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THE ENDEMIC CANID *CYNOTHERIUM* (MAMMALIA, CARNIVORA) FROM THE PLEISTOCENE DEPOSITS OF MONTE TUTTAVISTA (NUORO, EASTERN SARDINIA)

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Key words: Pleistocene, Italy, Sardinia, endemic evolution, Mammalia, Canidae, *Cynotherium*.

Abstract. This paper presents the main results related to the analysis of fossils of the endemic Sardinian canid *Cynotherium*, discovered during the past years within the rich fossiliferous karst deposits in the Monte Tuttavista area (Eastern Sardinia, Nuoro).

The analysis indicates that the remains from various fissure infillings differ in size and dental characters, which are suggestive of evolutionary phases under endemic conditions. The chronological sequencing of fissures obtained based on the evolutionary stage of the fossil canid is consistent with that emerging from the analysis of the whole mammal assemblages occurring in the same fissures.

The possible evolutionary relationships of the Sardinian canid to the Plio-Pleistocene mainland species are also considered; a derivation from a population of late *Canis arnensis* (or *Canis mosbachensis*) is supported.

Riassunto. Nel presente lavoro sono analizzati i resti fossili del canide endemico *Cynotherium*, scoperti nei riempimenti di fessure carsiche, affioranti nell'area del Monte Tuttavista (Sardegna nord-orientale, Nuoro). I fossili rinvenuti in fessure diverse si distinguono per taglia e per alcuni caratteri morfologici della dentatura che indicano livelli evolutivi distinti. In particolare le dentature semplificate (es. assenza del conide postero-labiale nel ferino inferiore), alle quali corrispondono dimensioni minori, indicano livelli evolutivi più avanzati rispetto a quelle più complesse e con taglia maggiore.

Sulla base delle caratteristiche biometriche e morfologiche dei reperti di *Cynotherium*, è possibile suggerire una successione cronologica dei riempimenti carsici, che è in sostanziale accordo con quella che emerge considerando anche gli altri elementi faunistici.

Nel presente lavoro vengono inoltre presi in considerazione i possibili legami tra il canide sardo e le specie diffuse nell'Europa continentale durante il Plio-Pleistocene. A questo proposito viene sostenuta la derivazione di *Cynotherium* dalla specie *Canis arnensis* o da una popolazione primitiva di *C. mosbachensis*.

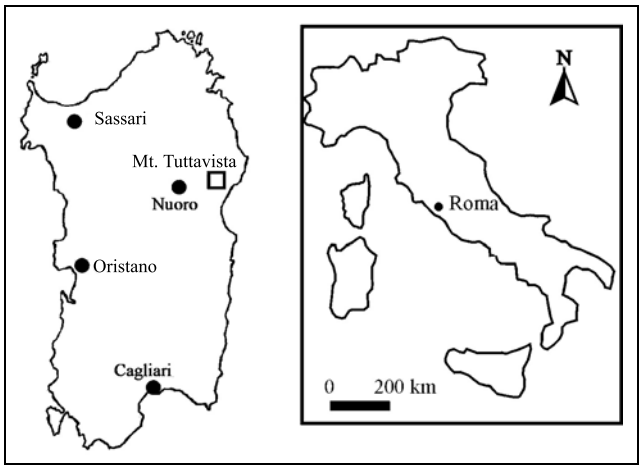

Fig. 1 - Location map of the Monte Tuttavista area.

Introduction

In the Pleistocene insular domain of Sardinia, a canid of the size of a coyote represents one of the most important elements in the mammal faunas. This canid has been referred to the genus *Cynotherium* and to date only one species, *C. sardous,* has been described from the Middle-Late Pleistocene Sardinian localities.

A fairly abundant sample of this canid has been found within the fillings of the karst fissures outcropping in the quarries of the Monte Tuttavista area (Orosei, Eastern Sardinia; Ginesu & Cordy 1997; Sondaar 2000; Abbazzi et al. 2004) (Fig. 1), from which a diverse

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vertebrate fauna is also known. The preliminary analysis of these vertebrates, recovered from eighteen fissures (Abbazzi et al. 2004), recognizes about 80 taxa, among them fishes, amphibians, reptiles, birds and mammals. These faunas contribute to a better understanding of the complex paleontology of the Sardinian insular domain, during the time interval from perhaps the Late Pliocene to the Late Pleistocene, and they provide information that adds to that obtained from other well-known Pleistocene faunas such as Capo Figari (Golfo Aranci), Dragonara (Alghero) and Corbeddu Cave (Oliena) (Dehaut 1911; Malatesta 1970; Gliozzi & Malatesta 1982). Indeed, the Plio-Pleistocene Sardinian mammals of Monte Tuttavista document a succession of different faunal complexes – characterized by arrivals and extinctions of species and in situ evolution of endemic taxa – that testifies to the colonisation phases from the European mainland and the subsequent periods of insularity (Sondaar 2000; Sondaar & van der Geer 2002). The species *Rhagapodemus minor*, *Tyrrhenoglis* cf. *figarensis*, *Macaca* cf. *majori*, *Pannonictis* sp. and *Nesogoral* spp. document the latest Pliocene-Early Pleistocene "*Nesogoral* complex" (Sondaar 2000), which represents the oldest assemblage in the Monte Tuttavista area. One of the most important features of this complex is the occurrence of the hunting-hyaena *Chasmaporthetes melei* (Rook et al. 2004), which could be indicative of an even older faunal assemblage, Middle-Late Pliocene in age. However the presence of such taxa as the megalocerine *Praemegaceros cazioti,* the canid *Cynotherium sardous* and the vole *Tyrrhenicola henseli* are indicative of the well-known and widespread Middle-Late Pleistocene and Early Holocene "*Praemegaceros-Tyrrhenicola* complex" (Sondaar et al. 1986; Klein Hofmeijer et al. 1987) in the Monte Tuttavista area. This assemblage can be further divided into two "sub-complexes", on the basis of successive morphotypes within lineages. In some quarries we find the occurrence of primitive representatives of endemic taxa, including *P. cazioti*, *C. sardous* and *T. henseli*.

The Sardinian Canid

Cynotherium sardous was established by Studiati (1857) based on the material from Monreale di Bonaria (Cagliari, see also Comaschi Caria 1968). It is fairly abundant in Late Pleistocene localities, such as Dragonara (Malatesta 1970) and Corbeddu Cave (Eisenmann 1990; Eisenmann & van der Geer 1999) and it is recognized from other sites in Sardinia (Gliozzi et al. 1984) and Corsica (Bonifay 1994; cfr. Pereira & Salotti 2002).

Although this species is documented by a good fossil record, its evolutionary relationships with continental representatives of the family Canidae have not yet been fully established. In earlier works (e.g. Major 1877) and even in later ones (Malatesta 1970; Comaschi Caria 1968), *Cynotherium* has been linked to *Cuon* based on the occurrence of an unicuspidate talonid on the lower carnassial (M_1). Eisenmann (1990) and Eisenmann & van der Geer (1999) stressed that even though some morphological and biometric parameters of the dentition, such as P^4-M^2 length, are actually close to those characterising *Cuon*, other cranial characters (e.g. the longer palate and shorter palatine fissures) do not support this affinity. The latter authors also showed a close similarity in skull morphology to the jackal-like canids, and did not rule out an origin from the small-sized *Canis arnensis*. On the other hand, Bonifay (1994) suggested that the ancestor of the Sardinian canid might also be found among the Early Pleistocene representatives of *Lycaon*, at present widespread in sub-Saharan Africa.

Malatesta (1970) described the canid fossil sample from the late Pleistocene site of Dragonara, referring it to the species *Cynotherium sardous*. According to this material, the species is characterised by a narrow, elongate and slender mandible; the cranium shows small bullae and presents some characters (narrow palate, high and bulging maxillaries) considered to be autoapomorphies (Malatesta 1970). Malatesta (1970) also suggested that the peculiar skull proportions of *Cynotherium* must be regarded as the result of an endemic evolution, in particular an adaptation to feed on small mammals, such as the ochotonid *Prolagus*. The development of an elongated and narrow muzzle is a typical case of iterative evolution in dogs, being characteristic of the Early Pliocene *Eucyon adoxus* and of the extant *Canis simensis*, both adapted (like *Cynotherium*) to prey on lagomorphs (cf. Rook & Azzaroli Puccetti 1996). Similarly, the unicuspidate talonid with a large centrally positioned hypoconid and no entoconid is probably not a good taxonomic character but, on the other hand, another case of parallelism among hypercarnivorous canids (Van Valkenburgh 1991).

The analysis of the fossil material from various fissure fillings of different age in the Monte Tuttavista area allowed us both to describe the evolutionary trends in this canid during the documented time interval and to contribute to the reconstruction of its evolutionary relationships with the canids widespread on the European Plio-Pleistocene mainland.

