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Journal of Vertebrate Paleontology

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Published online: 02 Aug 2010.

PLEASE SCROLL DOWN FOR ARTICLE

CYNOTHERIUM SARDOUS, AN INSULAR CANID (MAMMALIA: CARNIVORA) FROM THE PLEISTOCENE OF SARDINIA (ITALY), AND ITS ORIGIN

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ABSTRACT—The endemic insular canid *Cynotherium sardous* has been known for 1 ½ centuries, yet its phylogenetic position remained unsolved. This was because inherited ancestral characters and acquired adaptations to different ecological pressures could not be separated. In this study the problem is approached again, with the use of morphological features that were either overlooked or could not be explained properly, combined with results from recent major revisions of canid phylogeny. It appears that *Xenocyon* is the ancestor of *Cynotherium*, and that this large hypercarnivorous canid, once on the island, faced a rather different menu consisting of small prey only. The subsequent necessary adaptation resulted in a small-sized dog whose dentition remained much the same, whereas its skull lost the typical fortifications seen in the other hypercarnivorous canids; these are considered superfluous for *Cynotherium*, which had to exchange big and strong prey for small and fast prey.

INTRODUCTION

During the Plio-Pleistocene period, many islands of the world were inhabited by endemic mammals of mainland origin (for an overview, see Sondaar and Van der Geer, 2005). Today, most of these island endemics are extinct and are known to us only by their fossil remains (Alcover et al., 1998). The larger insular mammals present unique adaptations to the island environment compared to their mainland relatives, such as smaller size combined with robust and short limbs (Sondaar, 1977; Sondaar and Van der Geer, 2005).

A difficulty in the study of these mammals is that they are so highly adapted to their new environment; it is not easy to trace their direct mainland ancestor. The major problem is how to distinguish inherited characters from characters that were acquired during the adaptation to the island environment. *Cynotherium sardous*, a small canid from the Pleistocene of Sardinia and Corsica is such a case.

This canid has been known for almost 150 years (Studiati, 1857), and some works have been published on its morphology, among which Malatesta's (1970) descriptions of the Dragonara Cave (Sardinia) material is the most extensive one, followed by Eisenmann and Van der Geer (1999) for the skull's biometrics. The anatomical features of *Cynotherium* make it a unique species in canid evolution.

Several suggestions for a possible ancestor have been made: *Cynotherium* has been related to *Cuon* (Forsyth Major, 1877; Malatesta, 1970; Bonifay, 1971), *Canis* (Azzaroli, 1977; Kotsakis, 1980; Eisenmann, 1990; Eisenmann and Van der Geer, 1999), *Eucyon* (Van der Made, 1999), and *Xenocyon* (Schütt, 1973; Eisenmann, 1990; Van der Made, 1999). Finally, the possibility of a relationship to *Nyctereutes* (Van der Made, 1999) has been mentioned but was not further explored.

Hardly anything has been published about the animal's functional morphology and its possible ecological niche. The only comments were made by Malatesta (1970) who along with the detailed description of the Dragonara material gave some interpretations of a few muscle attachments, neck posture (more horizontal), body proportions (short legs) and cranial and dental characters (slender mandible and weak set of teeth). Based on these features, Malatesta (1970) suggested that *Cynotherium*

could not attack big game and that most probably its diet consisted of small vertebrates and carrion.

In this article, we present the results of the study of a *Cynotherium* skeleton that was found in 1984 during paleontological excavations by a Dutch-Italian team in Corbeddu Cave, province of Nuoro, Sardinia (Klein Hofmeijer et al., 1987; De Visser and Van Den Bergh, 1999). The absolute age of this skeleton was estimated at 11,350 +/– 100 years B.P. (Klein Hofmeijer, 1996). It belongs to the species *Cynotherium sardous* (Eisenmann, 1990; Eisenmann and Van Der Geer, 1999) and it is one of the youngest specimens of the species, as the species became extinct shortly thereafter (Klein Hofmeijer, 1996). The extensive work that has been carried out on canid phylogeny during the past decade (e.g. Rook, 1993, 1994; Tedford, Taylor and Wang, 1995; Wayne et al., 1997; Wang, Tedford and Taylor, 1999; Sotnikova, 2001; Lyras and Van Der Geer, 2003; Wang et al., 2005) has provided new data and insights.

MATERIALS AND METHODS

The Skeleton from Corbeddu Cave

The *Cynotherium* skeleton used for this study was found in Late Pleistocene terre rosse sediments of Corbeddu Cave (Lanaittu Valley, province of Nuoro, Sardinia, Italy). This cave yielded more than 20,000 fossils, for the major part belonging to the endemic deer "*Megaloceros*" *cazioti* and the endemic lagomorph *Prolagus sardus* (Klein Hofmeijer, 1996). The *Cynotherium* skeleton comes from the upper fossiliferous level of layer 3 in hall 2 (Fig. 1), is fairly complete (Table 1), and in an excellent stage of preservation. The skeleton is at present in the collection of the Archeological Survey of Sassari at Porto Torres (Sardinia, Italy).

Skeletal Morphology

For the description of the skeleton we follow the nomenclature of Evans (1993). To investigate the functional significance of the observed features, we compared the morphology of the Corbeddu skeleton with specimens from most living and some selected fossil canid species (Table 2).
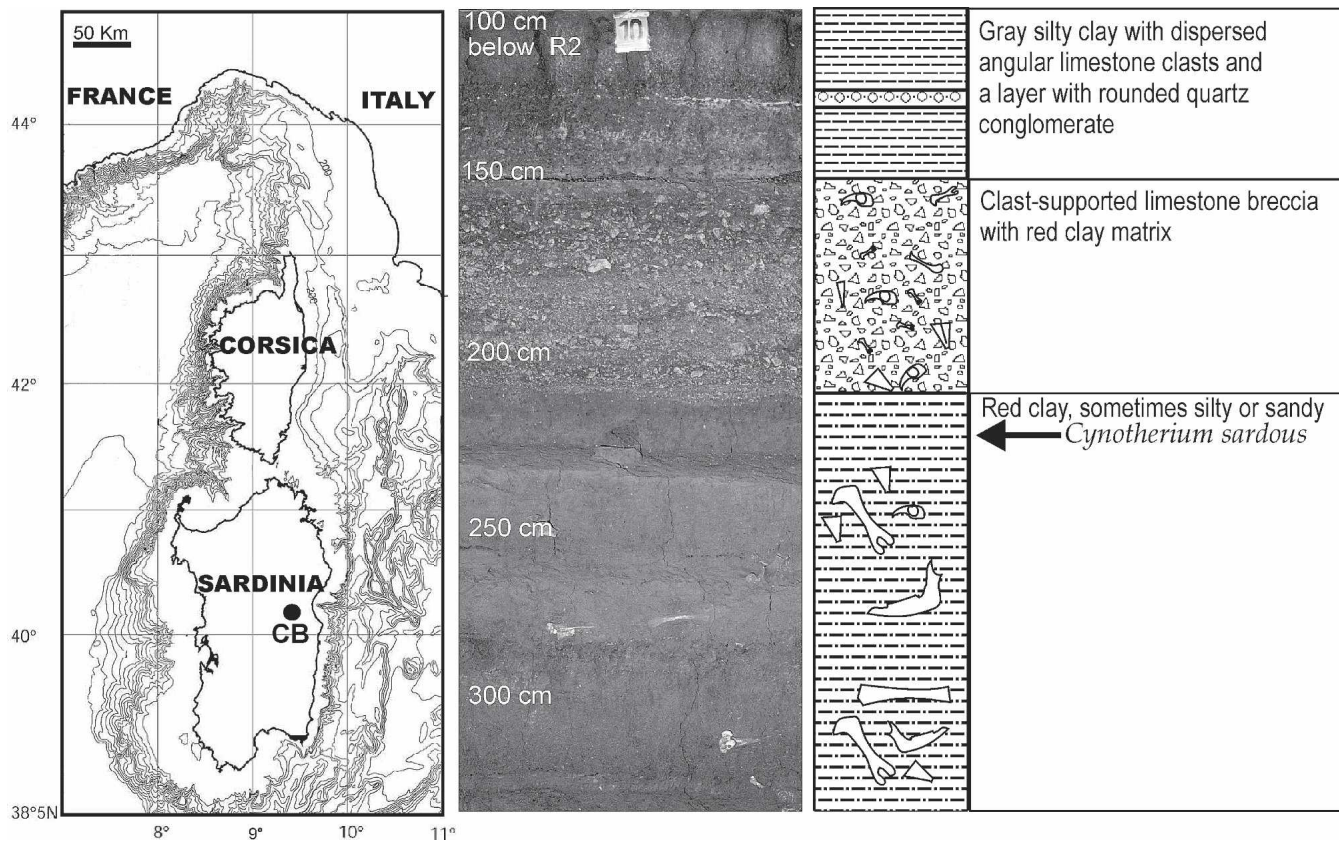
FIGURE 1. Location of Corbeddu Cave (CB on the map) and profile of Hall 2. The contours on the bathymetric map are every 200 m. The depths indicated on the profile are below reference point R2.

