Adaptations of the Pleistocene island canid *Cynotherium sardous* (Sardinia, Italy) for hunting small prey

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**Summary**

*Cynotherium sardous* is a small canid that lived on the island of Sardinia-Corsica during the Pleistocene. Once on the island, the species gradually adapted, and became specialized in hunting small prey like the lagomorph *Prolagus*. Moreover, in order to fulfil mass-related energetic requirements, the species had to reduce body size compared to its ancestor *Xenocyon*, which was larger than the grey wolf. *Cynotherium* carried its head much in the way foxes do, and was able to hold its body low to the ground when stalking. In addition, it could move its head laterally better than any living canid.

**Samenvatting**

*Cynotherium sardous* is een kleine hondachtige, die leefde op het eiland Sardinië-Corsica gedurende het Pleistocene. Eenmaal op het eiland paste de soort zich aan en specialiseerde zich in het jagen op kleine prooi zoals de haasachtige *Prolagus*. Om aan de energiebehoefte, gerelateerd aan lichaamsgewicht, te voldoen, moest de soort kleiner worden, vergeleken met zijn voorouder, *Xenocyon*, die groter was dan de huidige grijze wolf. *Cynotherium* hield zijn hoofd ongeveer zoals vossen doen, en hield het lichaam laag bij de grond bij het besluiten van de prooi. Daarbij kon hij zijn kop verder zijwaarts bewegen dan alle nu levende hondachtigen.

**Introduction**

When we hear about insular island mammals, we immediately make associations with pig-sized hippo’s, mini-mammoths, giant rodents, deer adapted for mountain climbing, apart from the scientific names of several Plio-Pleistocene insular ungulates and micro-mammals. We all think of the well-established model according to which mammals reached the islands by swimming or rafting. Once there, due to limited resources and the absence of terrestrial mammalian predators, their descendants gradually became adapted to the island environment by a change in body plan in several ways, e.g. by reducing or increasing their size, fusion of limb bones, etcetera.

That is in general true, but not in all cases. There are, for example, cases of mammalian predators that lived on islands. Such cases in the first instance disturb the nice picture. However, their study provides us with a better and more complete picture of island mammal evolution, not only because more and different taxa are involved, but also because of their relation with the other endemic animals on the island. It appears from such studies that also mammalian predators follow the earlier observations, and thus that also they show adaptations to the peculiar island environment.

![The studied skeleton of Cynotherium sardous (missing parts in white). The background outline represents the size of its ancestor Xenocyon lycanooides (based on data from Sotnikova, 2001).](image-url)
characterized by more faunal changes and a greater diversity than any other island with insular mammals (table 1). Of particular interest of all the Sardinian-Corsican extinct mammals, are the carnivores. Fossils of several carnivore groups have been recovered from Sardinia-Corsica: the hunting hyaena *Chasmaporthetes melei*, the canid *Cynotherium sardous*, and several otters (*Algarolutra majori, Sardolutra ichnusae, Enhydrictis galictoides, Megalenhydris barbaricina*).

*Cynotherium sardous* fossils are found in relatively large numbers, including not only skulls and dentition, but also postcranials. This species can therefore be studied in more detail. *Cynotherium* is a small canid with dental characters that are typical for hypercarnivorous canids (i.e., canids that include significant quantities of meat in their diet and prey mostly on large animals). Its cranial characters, however, indicate that it was not able to hunt large prey. A recent phylogenetic analysis by Lyras et al. (in press), led to the conclusion that *Cynotherium* originates from *Xenocyon lycaonoides*, a large-sized dog, related either to some extinct wolves (Wang et al., 2005) or to the Cape hunting dog, *Lycaon pictus* (Martinez-Navarro & Rook, 2003). *Xenocyon* reached Sardinia-Corsica at the end of the early Pleistocene and once isolated, it became a small and specialized small-prey hunter (Lyras et al., in press).

**Materials and Methods**

Here we present the results of the morphofunctional analysis of a *Cynotherium* skeleton that was excavated in Corbeddu Cave (Lanaittu Valley, Nuoro, Sardinia, Italy; see also Van der Geer & Van der Geer, 2001). The skeleton is fairly complete (fig. 1) and in an excellent state of preservation. The fact that the material belongs to one individual, provides an excellent opportunity for morphofunctional analysis. For the description of the skeleton we follow the nomenclature of Evans (1993). Data on the myology of the living canid species have been taken from Langguth (1969) and Evans (1993). To check these data and to see the nature of the different muscles and tendons, we dissected a red fox (*Vulpes vulpes*) and a domestic dog (*Canis familiaris*).