Cynotherium from Monte Tuttavista

Material

All the fossils from Monte Tuttavista are kept in the Operating Office of the Soprintendenza per i Beni

Archeologici in Nuoro and in the Archeological Museum of Nuoro. Canid remains were recovered from nine of the eighteen fissures that have been identified and sampled in the area of Monte Tuttavista. *Cynotherium* from various fissures often shows morphological differences, which suggest taxonomic distinctiveness as shown in Tab. 1. The detailed list of the material (inventory numbers in text and lists refer to field numbers) and the measurements of fossil remains are reported in Appendix I and II.

Fissure X-3 uccelli - From the deposit of this fissure only one specimen, a juvenile second phalanx without proximal epiphysis, attests to the occurrence of a canid (Fig. 2). The specimen is referred with doubt to Canidae indet. (see also Sondaar 2000). However, it is fairly important because is associated with one of the most primitive faunal assemblage identified in the Monte Tuttavista area, characterised by the occurrence of *Macaca* cf. *majori* and *Pannonictis* sp. This specimen therefore may represent the oldest record of a canid in Sardinia. In this respect it is worth mentioning that the occurrence of a canid significantly larger than *C. sardous* has also been recognized at Capo Figari (*Cynotherium*? sp. in van der Made 1999), dated to close to the Plio-Pleistocene boundary.

Fissure XI-canide - This fissure produced the only skull of *Cynotherium* in the whole Monte Tuttavista area. It is not very well preserved, lacking the anterior part of the muzzle and part of the brain case (Fig. 3); moreover, it is still embedded in breccia and its dimensions are not estimatable. The vertebrate assemblage from this fissure represents a primitive stage of the *Praemegaceros-Tyrrhenicola* complex and therefore may demonstrate a populating phase of early Middle Pleistocene age.

Fissure XI-Dicembre2001 - The few canid remains that have been recovered from this fissure are associated with a mammal assemblage indicative of a primitive stage of the *Praemegaceros-Tyrrhenicola* complex.

Fissures IV-20, V, IX cervo, IX Prolagus - Only very fragmented and un-diagnostic materials are found in these fissures (Fig. 4), which are referred to the classical Middle-Late Pleistocene *Praemegaceros-Tyrrhenicola* complex (Sondaar et al. 1986; Klein Hofmeijer et al. 1987; Sondaar 2000), based on the occurrence of *Raghamys orthodon*, *Tyrrhenicola henseli*, and *Prolagus* cf. *sardous* (Abbazzi et al. 2004). The canid remains, because of their incompleteness, are referred to *Cynotherium* sp.

Fissure VI-B6 - Seventy dog remains have been found within the sediment of this fissure, including two complete hemimandibles from the same individual (Figs 5, 6). The vertebrate assemblage from this fissure seems to represent one of the most recent in the area of Monte Tuttavista (Abbazzi et al. 2004).

Fissure VII-2 - The material from this fissure is the most abundant, with more than 160 specimens, consisting of craniodental elements (Figs 6, 7) as well as postcranial bones, giving an MNI of 5 based on the left lower carnassial. The classic *Praemegaceros-Tyrrhenicola* complex as described for the Late Pleistocene-Early Holocene of Sardinia has been recognised in the sediment of this karst fissure.

Description

The fossil canid from Monte Tuttavista shows the main features that characterise the endemic taxon *Cynotherium*, in agreement with the most detailed description of this species from the Dragonara site (Malatesta 1970).

The size of the dentition is comparable to that of recent jackals and it is on average smaller than that of the Late Pliocene *Canis arnensis* and the Early Pleistocene *Canis mosbachensis* (Rook 1993; Martínez-Navarro 2002) (Fig. 8), though some specimens from the supposedly oldest fissures (see below) fall within the size range of these species. The skull shows a poorly marked post-orbital constriction. The mandible is elongated and slender and the teeth, particularly the premolars, tend to have spaces between them. The dentition is reduced with P_1 missing in several specimens. The lower premolars are asymmetrical in lateral view and have poorly developed or absent cusps. M_1 has a unicusped talonid, with the hypoconid occupying a central position and the entoconid strongly reduced or lacking. M_3 is present.

For estimates of overall body size, Palmqvist et al. (1999) derived a multiple regression from some recent and fossil canid taxa. This type of equation allows a more accurate body mass estimate compared with single regressions using single variables, such as lower first molar length. Among canids, allometric differences related to diet tend to overestimate or underestimate body mass (the size of omnivores tends to be overestimated and the size of hypercarnivores tends to be underestimated). The application of the equation from Palmqvist et al. (1999) gives a mass estimate of around 13 kg for specimen VI-B6-991 from the Monte Tuttavista site VI-B6.

Comparisons

The fragmentary state and low number of *Cynotherium* fossils from Monte Tuttavista hinder the identification of diagnostic characters and the range limits of measurements. However, the comparative analysis performed here do suggest significant biometrical and morphological differences between the remains from the various fissures. These differences indicate different

Fissures / Taxa	X-3 uccelli	XI-canide	XI-Dic2001	IV-20	IX-*Prolagus*	IX-cervo	V	VI-B6	VII-2
Canidae indet.	X								
Cynotherium sp.		X	X	X	X	X	X		
C. cf. *sardous*								X	
C. sardous									X

Tab. 1 - Occurrence of canids in the fissures of the Monte Tuttavista area.

Fig. 2 - Canidae indet. from fissure X-3 uccelli. A - dorsal and B - lateral views of X-3u-6 second juvenile phalanx. Scale is 10 mm.

evolutionary stages of the samples, consistent with those of other from the same fissures.

The Monte Tuttavista canid has been compared with *C. sardous* from Dragonara (data from Malatesta 1970) which represents the best sample for this species, allowing the evaluation of the morphological range for this species.

On the whole, the material from fissure VII-2 is comparable in size and morphology with the Dragonara sample, suggesting referral to *Cynotherium sardous*, while the remains from quarries XI-Dicembre2001 and XI-canide are larger and possess dental features that indicate an earlier evolutionary stage. These remains are insufficient in our opinion for describing a new taxon, and for the moment are referred to *Cynotherium* sp.

Material from fissure VI-B6 is morphologically similar to that from the Dragonara and VII-2 sites, but it is not fully comparable, and it is therefore referred to *C.* cf. *sardous*.

Skull - The skull from fissure XI-canide (Fig. 3) although badly preserved allows us to observe a few features such as the occurrence of a weakly marked postorbital constriction (= about 35 mm) and protruding orbits (the external border is at the same level as the parietal bones; breadth at the orbit = 53.7 mm).

Dentition - The biometric comparison of the teeth gives interesting results. In Fig. 8 it can be seen that teeth from Dragonara show large variation, the remains

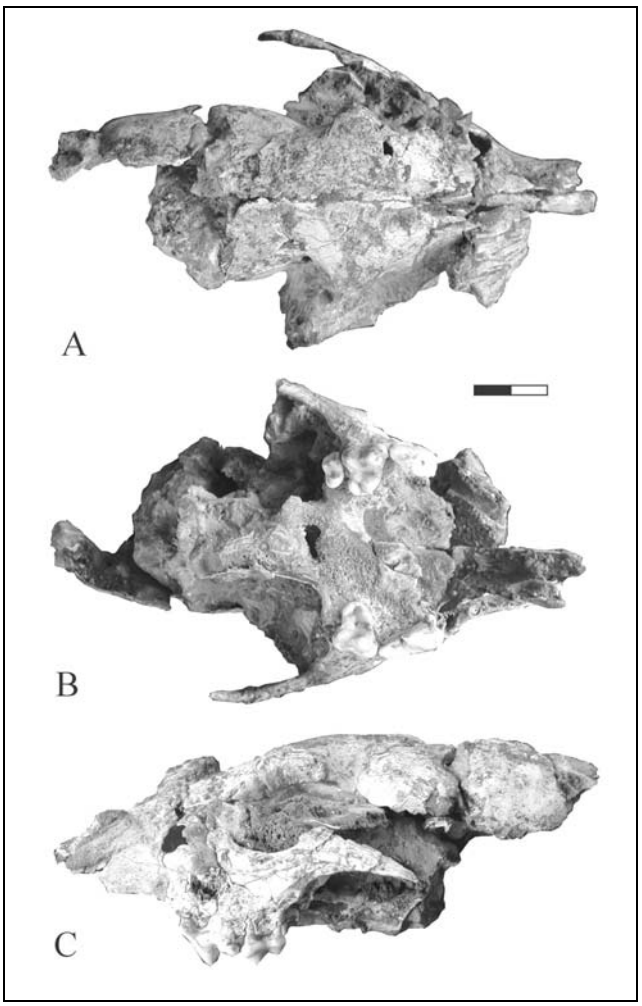

Fig. 3 - Fragmentary cranium of *Cynotherium* sp. from fissure XI-canide. A - dorsal, B - ventral and C - lateral views of skull XI-cn-1. Scale is 20 mm.

from VII-2 quarry show medium to low relative values, while the two hemimandibles from VI-B6 fall in the upper part of the range; the specimen from XI-Dicembre2001 is the largest. The comparison of upper dental series gives similar results confirming the larger size of the canids from fissures VI-B6, XI-Dicembre2001 and XI-canide, as evidenced in the graph relative to the dimensions of P^4 (Fig. 9).