Taxonomic Arrangement

The taxonomy in this work follows Wozencraft (1993) for the living taxa and Schütt (1974) for *Xenocyon*. According to her, *Xenocyon* includes only the two Old World species *X. lycaonoides* and *X. dubius* (formerly known as *Cuon dubius*). More recently, Martínez Navarro and Rook (2003) proposed that *Canis falconeri, Xenocyon lycaonoides*, and *Lycaon pictus*, form a series of chrono-species and therefore should be grouped within the genus *Lycaon*. Such an arrangement creates taxonomical problems, as in this way the genus *Canis* becomes paraphyletic (Werdelin and Lewis, 2005). In addition, a phylogenetic analysis in progress by Tedford, Wang and Taylor (published in part by Wang et al., 2005: fig. 2.1) suggests a closer relationship of *Xenocyon* to *Cuon* and *Lycaon* than to *Canis*. Therefore, as an extensive phylogenetic analysis of the wolf-like dogs is beyond the scope of this paper, we choose to follow Schütt's more narrow diagnosis for convenience.

TABLE 1. List of *Cynotherium* elements from Corbeddu Cave.

Elementary Description	Number	Elementary Description	Number
Skull with mandible	CB 84-8022	Tibia (sin)	CB-84-2045
Atlas	CB 84-2028	Radial	CB 88-13433
Axis	CB 84-2029	3rd metacarpal (dex)	CB 83-1063A
3rd cervical vertebra	CB 83-1031	4nd metacarpal (dex)	CB 83-1063B
4rd cervical vertebra	CB 84-2046	3th metacarpal (sin)	CB 83-1063C
6th thoracic vertebra	CB 82-154	5th metacarpal (dex)	CB 84-2025
4rd lumbal vertebra	CB 82-310	5th metacarpal (sin)	CB 84-2037
5rd lumbal vertebra	CB 83-1149	3rd metatarsal (sin)	CB 84-2023
6rd lumbal vertebra	CB 84-2030	2nd metacarpal (dex)	CB 84-2043
2rd caudal vertebra	CB 83-1027	4th metacarpal (sin)	CB 84-2031
Caudal vertebra	CB 83-1063F	1st metacarpal (dex)	CB 84-2042
Pelvis	CB 83-1027A	Phalange	CB 84-2039
Scapula (sin)	CB 84-2016	Phalange	CB 84-2048
Scapula (dex)	CB 83-1034	Phalange	CB 82-249
Humerus (sin)	CB 88-14.767	Phalange	CB 83-1063E
Humerus (dex)	CB 84-2019	Phalange	CB 84-2038
Radius (sin)	CB 88-14.765, 766	Femur (sin)	CB 84-1763
Radius (dex)	CB unnumbered	Rip	CB 83-1051
Ulna (sin)	CB 88-14.768	Rip	CB 84-2049
Ulna (dex)	CB 84-2027	Rip	CB 84-2049

TABLE 2. List of fossil canids used in this study.

Species	Material	Number
"*Canis*" *adoxus*	Skull and mandible	NMB-Rss-45
Canis cf. *falconeri*	Skull and mandible	F:AM 97051
Cynotherium sp.	Humerus (prox. fragment)	NMB Ty 5363
Cynotherium sp.	Humerus (dist. fragment)	NMB Ty 5362
Cynotherium sardous	Skull	MPUR S.G. 1
Cynotherium sardous	Skull	MPUR S.G. 2
Cynotherium sardous	Mandible	MPUR d. 7
Cynotherium sardous	Mandible	MPUR d. 7
Cynotherium sardous	Mandible	MPUR d. 8
Cynotherium sardous	Mandible	MPUR d. 9
Cynotherium sardous	Mandible	MPUR d. 11
Eucyon davisi	Skull and mandible	F:AM 129013
Eucyon davisi	Partial endocast	F:AM 63005
Nyctereutes sinensis	Skull and mandible	F:AM 96792
Xenocyon dubius	Mandible	IVPP CP82
Xenocyon lycaonoides	Mandible	IQW 1984/20196
Xenocyon lycaonoides	Mandible	IQW 1985/21000
Xenocyon lycaonoides	Endocast	GIN 3755-144

Institutional Abbreviations—AMNH(M), American Museum of Natural History, Department of Mammalogy New York, USA; **CB**, Corbeddu Cave, Sardinia, Italy; **F:AM**, Frick collection, American Museum; **GIN**, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China; **IQW**, Research Station of Quaternary Palaeontology Weimar, Senckenbergische Naturforschende Gesellschaft, Germany; **NMB**, Naturhistorisches Museum Basel, Switzerland; **MPUR**, Museo di Paleontologia, Universita' degli Studi di Roma "La Sapienza," Italy; **NNML**, Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands.

OBSERVATIONS AND COMPARISONS

The morphology of the skull and postcranial skeleton of *Cynotherium* from Corbeddu Cave is similar to that of the specimens found in Dragonara Cave, Sardinia. Since the Dragonara material is already described in detail by Malatesta (1970), we provide a brief description of the Corbeddu specimen, focusing only on those features that are either not recognized or not stressed in Malatesta's (1970) work and which are useful for phylogenetic analyses.

Cranial Anatomy

Skull—In lateral view, the skull gives a slender impression (Fig. 2). The muzzle slopes steadily from the nasal openings till the posterior part of the forehead so that the anterior part of the skull has a wedge-shaped lateral profile. The anterior part of the muzzle is narrower than in *Cuon, Lycaon* and *Speothos* (Figs. 2, 3) but broader than that in most foxes.

The postorbital constriction is broad. Although the neurocranium is relatively broad, the zygomatic arches are slender, with only a small lateral expansion. The skulls of *Cuon, Lycaon, Speothos*, and *Canis lupus* are also broad, yet their zygomatic arches are equally wide. In the jackals, the zygomatic arches are weaker, although not to the degree as seen in *Cynotherium*. An exception is provided by *Canis simensis*, which has slender zygomatic arches combined with a broad postorbital constriction (Rook and Azzaroli-Puccetti, 1997).

Cynotherium has a frontal sinus that is small for a *Canis* spp. of this size. The posterior expansion of the sinus is limited, and its margin lies far away from the parietofrontal suture. The sinus invades the postorbital process, leaving only a small bony edge at the tip on the exterior side, as in *Cuon*. The frontal shield is wide and surrounded by well-formed parasagittal ridges with just a slight elevation. The temporal crests unite and are lyrate in shape. The inion is rounded and, in lateral view, slightly overhangs the posterior edge of the occipital condyles. A similar configuration is seen only in some *Vulpes* species and in *Urocyon*.

