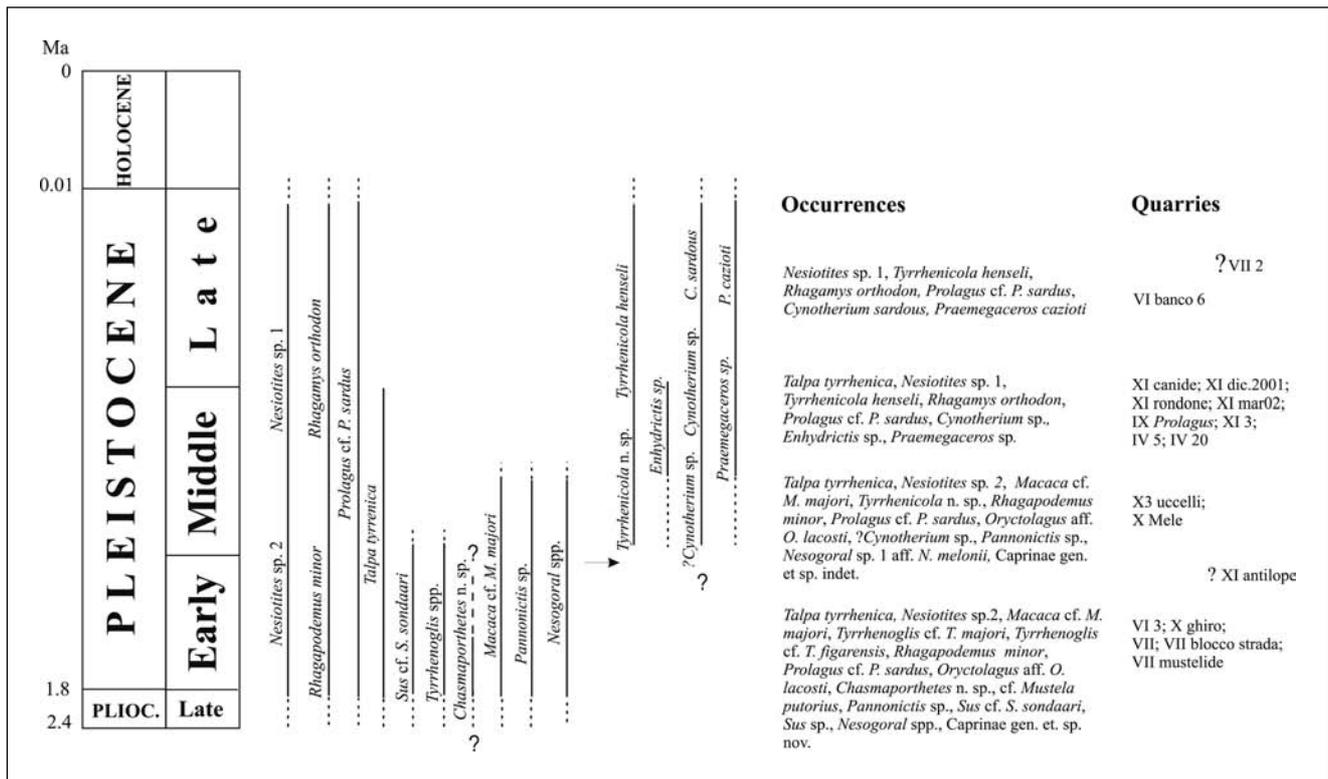


Fig. 16 - Chronological sequence of quarries of Monte Tuttavista and chronological range of mammal taxa documented in the fissure infillings.

*tyrrhenicola* complex" (Sondaar et al. 1986; Klein Hofmeijer et al. 1987). The new faunal complex is identified on the basis of the occurrence of new immigrants (*?Cynotherium* sp. and *Tyrrhenicola* n. sp.) coexisting with forms of the previous assemblage as *Macaca* cf. *M. majori* and *Rhagamys minor*. For this complex, we suppose an Early to early Middle Pleistocene age. *Tyrrhenicola* and *Cynotherium* would appear to not be especially endemic compared to later assemblages.

The classical Middle-Late Pleistocene "Praemegaceros-Tyrrhenicola complex" (Sondaar et al. 1986; Klein Hofmeijer et al. 1987) at Mt. Tuttavista can be subdivided in two "sub-complexes", on the basis of their successive stages of evolution. In quarries "XI canide", "XI dic.2001", "XI mar2002", "XI 3" and "XI rondone" is documented in fact the occurrence of primitive representatives of taxa characterising this complex, such as *Praemegaceros* sp. and *Cynotherium* sp. associated with *Tyrrhenicola henseli*. Other taxa appearing associated within this "primitive" "Praemegaceros-Tyrrhenicola complex" are *Enhydricteis* sp. and *Rhagamys orthodon*.

The "Praemegaceros-Tyrrhenicola complex" as described in the literature (Sondaar et al. 1986; Klein Hofmeijer et al. 1987) seems to be represented in quarries "VI banco 6" and "VII 2", where abundant samples of more evolved taxa occur, including *Cynotherium sardous* and *Praemegaceros cazioti*.

On the other hand, this interpretation is apparently in contradiction with the conclusion drawn by rodents and lagomorphs, since *Rhagamys orthodon*, *Tyrrhenicola henseli* and *Prolagus* cf. *P. sardus* from quarry "VII 2" seems characterized by primitive morphologies.

Palaeoecological and palaeoenvironmental indications come basically from the preliminary data of avifauna and herpetofauna. The fossil bird remains indicate that all sites are characterized by species of rocky habitat, dominated by cliffs. Moreover other taxa, such as Anatidae and Rallidae, suggest the presence of marshlands not so far from Monte Tuttavista, while others (*Coturnix*, *Alauda* and *Melanocorypha*) indicate also an important open dry area. The ongoing complete analysis of the entire bird collection (separated by fissure fillings) will allow us to reconstruct the evolution of the environment in the Oroisei area from the Pliocene to the Late Pleistocene.

The main palaeoecological indication derived from herpetofauna is the sharply contrasting apparent syntopy of members of the genera *Speleomantes* and *Agama* in quarry "VI 3": the first inhabits preferably areas that are relatively humid, while the latter ones are usually considered as proxies of arid environments. Nevertheless, since cave salamanders live in caves, crevices and interstices (or nearby), it is not unlikely that such cool and humid microhabitats were scattered in a relatively dry and sunny Mediterranean environment.

As far as concerns palaeobiogeographic indications derived from this study, two are the main points that are to be made. First, during the entire time span represented by the Mt. Tuttavista faunas, several episodes of colonization from mainland are evident, marking the turnovers or faunal changes that characterize the successive biochronological complexes. Such faunal events involve taxa all arriving to the island from the European bioprovince, thus confirming the biogeographic European affinity.

A second important point is the occurrence of large and medium-sized carnivores (active predators like the hunting-hyaena *Chasmaporthetes* and the large mustelid *Pannonictis*) into an endemic insular faunal assemblage. The occurrence of large carnivores in island ecosystems is an exception, especially if such taxa maintain a strictly carnivorous behaviour and diet. Island endemic faunal assemblages result in fact typically impoverished and ecologically unbalanced (cfr. MacArthur & Wilson 1963; Sondaar 1977). The identification of a large-sized hyaenid in the Mt. Tuttavista faunal assemblages is evidence that requires us to reconsider the biogeographic history of the Plio-Pleistocene Sardinia-Corsican massif.

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