As already reported above, one of the main diagnostic features in *Cynotherium* is the unicuspidate talonid on the first lower molar. The comparison between the relative development of the talonid (expressed by the ratio of total M_1 length/trigonid length*100) and the M_1 width (Fig. 10) indicates a lar-

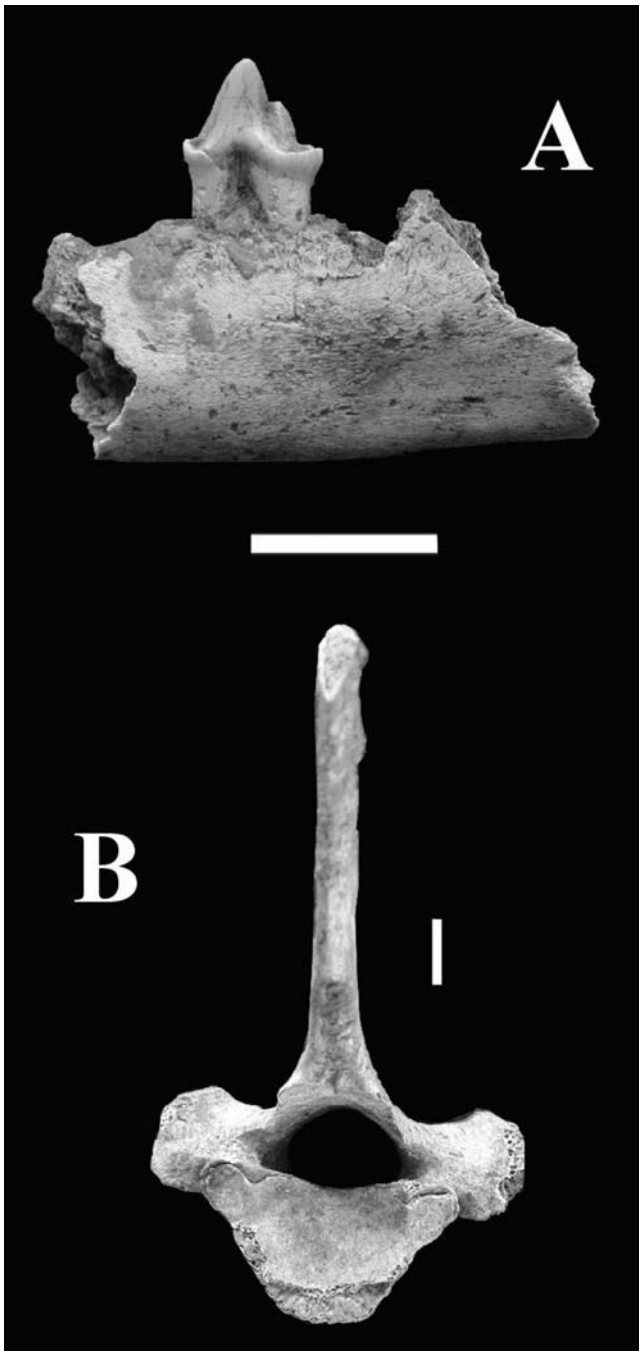

Fig. 4 - *Cynotherium* sp. A - IV-20-1 fragment of right mandible with D_3 from fissure IV-20; B - V-73 thoracic vertebra from fissure V. Scale is 10 mm.

ger talonid in the remains from XI-Dicembre2001 and VI-B6 than in those from VII-2. Considerable variation is evident in the M_1 talonid morphology among specimens from the VII-2 quarry, with the majority showing a well developed lingual cingulum (n. VII-2-1001, 1002, 1032, 5279), some a poorly developed cingulum (n. VII-2-952), and others a cusp-like feature which is interpreted as a vestigial entoconid (n. VII-2-1000 and 1003). The vestigial entoconid is also present on specimens from fissures VI-B6 (Figs 5, 6) and XI-Dicembre2001.

With regard to the M_2, the specimens from VI-B6 are larger and have a more developed antero-lingual cuspid (paraconid) than those from VII-2. In the upper series, the P^4 from XI-Dicembre2001 and XI-canide shows a larger postero-lingual cusp, and M^1 has a more developed and complicated lingual side, with a larger basin between protocone and hypocone, relative to the remains from VII-2.

All these differences are likely to be the result of a reduction of the crushing area with respect to the trenchant area of the teeth, probably due to a change in alimentary habits of the Sardinian canid during the time interval documented in the Monte Tuttavista deposits. This simplification of the talonid in canids is interpreted as a specialization towards hypercarnivory (Van Valkenburg 1991; Holliday cfr Steppan 2004). In this respect it is worth noting that the relative length of the carnassial blade (length of trigonid/length of M_1*100) in the Orosei VII-2, VI-B6 and Dicembre2001 samples is 70.83%, 67.65% and 65.61%, respectively. The value of the specimen from the first fissure is slightly smaller than that characterising the hypercarnivorous canids, such as the lycaon and the bush dog, where the length of the trigonid is between 72% and 74% of the total length of the lower carnassial (see Palmqvist et al. 1999).

The material from the VII-2 deposits permits more than systematic-evolutionary considerations. Thanks to the abundance of canine teeth it is possible to evaluate the composition of the sample in term of number of males and females. Based on the length and width of this tooth, it is evident from Fig. 11 that the remains fall into two groups of different size.

Post cranial skeleton - The fragmentary state of the bones of the skeleton does not allow a detailed comparative analysis. However some difference are again evident between the taxa from fissures VI-B6, XI-Dicembre2001, XI-canide, and VII-2. The comparison between the length and depth of metacarpal III (Fig. 12) confirms the larger size of the canid from the former group of fissures.

One of the most interesting trends in the evolution of modern canids is the reduction of the first metacarpal in the skeleton of the recent lycaon, *Lycaon pictus,* leading to the development of a tetradactyl forelimb linked to increased cursoriality. The tendency to reduce this bone is already evident in species of Early Pleistocene age such as *Lycaon lycaonoides* from Pirro Nord and Cava Dell'Erba (Rook 1994; Martínez-Navarro & Rook 2003), where the articular surface for this bone in the second metacarpal is markedly reduced. The record of *Cynotherium* from Sardinian sites demonstrates the occurrence of metacarpal I: second metacarpals from VI-B6 show a facet for the first metacarpal (Fig. 13), and first metacarpals have been

found in the rich sample of Dragonara (Malatesta 1970). The occurrence of such a feature in the Sardinian material allows us to exclude it from the lineage of *Lycaon*.

Conclusion and remarks on the evolutionary relationships of *Cynotherium*

Based on the results of the present analysis, the evolutionary trends of *Cynotherium* under insular conditions may be described in terms of a reduction of body size with changes in the dental morphology. The remains from fissures XI-Dicembre2001, XI-canide and, to a lesser extent, VI-B6, are larger in size and show more primitive dentitions (with more developed M_1 talonid and larger M_2) compared with the VII-2 material, which in turn is comparable with that from well-known Late Pleistocene sites such as Dragonara.

The canid phalanx from fissure X-3 uccelli represents the oldest record of a canid from the Monte Tuttavista area. However, the poor condition of the specimen does not allow additional interpretations, and therefore it is provisionally referred to Canidae indet. (? *Cynotherium* sp.).

The reconstruction of the phyletic relationship of *Cynotherium* with mainland Plio-Pleistocene canids is a controversial issue, especially due to the supposedly high degree of endemism in the Middle-Late Pleistocene record, and the development of homoplasies.