The mastoid is greatly enlarged and laterally expanded, and gives the impression of being merged with a continuation of the nuchal crest. The only canid in which the mastoid is also enlarged is the Falkland Island wolf (*Dusicyon australis*); here, the mastoid is modelled into a laterally extending knob structure, but not
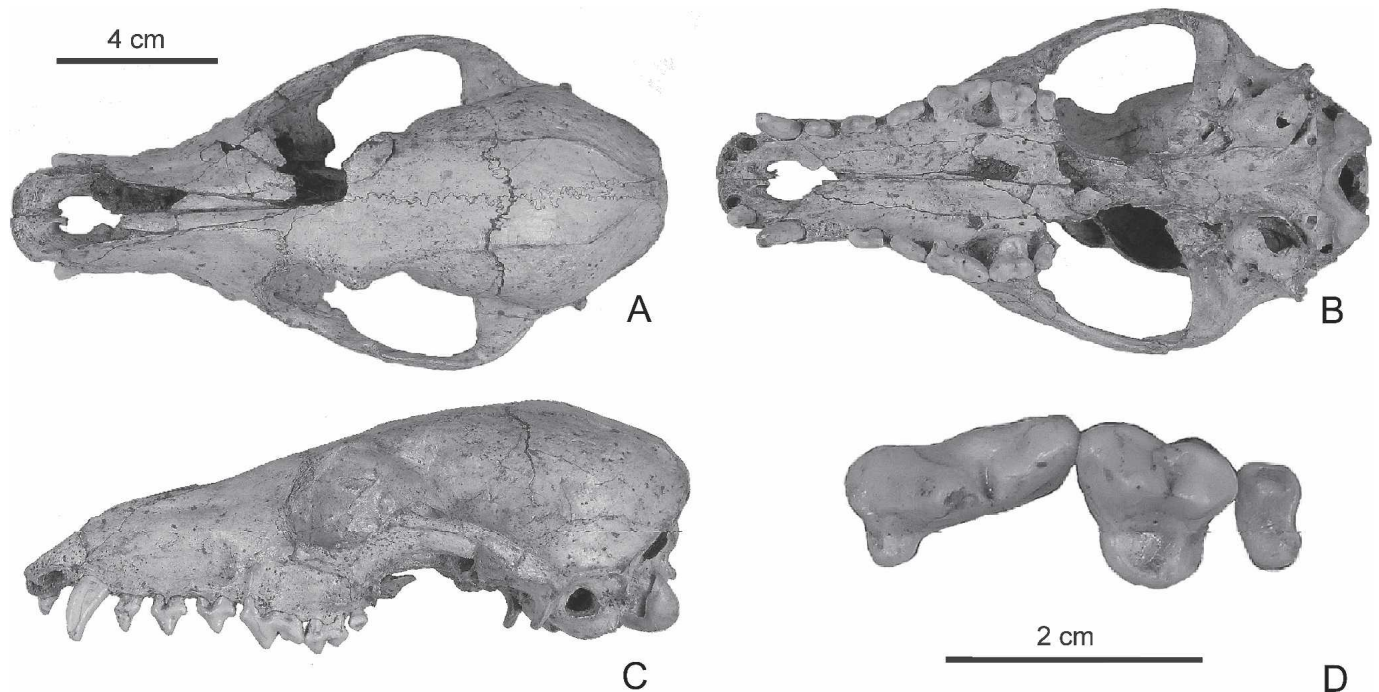

FIGURE 2. Skull of *Cynotherium sardous* CB 84–8022; **A**, dorsal; **B**, lateral; **C**, ventral view and **D** detail of P4-M2.
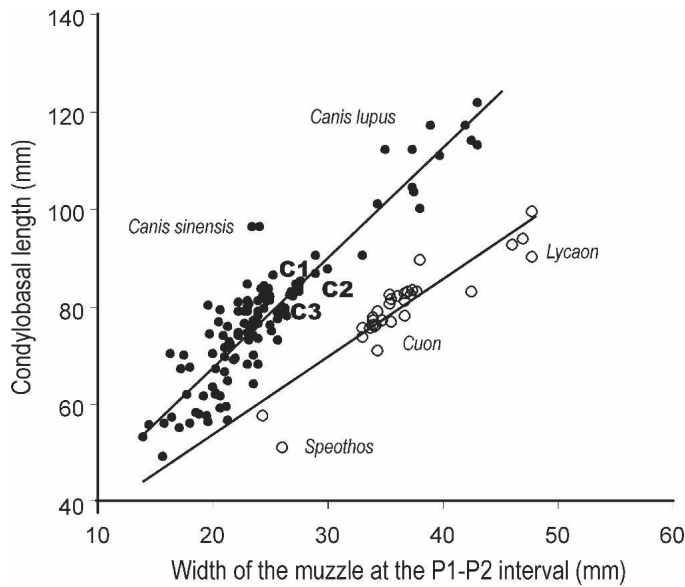
FIGURE 3. Width of the muzzle of living canids and *Cynotherium sardous*. Filled circles represent canids with a bicuspid talonid; open circles represent canids with one trenchant heel on the talonid. C1: *Cynotherium sardous* CB 84–8022; C2: *C. sardous* MPUR S.G. 1("no 2" of Malatesta, 1970) and C3: *C. sardous* MPUR S.G. 2 ("no 1" of Malatesta, 1970) from Dragonara Cave.

to the extent seen in *Cynotherium* (Fig. 4). In *Dusicyon* the knob-like mastoid makes no contact with the nuchal crest. This latter feature is the normal situation in canids: the mastoid stands always on its own, isolated, and not attached to any other structure. It seems that in fossil canids the process was as in the living canids (except for *Dusicyon*); see for example *Canis* cf. *falconeri* (Fig. 4). This seems also true for *Xenocyon*. Unfortunately, the described cranial material of *Xenocyon* is very poorly preserved (Schütt, 1974; Palmqvist et al., 1999). However, a complete and
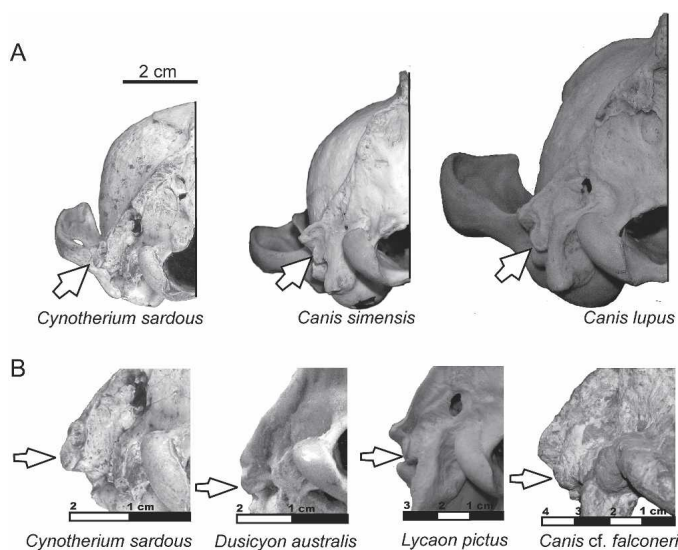

FIGURE 4. **A**, the occipital region of *Cynotherium sardous* (CB 84–8022) compared to *Canis sinensis* (AMNH(M) 214799) and *Canis lupus* (AMNH(M) 171172); **B**, the mastoid process of *Cynotherium sardous* (CB 84–8022), *Dusicyon australis* (NNML 19111), *Lycaon pictus* (AMNH(M) 169181) and *Canis* cf. *falconeri* (F:AM 97051). The arrow indicates the mastoid process.

well preserved skull, currently under description, is known from Siberia and its mastoid process is similar to that of *Canis lupus* (Sotnikova, personal communication, April, 2004).