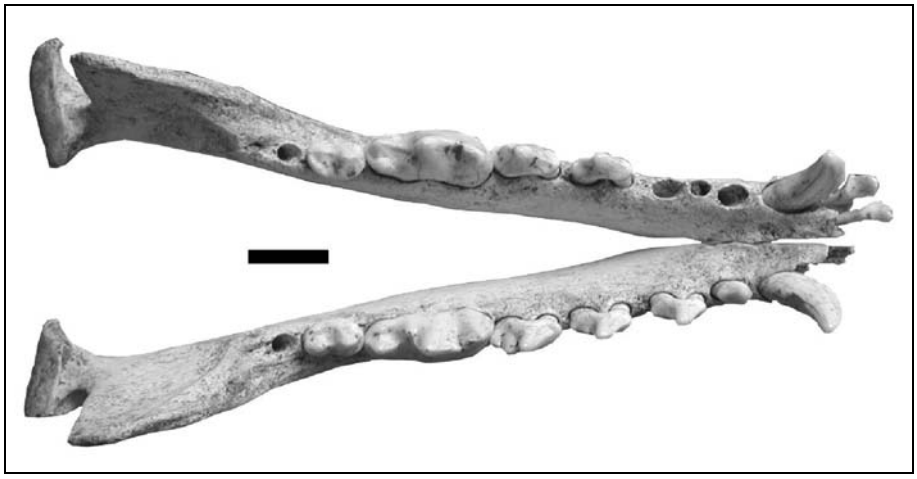

Fig. 5 - *Cynotherium* cf. *sardous* VI-B6-991 mandible from fissure VI-B6. Scale is 10 mm.

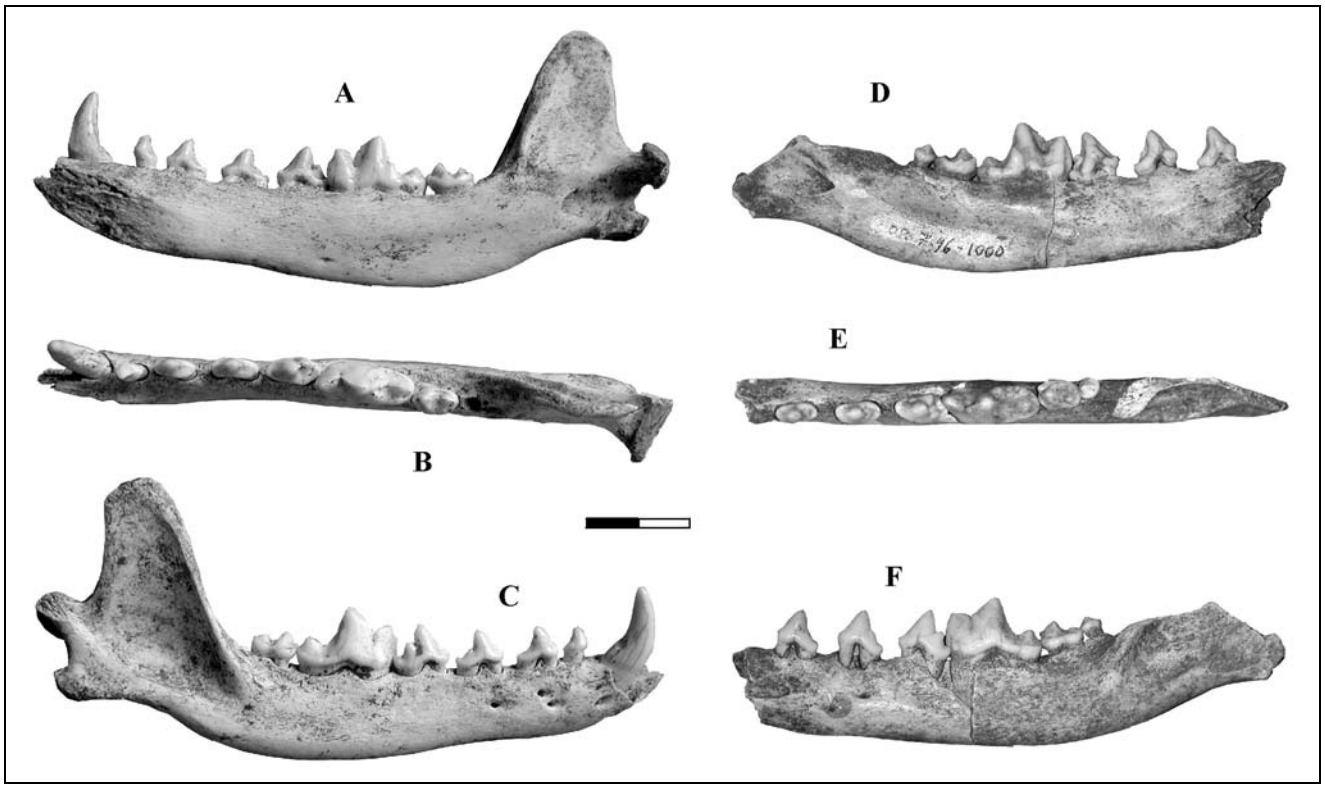

Fig. 6 - *Cynotherium* cf. *sardous* from VI-B6 fissure; A - lingual, B - occlusal and C - labial views of VI-B6-991 right hemimandible; *C. sardous* from VII-2 fissure; D - lingual, E - occlusal and F - labial views of VII-2-1000 left hemimandible. Scale is 20 mm.

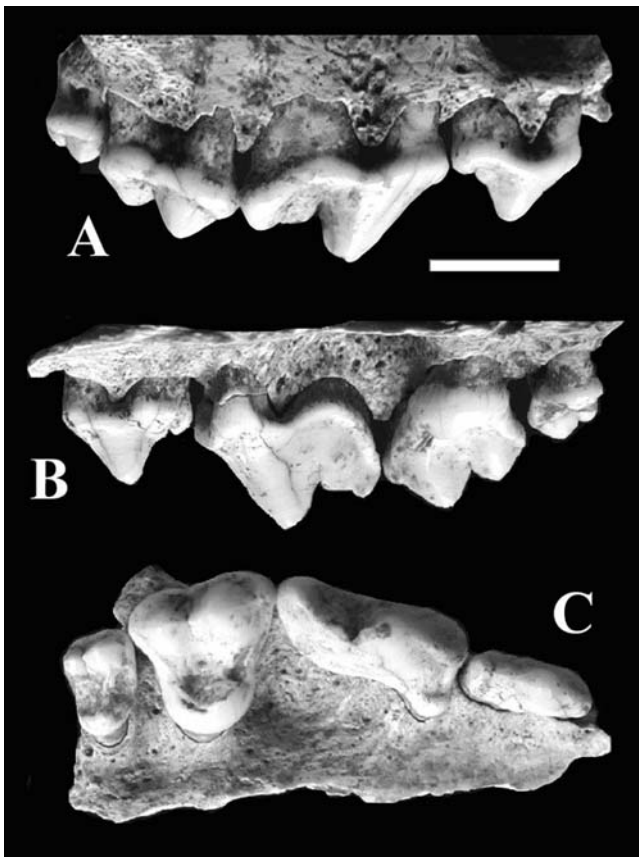

Fig. 7 - *Cynotherium sardous* from VII-2 fissure; A- labial, B - lingual and C - occlusal views of VII-2-5274 right maxillary with P^3-M^2. Scale is 10 mm.

The arrival of the ancestor of *Cynotherium* into the Sardinian-Corsica paleobioprovince is supposedly close to the Plio-Pleistocene boundary as suggested by the scanty canid postcranial finds at Capo Figari (van der Made 1999), and at Monte Tuttavista in the vertebrate assemblages referred to the *Nesogoral* complex. Therefore, the ancestor of *Cynotherium* may be sought among the species that dispersed into Europe during (or just after) the Late Pliocene "wolf-event" (Rook & Torre 1996), like *Canis etruscus* (wolf-like dog), *Lycaon falconeri* (lycaon-like dog), *Canis arnensis* (coyote-like dog), or the Early Pleistocene *Canis mosbachensis* (Rook 1993; Martínez-Navarro 2002).

As stressed by Eisenman (1990) and Eisenman & van der Geer (1999), *Cynotherium* has a close affinity with *Canis arnensis* (sensu lato). Although this could be an allometric result of size reduction, we support the hypothesis that the Sardinian dog (*Cynotherium*) was derived from a population of late *Canis arnensis* (or *Canis mosbachensis*). *Canis arnensis*, a small coyote-like dog, seems to be the first form to disperse into western Europe during the late Pliocene, being documented in Senéze (Rook & Torre 1996) and Slivnitsa (Spassov 1998).

The great similarity of *Cynotherium* to the modern jackals – evident, for example, in the outline of the ventral border of horizontal ramus of mandible, which is low and slender, as well as the shape of the neural part of the skull – is probably the result of morphological convergence. This convergence is especially evident in the case of *Canis simensis*, the most endangered of the living jackals, limited to restricted areas of the Ethiopian highlands, and adapted to prey on lagomorphs, endemic to the same region.