The ventral surface of the basioccipital of *Cynotherium* is broader than in similar sized living canids and bears a prominent, clearly triangular pharyngeal tubercle. Anterolateral of this tubercle, two rugose fossae for neck muscle attachment are present, which are deeper and wider than in *Canis*. The auditory bullae are small and dorsoventrally flattened. The paroccipital processes are well developed and are posteriorly expanded with a free tip as in *Cuon*. The caudal palatine border extends further caudally to the tooth row as in the short-faced canids *Speothos*, *Cuon*, *Nyctereutes procyonoides*, and *Lycaon*.

Endocranial Anatomy—The external brain anatomy of *Cynotherium* is typical of the living Canidae (Fig. 5). Seen in lateral view, the cerebrum is characterized by the arrangement of the three grooves—the ectosylvian, suprasylvian and ectolateral sulci—as a series of vertical arches wrapped around the sylvian sulcus and dorsally by the presence of two horizontal grooves— the lateral and entolateral sulci. The sigmoid gyri bow out laterally and the orbital and proreal gyri are well developed. The coronal and ansate sulci create an orthogonal outline on the dorsal side of the cerebrum. The proreal gyrus is long and bilaterally constricted. These last two features, the orthogonal outline of the coronal and ansate sulci and the long and bilaterally constricted proreal gyras, are typical for the wolf-like canids *Canis*, *Lycaon*, *Xenocyon*, and *Cuon* (Lyras and Van der Geer, 2003). The orthogonal outline of the coronal and ansate sulci is strikingly different from the pentagonal outline seen in *Eucyon* and also from the heart-shaped outline seen in *Nyctereutes*.

Mandible—The horizontal ramus of the mandible is slender and its inferior border is almost straight (Fig. 6). The two mental foramina are situated right below the diastema between c and p3. The tooth row is straight. The angular process is large as in *Canis*. The fossa for the medial pterygoid muscle occupies almost the complete medial surface of the process. The height of the coronoid process is less than the distance between the mandibular condyle and the ventral margin of the angular process, as in *Xenocyon* and *Lycaon*.

Dentition—The I3 is enlarged in comparison to the other incisors and has a posterior cingulum. P1 is single-rooted and monocuspid. Both P2 and P3 are double-rooted and posteriorly elongated with a small lingual cingulum. The P3 has a strong posterior accessory cusp, while P4 is robust, with a relatively small protocone slightly posterior to the anterior border of the parastyle. M1 is relatively small with the labial and lingual cinguli little developed. The paracone is considerably larger than the metacone. The metaconule is absent. The hypocone is very small and is practically represented only by a small ridge on the cingulum at the posterolingual corner of the tooth. M2 is also small with only two roots. The buccal cingulum is not well developed and the hypocone basin is reduced.

The lower tooth row (Fig. 6) is straight without an inclination at the p4-m1 interval as seen in *Canis lupus*. The p1 and p2 are missing. There is no trace of the corresponding alveolus. If this loss occurred during life, it took place long before the animal died, in view of the traceless repair. If the loss is an acquired feature, it may point to an evolutionary trend toward loss of the premolars.

Both p3–4 are robust with a strong posterior accessory cuspid and a strong distal cingular projection; in addition, p4 has a second posterior cuspid. None of the premolars bears anterior cuspids as in *Lycaon*. There is a small diastema between p3 and p4 and the latter slightly overlaps m1 on its labial side. The tip of the p4 protoconid is higher than the tip of the m1 paraconid. The trigonid of m1 is wider than its talonid. There is a small metaconid. The hypoconid is strong and centrally positioned and there is a vestigial entoconid. The m2 is short and bears two
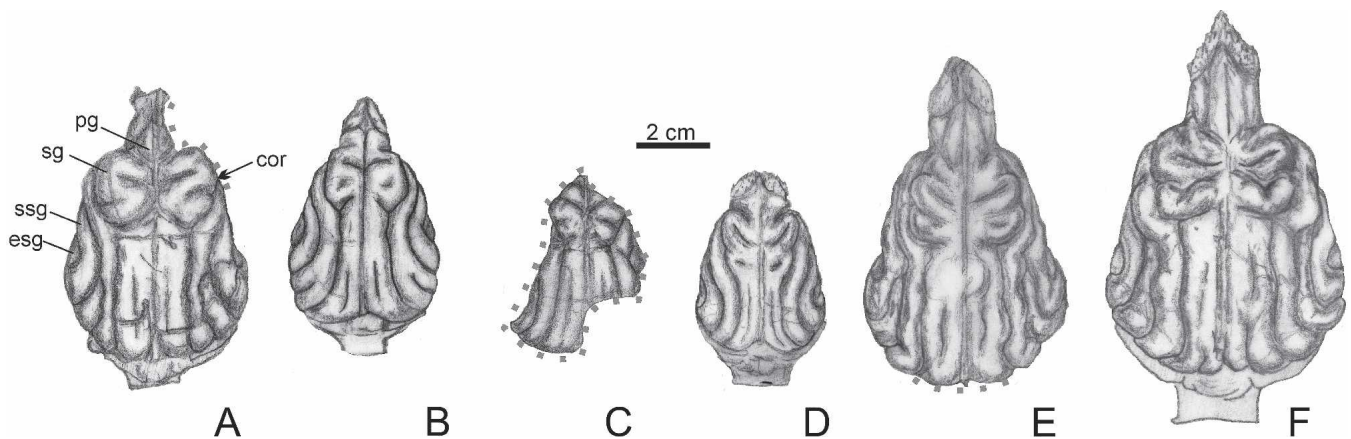
FIGURE 5. Dorsal view of the endocranial casts. **A**, *Cynotherium sardous* CB 84–8022; **B**, *Vulpes vulpes*; **C**, *Eucyon davisi* F:AM 63005; **D**, *Nyctereutes procyonoides*; **E**, *Xenocyon lycaonoides* GIN 3755–144; **F**, *Canis lupus*. **Abbreviations**: **pg**, proreal gyrus; **sg**, sigmoid gyrus; **ssg**, suprasylvian gyrus; **esg**, ectosylvian gyrus; **cor**, coronal sulcus.

cuspids: the protoconid and the metaconid. The former is much stronger than the latter, which is, however, considerably worn, possibly related to the antemortem loss of m3. The alveolus of m3 indicates the earlier presence of a small, single-rooted tooth (Fig. 6).

In summary the dental morphology of *Cynotherium* is very similar to that of *Xenocyon*. Differences from *Lycaon pictus* are that the latter lacks a vestigial endoconid on m1 and has anterior cuspids on p3-p4 (Tedford, Taylor and Wang, 1995). The cheek teeth of *Cynotherium* have an enlarged cutting section and a reduced grinding part. Similar cheek teeth are seen in canids that include significant quantities of meat in their diet, in other words, that are hypercarnivorous (Van Valkenburgh, 1991). These teeth are opposite to those with shortened shearing blades, combined with an enlarged and complex grinding part—a hypocarnivorous dentition.

Postcranial Skeleton

In general, all available vertebrae and limb bones of *Cynotherium* have very prominent muscle scars and more accentuated rugosities compared to canids of similar size. This has also been noted for the Channel Islands fox, *Urocyon littorals* (Hildebrand, 1954). In addition, all postcranial elements give a more robust and massive impression. This is common for many fossil island mammals (Sondaar, 1977; Van der Geer, 2005), and is also observed in the Channel Island fox (Hildebrand, 1954).

Vertebrae—The atlas shows, on the whole, a canine framework with, however, some important distinguishing features in its wings (Fig. 7F): They are expanded laterally as in *Canis*, *Cuon* and *Lycaon*; however, with reduced anterior parts, which gives the impression of a proportionally lesser cranio-caudal development. The dorsal openings of the transverse foramina are situated very close to the border of the caudal articular surface. The posterior tips of the atlas wings are clearly pointed, and not round as in other canids.

The axis (Fig. 7E), too, is canine in appearance, yet can be distinguished from other species by the following features: The posterior border of the spinous process is vertical and there is no tip for the attachment of the nuchal ligament. On the anteroventral border of the spinous process a tiny notch is present for additional insertion of the dorsal atlantoaxial membrane, not seen in any living canid, but seemingly present in *Hyaena hyaena* (as figured in Argot, 2003: fig. 10i).

Anterior Limb—The general shape of the scapula is canid-like. The cranial border, however, lacks the typical elliptical out-line, but changes direction about midway, forming angle (Fig. 7G), more or less similar to the condition observed in *Lycaon*. The attachment area for the M. triceps brachii on the scapula consists of the lower (caudal) border. The caudal border slopes gradually, and is broad as in *Cuon* and *Speothos*. A difference with *Cuon* is the more acute angle directly behind the glenoid in the latter. The acromion is large and triangular, and bears a large rugose surface for muscle insertion (Fig. 7L), much larger than in any living canid. Only in *Lycaon* and *Chrysocyon* is the acromion larger, but not to the extent seen in *Cynotherium*. The triangular shape is unique to *Cynotherium*; the other canids have a more or less ovate or drop-like shape.

The deltoid ridge on the humerus is large, sharp and high, and reaches almost to midshaft (Fig. 7A). The ridge functions as the insertion for the lateral head of the triceps. The scar for the M. deltoideus is located on the caudal surface of the posterior end of the deltoid ridge, which is rugose and large, larger than in any living canid. The tubercle for attachment of the M. teres minor is pronounced and well-developed (Fig. 7G). The posterior part of the greater tubercle of the humerus is only weakly developed.

Seen from above, the olecranon of the ulna is broad and square, and its attachment area for the M. triceps tendon is large (Fig. 7K). The two tubercles just in front of the olecranon on the processus anconeus of the ulna, one at the medial and the other at the lateral side, are present and well developed. Their height is low, but they are very broad, not slender and high as in most canids. The only exception is *Speothos*, in which the morphology of these two tubercles approaches the condition seen in *Cynotherium*. The trochlear notch is less deep than in the other canids, which makes it appear more open.

The maximal flexion in the humero-ulnar joint is greater than observed in *Canis*, *Cuon* and *Vulpes* (Fig. 7N; 40° in *Cynotherium*, approximately 60° in *Cuon, Canis* and *Vulpes*). This is due to an extension of the articular surface on the ulnar notch on the anterior side of the trochlea of the humerus.

The relative length and robustness of the metacarpals is comparable to that of *Canis aureus*. A short first metacarpal is present, as in all living *Canis* species and unlike *Lycaon pictus* (the only living canid with a tetradactyl forelimb).

Functional Deductions

Cynotherium has a low sagittal crest, a wide postorbital constriction, weak zygomatic arches and a slender mandible, that are features pointing to a lack of powerful masticatory muscles (Ewer, 1973). Features like these are typical of canids with a
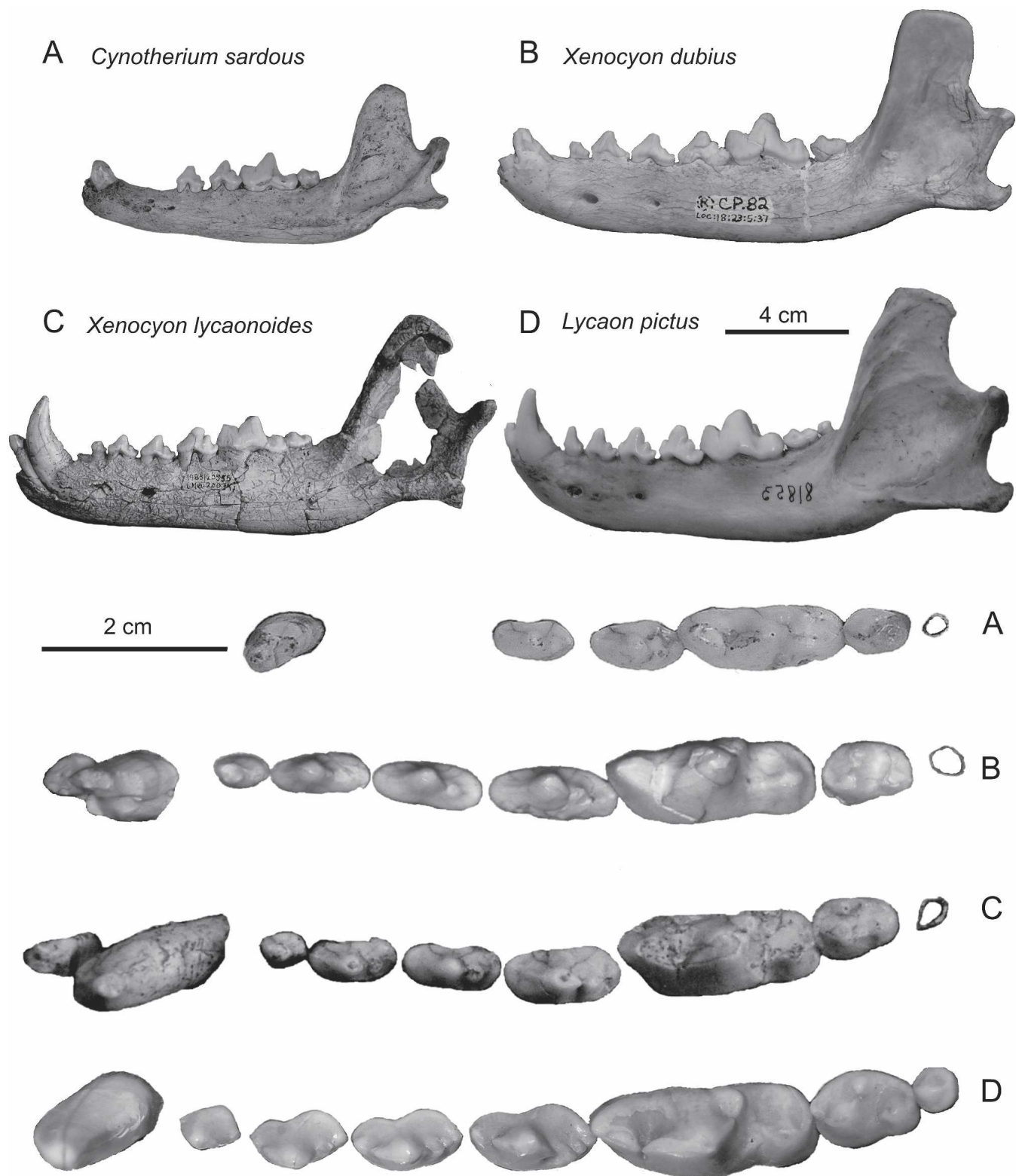
FIGURE 6.   Mandibles and lower dentition. **A**, *Cynotherium sardous* CB 84–8022; **B**, *Xenocyon dubius* IVPP CP 82; **C**, *Xenocyon lycaonoides* IQW 1985/20555; **D**, *Lycaon pictus* AMNH(M) 81853. The mandible of *Lycaon* is mirrored and the coronoid process of *Xenocyon dubius* is restored with plaster.

reduced carnassial dentition. This is in sharp contrast to the dentition of canids with a derived carnassial dentition, which hunt large prey. In these canids, this dentition goes together with craniofacial adaptations for resisting mechanical stresses that

arise during forceful mastication and killing of large prey. Two of the ratios used to estimate the possible prey size of carnivores (Fig. 8) are the relative resistance of the dentary to bending in the parasagittal plane and the relative lower molar grinding area