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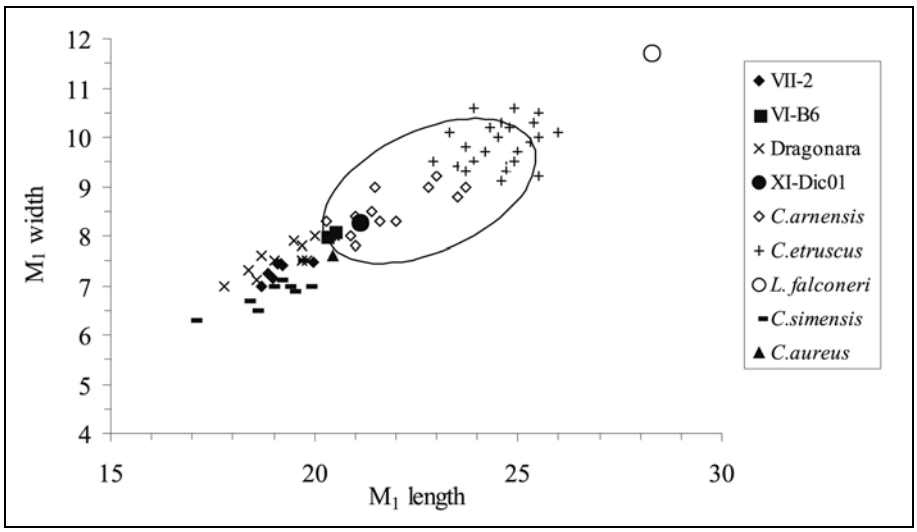

Fig. 8 - Scatter diagram of length and width of lower carnassial (M_1). Data on the Dragonara specimens of *Cynotherium sardous* are from Malatesta (1970), those on *C. arnensis*, *C. etruscus*, *C. mosbachensis* and *L. falconeri* are from Rook (1993), those relative to *C. simensis* and *C. aureus* are from Rook & Azzaroli Puccetti (1996). The ellipse corresponds to *C. mosbachensis* sample range.

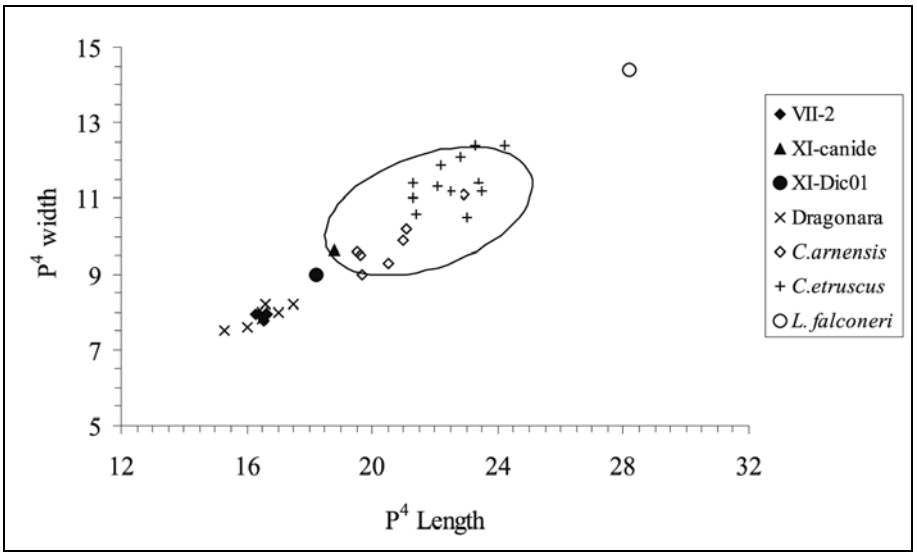

Fig. 9 - Scatter diagram of length and width of upper carnassial (P^4). Data on the Dragonara specimens of *Cynotherium sardous* are from Malatesta (1970), those on *C. arnensis*, *C. etruscus*, *C. mosbachensis* and *L. falconeri* are from Rook (1993). The ellipse corresponds to *C. mosbachensis* sample range.

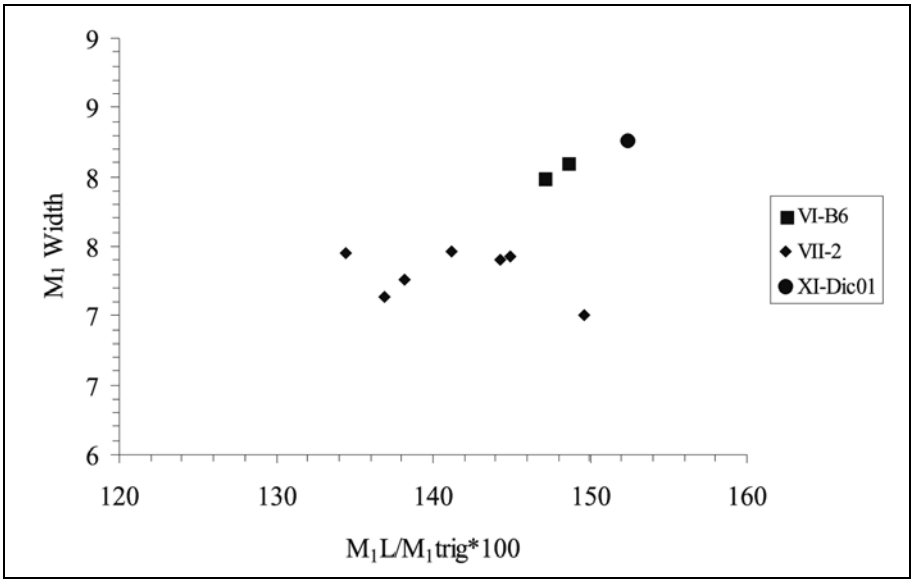

Fig. 10 - Scatter diagram of total M_1 length /trigonid length*100 ratio and width of M_1 of *Cynotherium* from fissures VII-2, XI-Dicembre2001 and VI-B6.

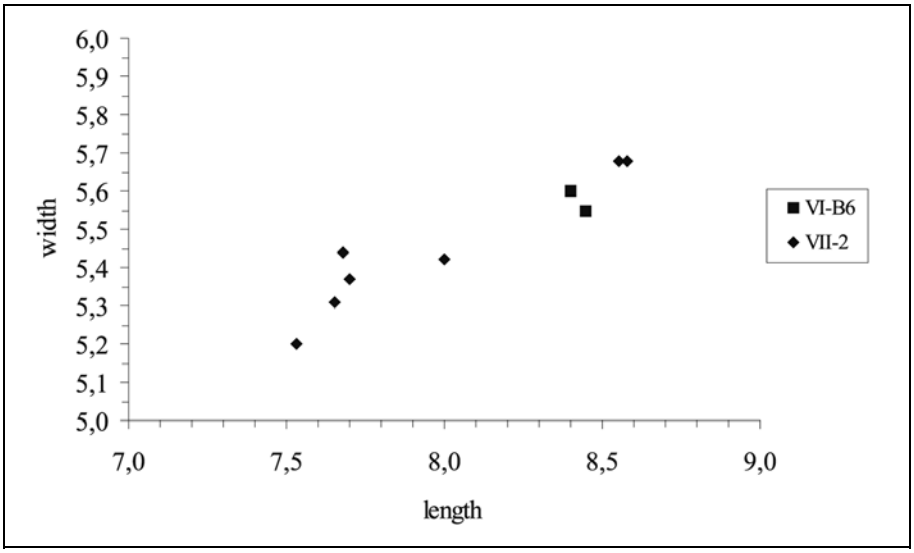

Fig. 11 - Scatter diagram of length and width of lower canines of *Cynotherium* from fissures VI-B6 and VII-2.

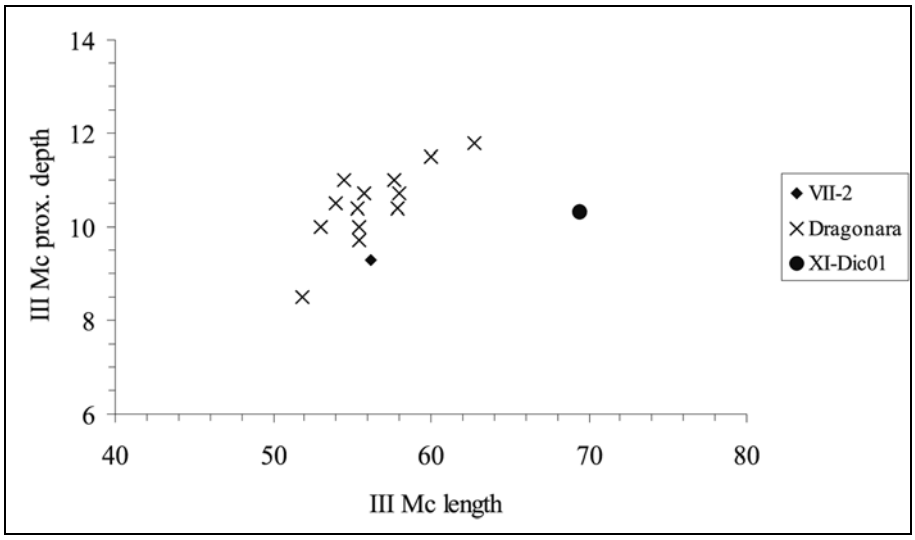

Fig. 12 - Scatter diagram of global length and depth of the proximal end of metacarpus III of *Cynotherium* from fissures VII-2, XI-Dicembre2001 and from Dragonara (data in Malatesta 1970).