FIGURE 7. Postcranial elements of *Cynotherium.* **A**, *Cynotherium sardous* CB 84–84–2019 right humerus, dorsal, caudal, anterior and lateral view; **B**, *C. sardous* CB 84–2027 right ulna, anterior and lateral view; **C**, *C. sardous* CB 84- n.n. right radius, dorsal and caudal view; **D**, *C. sardous* CB 84–2045 left tibia anterior view; **E**, *C. sardous* CB 84–2019 axis lateral view; **F**, *C. sardous* CB 84–2028 atlas, dorsal and ventral view; **G**, *Cynotherium sardous* CB 88–1034 left scapula lateral view. **K**, *Cynotherium sardous* CB 84–2027 right ulna dorsal view; **L**, *Cynotherium sardous* CB 88–1034 acromion of the left scapula; **M**, *Cynotherium sardous* CB 88–14.767 lateral view of the left humerus head; **N**, angle of maximum flexion of the elbow of *Cynotherium sardous.*

(Van Valkenburgh and Koepfli, 1993; Van Valkenburgh, Sacco and Wang, 2003). If we plot these two ratios in a diagram (Fig. 8), we see that *Xenocyon, Cuon, Lycaon, Canis lupus, Canis* cf. *falconeri* and *Speothos* (which have robust mandibles and small grinding areas) are clearly separated from the other taxa. The living representatives of the former group are able to attack animals larger than themselves. The members of the latter group on the other hand hunt only small prey.

From the diagram (Fig. 8) it appears that *Cynotherium* has the lowest grinding area, but not a massive mandible. *Cynotherium* plots with the other canids, though on the very right of the group. Based on this, we conclude that *Cynotherium* hunted small prey only. For Sardinia this implies *Prolagus* and birds. These animals were abundant on Sardinia (Klein Hofmeijer, 1996 for *Prolagus*, and Sondaar (1998, unpubl. report on Orosei) for birds).

ORIGIN OF *CYNOTHERIUM*

As noted previously, a number of mainland canid species have been proposed as the possible ancestor of *Cynotherium*, actually covering what is phylogenetically possible for any Eurasian dog. This is for two reasons; firstly, the strong impact of endemism obscures phylogeneticaly informative characters shared with mainland species, and secondly, the time of the arrival on the island is as broad as the entire canid history in Eurasia, since Sardinia-Corsica was repeatedly colonized from the Late Miocene till the Late Pleistocene (Ginesu and Cordy, 1997; Van der Made, 1999; Sondaar, 2000; Sondaar and Van der Geer, 2005). Therefore, the absence of concrete evidence has led to an unresolved controversy concerning *Cynotherium*'s origin.

The only phylogenetic position that is agreed upon is that *Cynotherium* has all the morphological features that distinguish the Canini (dogs) from the Vulpini (foxes): all known Canini have a frontal sinus (Huxley, 1880; Berta, 1988; Tedford, Taylor and Wang, 1995), lack the lateral flare and eversion of the dorsal border of the orbital part of the zygomatic bone (Tedford, Taylor and Wang, 1995), and have a very well-developed proreal gyrus on the brain, which is bilaterally constricted (Radinsky, 1973; Lyras and Van der Geer, 2003). A further division of the Canini is based upon morphological studies (e.g. Berta, 1988; Rook, 1993, 1994; Tedford and Qiu, 1991; Tedford, Taylor and Wang, 1995), suggest that the Canini is divided into three groups: the South American canids (including *Nyctereutes*), the *Eucyon*-like species of the Neogene, and the *Canis*-like species (which include *Canis, Xenocyon, Lycaon,* and *Cuon*). Members of all three groups have been suggested as the possible ancestor of *Cynotherium*.

To further constrain the phylogenetic position of *Cynotherium*, we critically examine the suggestions of previous authors, guided by reference studies on canid evolution (Berta, 1988; Rook, 1993; Van Valkenburgh and Koepfi, 1993; Tedford, Taylor and Wang, 1995; Wayne et al., 1997, Sotnikova, 2001; Lyras and Van Der Geer, 2003; Van Valkenburgh, Sacco and Wang, 2003).

Nyctereutes as the Ancestor

The proportions and general appearance of the *Cynotherium* skull resemble those of *Nyctereutes*. Based on this similarity Van der Made (1999) suggested that *Nyctereutes* could be its ancestor. However, this resemblance is only superficial, as several cranial features distinguish *Cynotherium* from *Nyctereutes*. For example, in *Cynotherium* the maxillary bones lack the shallow depression on their frontal process anterior to the orbit, the parasagittal crests are low, the sagittal crest is weak and the mandible lacks the subangular lobe. *Nyctereutes*, on the other hand, has strong sagittal and parasagittal crests and the subangular lobe is always present (Tedford and Qiu, 1991). Additional differences can be found in the dentition: the grinding section in *Nyctereutes* is far more developed than the cutting section (Ficcarelli, Torre and Turner, 1985), a situation opposite to that observed in *Cynotherium*. Finally, *Nyctereutes* lacks a second cusp on its p3, contrary to *Cynotherium*.

An *Eucyon*-like Ancestor

A second possibility is that *Cynotherium* is an independent evolutionary lineage, originating from an *Eucyon*-like animal, which developed characters of the *Canis* group during its long isolation under island conditions. Such an origin (from *Eucyon monticinensis*) has been suggested by Van der Made (1999). There are, indeed, four features of *Cynotherium* reminiscent of *Eucyon*: the frontal sinus is small, the zygomatic arches are slender and slightly arched, the supraoccipital shield is fan-shaped and the anterior limbs are relatively short. This anterior short-
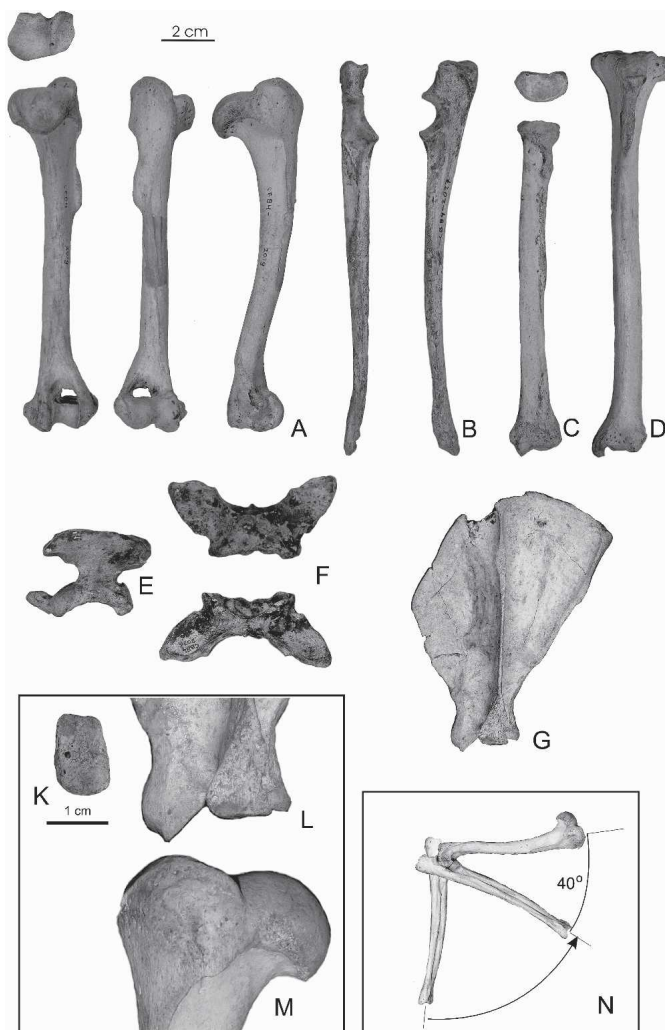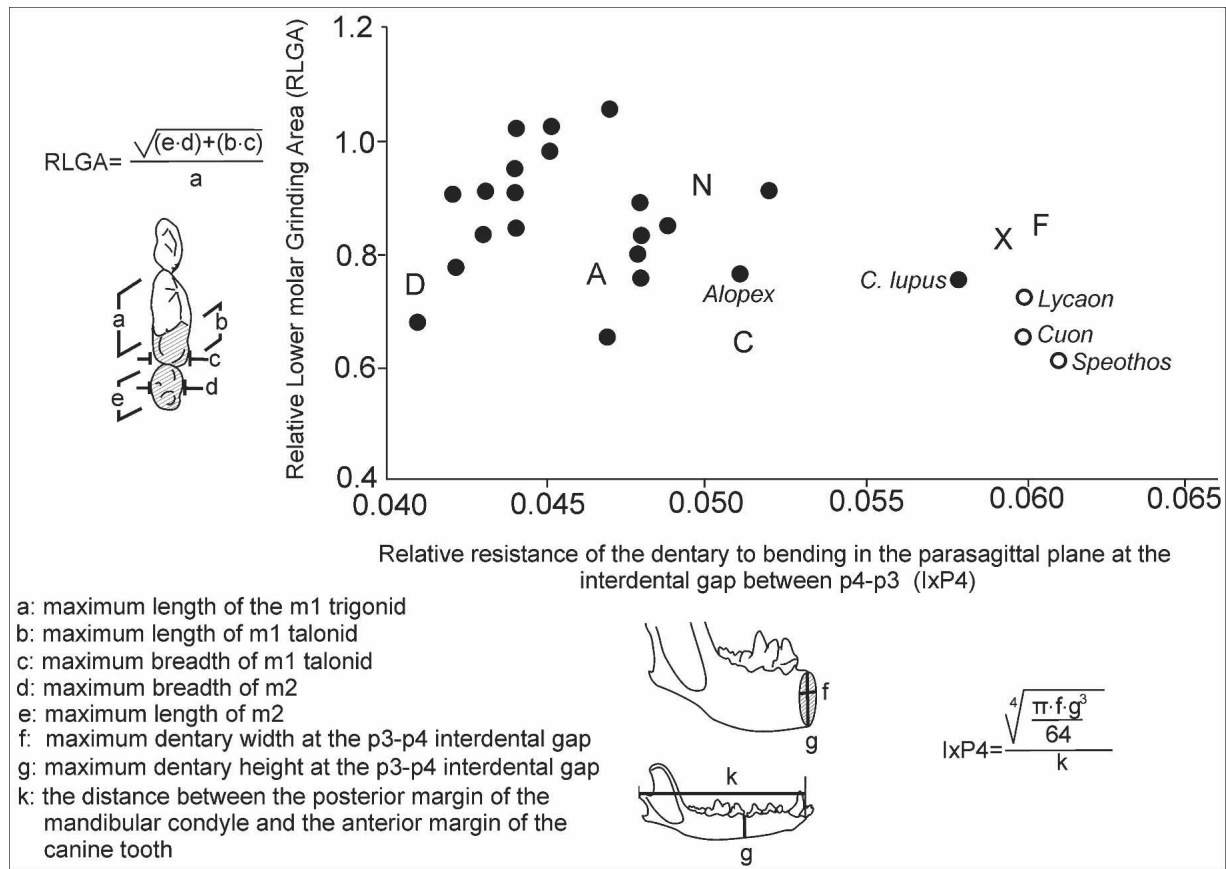
FIGURE 8. Plot of relative lower molar grinding area (RLGA) against relative resistance of the dentary to bending in the parasagittal plane as estimated by the second moment of area of the dentary relative to dentary length at the interdental gap between the third and fourth lower premolars (IxP4). The two ratios have been developed by Van Valkenburgh and Koepfli (1993) for an analysis concerning craniodental adaptations in living canids. Fossil canids: C: *Cynotherium sardous* CB 84–8022 (RLGA = 0.643, IxP4 = 0.051); X: *Xenocyon dubius* IVPP CP82 (RLGA = 0.827, IxP4 = 0.059); F: *Canis* cf. *falconeri* F:AM 97051 (RLGA = 0.849, IxP4 = 0.060); N: *Nyctereutes sinensis* F:AM 96792 (RLGA = 0.916, IxP4 = 0.0496); A: *'Canis' adoxus* NMB-Rss-45 (RLGA = 0.764, IxP4 = 0.046); D: *Eucyon davisi* F:AM 129013 (RLGA = 0.737, IxP4 = 0.041). Living canids (data from Van Valkenburgh and Koepfli, 1993): filled circles represent canids with a bicuspid talonid; open circles represent canids with a trenchant heel on the talonid.

ness is inferred from the ratio radius/tibia, which is less than 80% in *Eucyon* (Rook, 1992), more than 90% in *Canis* (Tedford, Taylor and Wang, 1995), and 85% in *Cynotherium* (Figs. 7C and 7D). However, though these features are shared with the more primitive members of the Canini, they are more likely the result of *Cynotherium*'s adaptation to the island environment, and thus constitute a parallel development. In addition, if the hypothesis of an origin from *Eucyon* is correct, then we have to assume that during the Late Miocene- Pliocene a primitive member of the Canini became isolated on Corsica-Sardinia, and independently developed characters which are typical for the derived *Canis*-like dogs of the rest of the world. Although such a case of parallel evolution is not impossible, it is less probable, especially because it is not just one feature that is paralleled, but several.

A *Canis*-like Ancestor

Many dental and cranial features that are typical of the *Canis*-like species (Berta, 1988; Tedford, Taylor and Wang, 1995) are found in *Cynotherium* (Fig. 9): the paroccipital process expands posteriorly from the bulla, and has a free tip, I3 is enlarged with a posterior cingulum, p4 has two posterior accessory cusps, the M1 paracone is larger than the metacone, the angular process of the jaw is hooked and the fossa for the insertion of the superior

branch of the pterygoid muscle is larger than that for the inferior (type "C" of Gaspard, 1964).

Additional characters can be seen in its external brain anatomy: there is a lateral expansion of the sigmoid gyri, and the proreal gyrus is bilaterally compressed, a combination seen only in *Canis*-like species (Lyras and Van der Geer, 2003).