Fig. 13 - *Cynotherium* cf. *sardous* from VI-B6; A and B medial and lateral views of VI-B6-999, left metacarpal II. Arrow indicates the articular surface for metacarpal I. Scale is 10 mm.

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Appendix I:

Examined Material

Fissure IV-20

IV-20-1 fragmented right mandible with D_3

Fissure V

V-65 distal part of right femur; **V-66** fragmented diaphysis of left femur; **V-67** fragmented diaphysis of long bone (femur?); **V-68** distal end of femur; **V-69** proximal fragment of right scapulae; **V-70** fragmented pelvis with acetabulum

V-71 fragmented lumbar vertebra; **V-73** fragmented thoracic vertebra.

Fissure VI-B6

VI-B6-955 proximal caudal vertebra (c2?); **VI-B6-956** three III phalanges; **VI-B6-957** three distal caudal vertebrae; **VI-B6-958** right P_3; **VI-B6-959** M_3; **VI-B6-960** left incisive; **VI-B6-961** undetermined fragmented bone; **VI-B6-962** fragment of right occipital condile; **VI-B6-963** proximal fragment of right scapula; **VI-B6-964** fragment of skull; **VI-B6-965** fragment of skull; **VI-B6-966** left maxillary with M^1-M^2; **VI-B6-967** fragment of skull (left parietal); **VI-B6-968** fragmented ribs; **VI-B6-969** fragmented atlas; **VI-B6-970** fragment of sacrum; **VI-B6-971bis** fragmented dorsal vertebrae; **VI-B6-971** II phalanx; **VI-B6-972** II phalanx; **VI-B6-974** II phalanx; **VI-B6-975** V right metacarpus; **VI-B6-976** IV left metacarpus; **VI-B6-977** III metatarsus without distal end; **VI-B6-978** fragmented diaphysis of humerus; **VI-B6-979** distal fragment of left humerus; **VI-B6-980** fragmented left ulna; **VI-B6-981** distal fragment of right radius; **VI-B6-982** distal fragment of right radius; **VI-B6-983** proximal fragment of right humerus; **VI-B6-984** fragmented diaphysis of tibia; **VI-B6-985** deciduous canine; **VI-B6-986** root of incisive; **VI-B6-987** right I^3; **VI-B6-988** right I^3; **VI-B6-989** left I^3; **VI-B6-990** distal caudal vertebra; **VI-B6-991** right and left mandibles with C, P1-M2 and I2-3, C, P3-M2, respectively; **VI-B6-992** left II metacarpus; **VI-B6-993** distal end of V metapodial; **VI-B6-994** distal end of III or IV metapodial; **VI-B6-995** distal end of III or IV metapodial; **VI-B6-996** right II metatarsus; **VI-B6-997** right III metacarpus without distal end; **VI-B6-998** left IV metacarpus without distal end; **VI-B6-999** left II metacarpus; **VI-B6-1045** distal end of left radius; **VI-B6-1047** distal fragment of right femur; **VI-B6-1069** root of canine; **VI-B6-1071** root of canine; **VI-B6-1072** proximal fragment of right tibia;

VI-B6-1075 fragmented mandible; **VI-B6-1076** fragmented maxillary; **VI-B6-1078** fragmented praemaxillary; **VI-B6-1079** proximal end of radius; **VI-B6-1080** distal end of ulna; **VI-B6-1081** fragmented ribs; **VI-B6-1083** I phalanx; **VI-B6-1084** I phalanx; **VI-B6-1085** I phalanx; **VI-B6-1087** right astragalus; **VI-B6-1088** left fragmented juvenile calcaneum (same specimen as 1087 and 1090); **VI-B6-1090** tarsal bone; **VI-B6-1092** fragmented thoracic vertebra; **VI-B6-1093** fragmented cervical vertebra; **VI-B6-1094** fragmented thoracic vertebra; **VI-B6-1124** radius without distal end; **VI-B6-1129** fragmented diaphysis of left tibia; **VI-B6-1139** left IV metatarsus; **VI-B6-1148** right I^3; **VI-B6-1149** right P_3; **VI-B6-SN** fragmented diaphysis of ulnae

Fissure VII-2

VII-2-936 Frontal and parietal bones; **VII-2-946** upper left canine; **VII-2-947** upper right canine; **VII-2-948** lower left canine; **VII-2-949** lower left canine; **VII-2-950** lower right canine; **VII-2-951** lower right canine; **VII-2-952** left M_1; **VII-2-953** fragment of occiput with right condile; **VII-2-954** fragment of right mandible without teeth; **VII-2-955** two fragment of left and right zygomatic arc; **VII-2-956** fragment of right frontal and parietal bones; **VII-2-957** three cuneiforms and one navicular; **VII-2-958** proximal caudal vertebra (cd2?) and distal caudal vertebra; **VII-2-959** 9 fragmented costae, 2 fragmented spines of thoracic vertebrae, 4 vertebral corpus, distal fragment of metapodial; **VII-2-960** thoracic vertebra; **VII-2-961** thoracic vertebra; **VII-2-962** thoracic vertebra; **VII-2-963** fragmented scapula; **VII-2-964** right fragmented scapula; **VII-2-965** left fragmented scapula; **VII-2-966** left fragmented scapula; **VII-2-967** left fragmented scapula; **VII-2-968** I phalanx (?); **VII-2-969** 4 fragmented pelvis; **VII-2-970** 8 fragmented metapodials, 2 fragmented diaphysis, distal epiphysis of metapodial; **VII-2-971** III right metatarsus; **VII-2-972** IV right metatarsus; **VII-2-973** III right metatarsus; **VII-2-974** II right metatarsus; **VII-2-975** IV left metacarpus; **VII-2-976** III left metacarpus; **VII-2-977** IV metatarsus; **VII-2-978** V left metatarsus; **VII-2-979** IV metatarsus; **VII-2-980** III metatarsus VII-2-981 II metatarsus; **VII-2-982** left ulna; **VII-2-983** left ulna; **VII-2-984** right ulna; **VII-2-985** right ulna; **VII-2-986** right ulna; **VII-2-987** right calcaneum; **VII-2-988** fragment of diaphysis of right humerus; **VII-2-989** proximal end of left humerus; **VII-2-990** diaphysis of left femur; **VII-2-991** diaphysis of left femur; **VII-2-992** right femur without distal end; **VII-2-993** right femur without distal end; **VII-2-994** right femur without distal end; **VII-2-995** proximal fragment of right tibia; **VII-2-996** proximal fragment of left tibia; **VII-2-997** left tibia without proximal end; **VII-2-998** fragment of distal left tibia; **VII-2-999** left tibia without distal end; **VII-2-1000** left mandible with M_3-P_2; **VII-2-1001** right mandible with M_1 and P_3; **VII-2-1003** right M_1; **VII-2-1004** right maxillary; **VII-2-1005** upper left canine; **VII-2-1006** upper left canine; **VII-2-1007** lower left canine; **VII-2-1008** lower left canine; **VII-2-1009** right lower canine; **VII-2-1010** right mandible with P_4; **VII-2-1011** I phalanx; **VII-2-1013** right P_3; **VII-2-1030** right P_4; **VII-2-1031** left fragmented mandible with M_2; **VII-2-1032** left M_1; **VII-2-1034** right P_3; **VII-2-1035** right P_3; **VII-2-1036** left I_2; **VII-2-1075** I phalanx; **VII-2-1120** left V metacarpus; **VII-2-1122** IV metacarpus (?); **VII-2-1123** IV metacarpus (?); **VII-2-1133** distal caudal vertebra (cd8?); **VII-2-1135** atlas; **VII-2-1136** axis; **VII-2-1153** right fragmented mandible without teeth; **VII-2-1213a** left ulna; **VII-2-1213b** right ulna; **VII-2-1254** III right metacarpus; **VII-2-3764** I phalanx; **VII-2-3765** I phalanx; **VII-2-3766** I phalanx; **VII-2-3767** I phalanx; **VII-2-3768** I phalanx; **VII-2-3807** right fragmented mandible without teeth; **VII-2-3808** right fragmented mandible with P_3; **VII-2-3809** fragmented praemaxillary bone; **VII-2-3810** left I^2; **VII-2-3811** right I^1; **VII-2-3812** left I^1; **VII-2-3813** left P^1; **VII-2-3817** distal caudal vertebra; **VII-2-3818** distal caudal vertebra; **VII-2-3819** distal caudal vertebra; **VII-2-3820** distal caudal vertebra; **VII-2-3841** right tibia without distal end; **VII-2-3842** left diaphysis humerus; **VII-2-3843** right tibia without proximal end; **VII-2-3848** cervical vertebra; **VII-2-3849** cervical vertebra; **VII-2-3850** cervical vertebra; **VII-2-3851** axis; **VII-2-3879** right calcaneum; **VII-2-3880** right astragalus; **VII-2-3889** right V metatarsus; **VII-2-3890** left V metatarsus; **VII-2-3893** fragmented mandible without teeth; **VII-2-3894** fragmented mandible without teeth; **VII-2-3895** fragmented mandible without teeth; **VII-2-5022** right astragalus; **VII-2-5148** proximal caudal vertebra; **VII-2-5149** proximal caudal vertebra; **VII-2-5150** proximal caudal vertebra; **VII-2-5151** proximal caudal vertebra; **VII-2-5265** distal caudal vertebra; **VII-2-5266** distal caudal vertebra; **VII-2-5267** distal caudal vertebra; **VII-2-5268** distal caudal vertebra; **VII-2-5269** distal caudal vertebra; **VII-2-5273** right calcaneum; **VII-2-5274** right maxillar with M2-P3; **VII-2-5275** left maxillar with M2-P3 (same specimen as 5274); **VII-2-5276** right premaxillar; **VII-2-5277** right P2; **VII-2-5278** left P2; **VII-2-5279** left M1; **VII-2-5280** left M2; **VII-2-5478** cervical vertebra.

Fissure IX Cervo

IX Cervo-1 distal part of humerus.

Fissure IX-Prolagus

IX-*Prolagus*- NN distal epiphysis and incomplete diaphysis of right humerus.

Fissure X-3uccelli

X-3u-6 II phalanx.

Fissure XI-canide

XI-cn-1 skull right and left maxillary with M^1-M^2 and P^4-M^1 resp.; **XI-cn-2** right mandible with P_1-M_2; **XI-cn-3.1** skull and mandible in the breccia; **XI-cn-3.2** radius in the breccia; **XI-cn-3.3** anterior fragment of right maxillary in the breccia; **XI-cn-3.4** anterior fragment of right maxillary in the breccia; **XI-cn-4** left maxillary with M^1-M^2; **XI-cn-5** left P_1 belonging to the same specimen as 2 and 6; **XI-cn-6** left C_1.

Fissure XI-dicembre 2001

XI-dic.01-1 right fragmented horizontal mandibular ramus with M_1; **XI-dic.01-2** fragmented left horizontal mandibular ramus without teeth; **XI-dic.01-3** right M_2; **XI-dic.01-4** right P^4; **XI-dic.01-5** left I^3; **XI-dic.01-6** left P^1; **XI-dic.01-7** left I_3; **XI-dic.01-8** fragment of cranium; **XI-dic.01-9** fragment of cranium; **XI-dic.01-10** fragment of cranium; **XI-dic.01-11** right calcaneum; **XI-dic.01-12** fragment of left pelvis (acetabulum); **XI-dic.01-13** fragment of right pelvis (acetabulum); **XI-dic.01-14** fragment of ischium; **XI-dic.01-15** fragment of pelvis; **XI-dic.01-16** right III metacarpus; **XI-dic.01-17** right II metacarpus; **XI-dic.01-18** right V metacarpus; **XI-dic.01-19** distal fragment of lateral metapodial; **XI-dic.01-20** I phalanx; **XI-dic.01-21** I phalanx; **XI-dic.01-22** I phalanx; **XI-dic.01-23** dorsal vertebra; **XI-dic.01-24** distal fragment of radium.

Appendix II - Measurements of fossil remains.

Measurements / Specimens	C_1 L	C_1 B	P_1 L	P_1 B	P_2 L	P_2 B	P_3 L	P_3 B	P_4 L	P_4 B	M_1 L	M_1 B	L trig.	B tal.	M_2 L	M_2 B	M_3 L	M_3 B	L M_3-C	LM_3-P_2	H mand	B mand	trig/M_1
VI-B6-991 r	8.40	5.60	5.20	3.70	8.65	3.85	9.80	4.00	11.40	5.60	20.30	8.00	13.80	6.91	9.30	6.10			76.00		19.50	10.50	67.98
VI-B6-991 l	8.45	5.55					9.80	4.00	11.40	5.55	20.50	8.10	13.80	7.07	9.10	6.20			76.30		20.00	10.50	67.32
VI-B6-958							9.40	4.00															
VI-B6-959																	4.70	4.10					
VII-2-948	8.58	5.68																					
VII-2-949	7.68	5.44																					
VII-2-950	8.55	5.68																					
VII-2-951	7.65	5.31																					
VII-2-952											18.85	7.26	13.64	5.48									72.36
VII-2-1000					8.08	4.02	9.27	4.25	10.90	5.76	19.17	7.43	13.23	6.10	8.92	5.95	4.98	4.44		64.75	18.00	8.30	69.01
VII-2-1001											18.98	7.14	13.86	6.06							16.62	7.75	73.02
VII-2-1002											18.70	7.00	12.50	5.40							17.00	7.50	66.84
VII-2-1003											19.10	7.45	14.21	6.30									74.40
VII-2-1007	7.53	5.20																					
VII-2-1008	7.70	5.37																					
VII-2-1009	8.00	5.42																					
VII-2-1010									10.82	5.97													
VII-2-1013							9.34	4.27															
VII-2-1031															8.01	5.80							
VII-2-1032											19.98	7.46	14.15	6.01									70.82
VII-2-1034							9.56	4.24															
VII-2-1035							9.77	4.16															
VII-2-3808							9.90	4.07													17.04	8.41	
VII-2-5279											19.23	7.40	13.33	6.25									69.32
VII-2-5280															8.71	6.74							
XI-Bc-1											20.02												
XI-Dic 01-1											21.11	8.26	13.85	7.06									65.61
XI-Dic01-2																					17.76	10.59	
XI-Dic 01-3															10.52	6.37							
XI-Bc-50 r			4.90	3.30	*7.00		10.20	3.80	11.50	5.50	*18.00				9.00					63.70	19.40	8.80	
XI-Bc-50 l			5.50	3.50																			

Tab. 1 - Measurements (mm) of mandibles and dentitions of *Cynotherium*. Legend: L= total length; B= maximum breight; H mand= height of mandibular ramus at M_1; B mand= breight of mandibular ramus at M_1; * inferred measurements.

Measurements / Specimens	C^1 L	C^1 B	P^1 L	P^1 B	P^2 L	P^2 B	P^3 L	P^3 B	P^4 L	P^4 B	M^1 L	M^1 B	M^1B tot.	M^2 L	M^2 B	D^3 L	D^3 B	D^4 L	D^4 B
VI-B6 966											12.1	13.2		6.6	9.9				
VII-2-944							10.95	4.34											
VII-2-946	8.42	5.76																	
VII-2-947	8.35	5.62																	
VII-2-1005	8.47	5.75																	
VII-2-1006	8.62	5.68																	
VII-2-1004							10.85	4.43	16.64	7.96									
VII-2-1030									16.28	7.95									
VII-2-5274							11.26	4.37	16.56	7.79	11.86	11.10		6.59	8.04				
VII-2-5275							10.87	4.42	16.39	7.96	11.70	11.45		5.56	8.31				
VII-2-5277					9.12	4.22													
VII-2-5278					8.83	3.94													
XI-Bc-1 l									18.79	9.65	12.93	14.76							
XI-Bc-1 r											13.26	14.11		5.67	8.90				
XI-Bc-4											13.09	15.33		6.49	9.56				
XI-Dic 01 4 l	6.20	5.58																	
XI-Dic 01 6					6.93	4.70													
XI-Dic 01 4 r									18.24	8.97									
IV-20-1																7.58	3.44		
XI-Bc 2											9.59					11.41	6.03	8.91	8.9

Tab. 2 - Measurements (mm) of upper dentitions of *Cynotherium*. Symbols are the same as tab. 1; D= deciduous premolar

Measurements / Specimens	TD prox	APD prox	TD Dia	APD Dia	TD dist	APD dist
VII-2-988			8.87	10.68		
VII-2-989	37.06	23.12				
VII-2-3842			9.72	10.25		
VI-B6-983	36.6	27.3				
VI-B6-979			11.3	12.3	30.6	26.3
VI-B6-978			10.5	12.6		
IX-*Prolagus* nn			12.29	13.33	*30	24.4

Tab. 3 - Measurements (mm) of humeri of *Cynotherium*. Legend: TD= transversal width; APD= depth. *= inferred measurement.