Most authors agree that *Cynotherium* is related to the *Canis*-like species, yet its exact phylogenetic position within this group is still a matter of discussion. What seems to be the source of most disagreements is its dentition (see previous description). Based on its dental morphology, some authors consider *Cynotherium* to be related either to *Cuon* or to *Xenocyon* (Forsyth Major, 1900; Malatesta, 1962, 1970; Schütt, 1974; Bonifay, 1971), both of which have a trenchant heel on the m1 talonid. Others, based on the assumption that such a unicuspid talonid in itself has but little taxonomic value, since it appeared several times in canid history (Van Valkenburgh, 1991), have suggested that *Cynotherium* originates from *Canis* (Azzaroli, 1977; Kotsakis, 1980; Eisenmann, 1990; Van der Made, 1999; Eisenmann and Van der Geer, 1999). Consequently, *Cynotherium* should then originate from an ancestor with a bicuspid talonid on m1, which later, once on the island, became reduced to a unicuspid talonid.
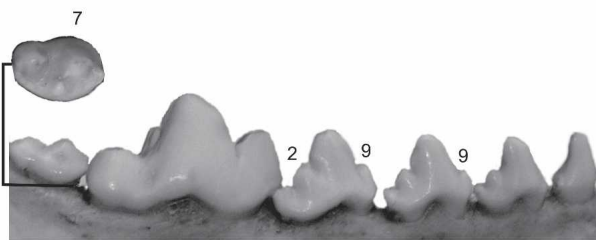
In our view, a key step toward a better understanding of the phylogenetic position of the Sardinian dog is the observation,
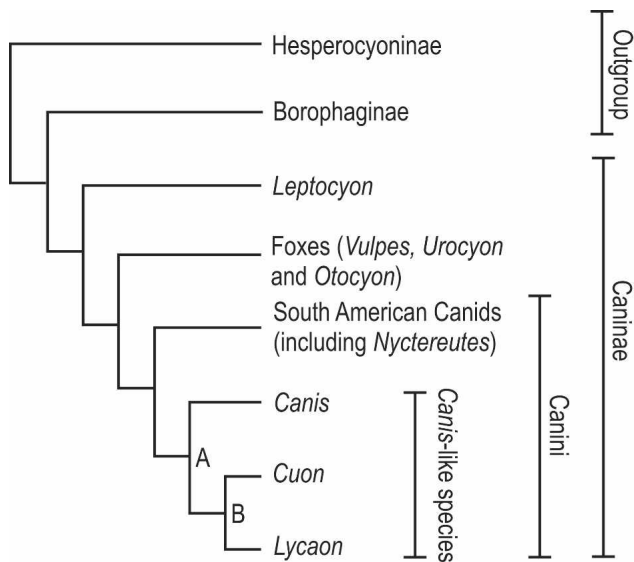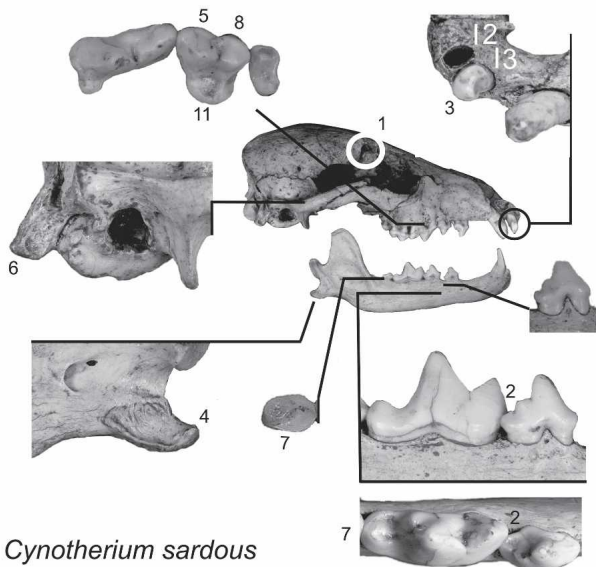
that although it has a hypercarnivorous dentition, its cranial characters differ from those that are typical for hypercarnivorous taxa. The latter all have broad muzzles, strong and wide zygomatic arches, well-developed sagittal crests and deep mandibles (Van Valkenburgh and Koepfli, 1993; Van Valkenburgh, Sacco and Wang, 2003). As we saw above, *Cynotherium* lacks all these characters: it has a narrow anterior point of the muzzle, weak and narrow zygomatic arches, a very low sagittal crest, and a slender mandible.

This enigmatic combination of a hypercarnivorous dentition and a hypocarnivorous skull can be explained in two ways.

(1) *Cynotherium* originates from a hypo- or mesocarnivorous ancestor, and developed a hypercarnivorous dentition on the island. The problem here is that never in canid history has a species developed a hypercarnivorous dentition without the associated cranial characters (see for descriptions of the species Berta, 1988; Rook, 1993; Schütt, 1974; Wang, 1995; Wang, Tedford and Taylor, 1999). These special cranial adaptations are necessary to avoid damage to the skull due to the heavy loads applied to it during the killing and eating of the prey (Van Valkenburgh and Koepfi, 1993; Biknevicius and Van Valkenburgh, 1996).

(2) *Cynotherium* originates from a hypercarnivorous ancestor, and developed hypocarnivorous cranial characters on the island. In this scenario, the dental morphology of *Cynotherium* reflects the retention of an ancestral character. There are only three Old Word mainland canid genera known, that developed hypercarnivory: *Xenocyon*, *Cuon*, and *Lycaon*. As living, as well as fossil *Cuon* lack the m3, *Xenocyon* and *Lycaon* are the most probable ancestors. Other features of the mandible of *Cynotherium* are shared by both *Xenocyon* and *Lycaon*, such as straight tooth row, position and number of mental foramina (see previous description). *Xenocyon* and *Lycaon* are related taxa (Rook, 1994; Wang et al., 2005). *Xenocyon* resembles *Lycaon* in dental morphology, whereas its cranial structure shows *Canis*-like features. At the same time it differs from the similarly sized *Canis lupus*, as well as from *Lycaon* in a series of primitive cranial features (Sotnikova, 2003). The systematic and evolutionary positions of *Xenocyon* and *Lycaon* are not yet solved, and therefore we opt for *Xenocyon* on the basis of two selection criteria. One is a weak criterium: geography. With the exception of a single specimen from Israel (Stiner et al., 2001), *Lycaon* is restricted to Africa,

A Cladogram of the Caninae

B *Cynotherium sardous*

C *Lycaon pictus*

D *Xenocyon lycaonoides*

←

FIGURE 9. Cladogram of the Canidae (**A**) and views of certain anatomical characters of *Cynotherium sardous* (**B**), *Lycaon pictus* (**C**), and *Xenocyon lycaonoides* (**D**). The cladogram shows the phylogenetic relationships of genera within Caninae and has been adapted from Tedford et al. (1995). *Canis*-like species (node A) are united by the following characters: large frontal sinus that penetrates the postorbital processes (indicated by number 1 on the figure), presence of a second posterior cusplet on p4 (number 2), enlargement of I3 relative to I2 (number 3), enlarged angular process with a dorsal hook and with a fossa for the insertion of the superior branch of the pterygoid muscle larger than that for the inferior (number 4), reduced M1-M2 buccal cingulum, larger M1-M2 paracone relative to the hypocone (number 5), posteriorly expanded paroccipital process with a free tip (number 6), supraoccipital shield triangular in shape and the inion overhanging the condyles. *Cuon* and *Lycaon* (node B) are united by reduced endoconid and metaconid on m1 and m2 (number 7), reduced buccal cingulum and hypocone on M1-M2 (number 8), relatively small canines, and a wide palate. Furthermore, *Cuon* lacks m3 and the endoconid and metaconid on m1 are even more reduced and *Lycaon* has an even wider palate, large multicuspid premolars (number 9) and reduction of the pollex. *Xenocyon* and *Cynotherium* are not represented in the Tedford et al. (1995) cladogram, as their study emphasized on the living Caninae. From the characters listed above, it becomes evident that they are both members of the *Canis*-like clade, although not so derived as *Cuon* (as an m3 is present) and *Lycaon* (as their premolars do not have anterior cusplets).

while *Xenocyon* has a wide Eurasian distribution, ranging from China to England (Sotnikova, 2001). The other is based on dentition: *Lycaon* has strong anterior cusplets on p3-p4 (Tedford, Taylor and Wang, 1995), whereas such cusplets are not present in either *Xenocyon* or *Cynotherium* (Figs. 6 and 9).

From the previous discussion, it is clear that *Cynotherium* is a derived member of the *Canis*-like canids (Fig. 9). Dental and mandibular characters indicate that *Xenocyon* is the ancestor of *Cynotherium*. This implies that *Xenocyon* must have come to the island Sardinia-Corsica somewhere during the late Early–Middle Pleistocene because it is from that period that *X. lycaonoides* is recorded at several Eurasian localities (Sotnikova, 2003). This is in accordance with the faunal record of Sardinia, because *Cynotherium sardous* belongs to the *Tyrrhenicola-Megaloceros*-fauna of the late Middle to Late Pleistocene (Sondaar et al., 1986; Sondaar and Van der Geer, 2005). There is evidence (two parts of a humerus) of a *Cynotherium* sp. in Sardinia-Corsica from the Middle Pleistocene of Capo Figari, North Sardinia (Van der Made, 1999).

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