Measurements / specimens	TD prox	APDprox	TD Dia	APD Dia	TD dist	APD dist
VI-B6-1045			22.8	14.08	15.83	10.48
VI-B6-1124	17.75	11.08	12.91			
VI-B6-981			11.6	8.4	21.8	13.8
VI-B6-982			10.8	8.6	22.7	12.3

Tab. 4 - Measurements (mm) of radii of *Cynotherium*. Legend: TD= transversal width; APD= depth

Measurements / Specimens	TD prox	APD prox	TD Dia	APD Dia	H
VII-2-982	10.53	16.56			
VII-2-983	10.13	16.69			
VII-2-984	10.71	17.00			
VII-2-985			7.00	8.49	
VII-2-986				8.59	
VII-2-1213a	7.47	15.99	7.00	6.53	16.27
VII-2-1213b	6.86	16.15	8.17	8.25	15.55
VI-B6-980	8.80	17.60	9.5	9.81	17.20

Tab. 5 - Measurements (mm) of ulnae of *Cynotherium*. Legend: TD= transversal width; APD= depth; H= height of holeocraneon.

Measurements	GL	TD prox	APD prox	TD Dia	APD Dia	TD dist	APD dist
Specimens							
VI-B6-975 V mtc	46.8	10	9.5	6.8	4.7	9.5	8.5
VI-B6-976 IV mtc	55.7	6.6	9.3	5.7	4.1	8.3	8.7
VI-B6-992 II mtc	48.94	6.21	10.26	6.44	5.15	8.40	
VI-B6-997 III mtc		6.88	9.71	6.05	4.67		
VI-B6-998 IV mtc		5.98	9.79	6.55	4.65		
VI-B6-999 II mtc	54.97	6.53	12.15	5.94	5.00	8.80	8.38
VII-2-975 IV mtc		8.56	12.38	6.35	5.14		
VII-2-976 III mtc		6.55		6.30	5.01		
VII-2-1120 V mtc	47.09	9.33	9.55	5.76	4.23	8.66	7.70
VII-2-1121 III mtc	56.17	7.48	9.30	5.62	4.26	8.33	8.54
VII-2-1122 IV mtc	55.63	6.66	8.52	5.64	4.37	8.31	9.27
VII-2-1123 IV mtc				5.66	4.19	8.14	7.66
VII-2-1254 III mtc	64.17	11.58		6.42	5.08	8.59	8.65
XI-Dic 01 16 III mtc	69.41	9.86	10.32	6.87		8.69	9.31
XI-Dic 01 17 II mtc		6.62	10.71	6.68	4.95		
XI-Dic 01 18 V mtc		7.74	9.74	6.79	5.07		

Tab. 6 - Measurements (mm) of metacarpals of *Cynotherium*. Legend: GL= global length; TD= transversal width; APD= depth.

Measurements	TD prox	DAP prox	TD Dia	DAP Dia	TD dist	DAP dist
Specimens						
VII-2-990	29.39	29.57	12.43	11.85		
VII-2-991			10.82	10.61		
VII-2-993			12.06	9.52		
VII-2-994	29.39	29.57	12.43	11.85		
V-65					32.7	33.58
VI-B6-1047			12.70	14.50	30	31.3

Tab. 7 - Measurements (mm) of femura of *Cynotherium*. Legend: TD= transversal width; APD= depth.

Measurements	TD prox	APD prox	TD Dia	APD Dia	TD dist	APD dist
Specimens						
VII-2-995	32.19					
VII-2-996	31.64	33.06				
VII-2-997					21.68	15.95
VII-2-998			9.04	10.61	20.66	15.09
VII-2-999			8.77	8.88	17.24	14.16
VII-2-3841			10.40	11.06		14.25
VII-2-3843	22.46		9.35	9.14		
VI-B6-984			12.50	11.80		
VI-B6-1072	31.20	33.20				
VI-B6-1129			12.40	11.50		

Tab. 8 - Measurements (mm) of tibiae of *Cynotherium*. Legend: TD= transversal width; APD= depth.

Measurements	GL	L *corpus calcanei*	TD *corpus calcanei*	APD *corpus calcanei*	TD tuberosity	APD tuberosity	TD prox	APD prox
Specimens								
VI-B6-1088			6.89	12.27	12.07		18.08	17.32
VII-2-987		24.02	7.35	11.99	12.2	13.51		
VII-2-3879	38.57	27	7.38	11.4	11.6	12.63	16.12	18.02
VII-2-5273	39.12	27.53	7.05	11.55	11.94	13.81	16.26	17.91
XI-Dic01-11			7.05	12.45	11.35	12	15.7	16.4

Tab. 9 - Measurements (mm) of calcanei of *Cynotherium*. Legend: GL= global length; TD= widht; APD= depth.

Measurements	GL	GTD	APD	TD art
Specimens				
VI-B6-1087	22.15	18.87	11.87	12.66
VII-2-3880	22.02	19.16	13.13	13.93
VII-2-5022	22.59	20.09	13.88	13.45

Tab. 10 - Measurements (mm) of astragali of *Cynotherium*. Legend: GL= global length; GDT= global widht; APD= depth; TD= transversal diameter.

Measurements	GL	TD prox	APD prox	TD Dia	APD Dia	TD dist	APD dist
Specimens							
VI-B6-996 II mtt		5.37	10.14	5.92	5.05		
VI-B6-1139 IV mtt		5.74	12.49				
VI-B6-977 III mtt		7.70	10.00	6.50	4.60		
VII-2-971 III mtt		5.72	9.94	5.36	3.67		
VII-2-972 IV mtt		6.04	12.50	6.30	3.80		
VII-2-973 III mtt		6.62	11.52	6.02	4.38		
VII-2-974 II mtt				6.34	5.67		
VII-2-977 IV mtt						8.36	8.62
VII-2-978 V mtt		5.91	9.55	5.75	5.30		
VII-2-979 IV mtt		7.79	10.33	6.59	5.09		
VII-2-980 III mtt		9.02	11.05				
VII-2-981 II mtt				5.63	7.30		
VII-2-3889 V mtt	58.30	5.06	11.43	5.19	4.79	8.87	7.97
VII-2-3890 V mtt						8.36	8.62

Tab. 11 - Measurements (mm) of metatarsals of *Cynotherium*. Legend: GL= global length; TD= widht; APD= depth.

Measurements	GL	TD prox	APD prox	TD Dia	APD Dia	TD dist	APD dist
Specimens							
VI-B6-1083 j.	18.13	7.00	6.00	4.84	4.94	5.90	4.60
VI-B6-1084	27.90	9.57	7.98	5.78	5.23	7.93	5.91
VI-B6-1085	25.89	9.13	7.84	5.41	4.61	7.28	5.51
VI-B6-971	22.10	8.50	7.20	4.70	4.50	6.70	5.70
VI-B6-972	22.60	9.00	7.50	5.50	4.50	7.00	5.40
VI-B6-974	23.10	8.40	7.00	4.90	4.60	6.90	4.90
VII-2-968		8.36	6.21	5.12	3.53		
VII-2-1011	23.71	8.00	6.28	4.68	4.12	6.55	4.62
VII-2-1075	25.90	8.32	6.41	4.93	4.02	6.42	4.84
VII-2-3763	24.48	8.12	7.12	4.66	3.78	6.45	4.39
VII-2-3764	25.73	8.35	7.27	5.00	3.96	6.71	4.77
VII-2-3765	25.92	8.59	7.58	5.25	4.32	6.80	5.11
VII-2-3766	23.91	8.07	6.98	4.62	3.98	6.53	4.90
VII-2-3767	24.81	8.02	6.69	4.61	3.70	6.08	4.49
VII-2-3768	25.80	8.55	7.28	4.51	4.04	6.50	5.10
XI Dic 01 20	23.20	8.78	7.30	5.10	5.16	7.08	5.30
XI Dic 01 21	25.51	8.39	7.03	5.08	4.57	6.33	4.62
XI Dic 01 22	22.21	8.53	7.33	5.41	5.28	7.35	5.45
X-3u-6				5.00	3.00	6.70	4.40

Tab. 12 - Measurements (mm) of I phalanx of *Cynotherium*, except but VI-B6-971, 972, 974 and X-3u-6 which are second phalanges. Legend: GL= global length; TD= transversal width; APD= depth. J= juvenile.