In order to investigate the functional significance of the observed features we followed the form-function correlation method of analysis. This method extrapolates the correlation that is observed between anatomical forms and certain functions or behaviours of living animals to the

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**Fig 2** Greatest width of the distal end of the humerus of *Xenocyon lycaonoides* from Stránska Skála, Czech Republic, and Undermassfeld, Germany (data from Sotnikova, 2001), compared with *Cynotherium* spp. from Sardinia: C. sp. NMB Ty-5362 from Capo Figari (data and photograph from van der Made, 1999), *C. sardous* from Dragonara Cave (data from Malatesta, 1970) and from Corbeddu Cave (CB 84-8022).

Grootste breedte van het onderuiteinde van het opperarmbeen van *Xenocyon lycaonoides* van Stránska Skála, Tsjechië, en Undermassfeld, Duitsland (data uit Sotnikova, 2001), vergeleken met *Cynotherium* spp. van Sardinië: C. sp. NMB Ty-5362 van Capo Figari (data en foto uit Van der Made, 1999) en *C. sardous* van de grot Dragonara (data uit Malatesta, 1970) en de grot Corbeddu (CB 84-8022).
fossil species (Radinsky, 1987). In order to do so, we compared the morphology of the Corbeddu skeleton with specimens from most living canid species (see table 2).

Material of the living and of the fossil species was studied at and belongs to the following institutes: AMNH(M): American Museum of Natural History, Department of Mammalogy New York, USA; CB: Corbeddu Cave, Sardinia, Italy; FMNH: Field Museum of Natural History, Chicago, USA; MNHN: Muséum National d’Histoire Naturelle, Paris, France; NMB: Naturhistorisches Museum Basel, Switzerland; NNML: Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands.

Size reduction

Findings of Cynotherium in Corsica are limited (Robert & Vigne, 2001), but Sardinia has many localities with fossil remains of that canid. The oldest remains found till now come from breccia deposits on Capo Figari, Sassari (Van der Made, 1999) and from fissure fillings at Monte Tuttavista near Orosei, Nuoro (Abbazzi et al., 2005). A stratigraphically younger locality is Dragonara Cave, Sassari, from which material belonging to several Cynotherium, individuals has been excavated (Malatesta, 1970). The youngest material comes from Corbeddu Cave near Oliena, Nuoro (hall II and hall IV, see Van der Geer & Van der Geer, 2001). The skeleton from hall II, under study here, is the youngest Cynotherium specimen (Klein Hofmeijer, 1996) known till now. Its postcranial is of a smaller size than any specimen from Dragonara (fig. 2). The latter specimens are in turn smaller than the humerus from Capo Figari.

Although the data are limited, it is tempting to suggest that they provide us with an indication of size reduction of Cynotherium through time. The phenomenon of size reduction becomes even more evident when we compare Cynotherium with its probable mainland ancestor. As shown in figure 2, the humeri of Xenocyon (data from Sotnikova, 2001) are considerably larger than those of Cynotherium.

In theory, body mass can be estimated with the use of a number of dental and skeletal measurements (Damuth & MacFadden, 1990). In dwarf forms, however, dental measurements are not reliable in such estimations, as their relation with body proportions differs essentially from those of their mainland relatives (e.g. Sondaar, 1977; Lister & Davies, 2003). Thus, the body mass of Cynotherium can only be estimated based on postcranial elements. The method based on the circumference of the femur at the midshaft, developed by Anyonge (1993), gives the best estimation of body mass in living canids. Applying this method results in a body mass for Cynotherium from Corbeddu Cave of approximately 10 Kg, which is the size of an average jackal.

Reduction in body size is a common phenomenon in island ungulates, combined, amongst others, with changed interlimb ratios and the tendency of distal elements to fuse. This phenomenon coincides with a simultaneous absence of large mammalian predators and limited food resources (Sondaar, 1977). Cynotherium, on the other hand, is not an ungulate but a predator, and thus may have followed a different evolutionary path on the island. What seems to have followed the ungulate pattern is its size reduction. It is known that the size of a carnivore is closely related to that of its prey (Carbone et al., 1999). According to them, in order to fulfil mass-related energetic require-

Fig 3 Comparison of the skulls of Xenocyon lycaonoides (a, b and c) from Venta Micena (Spain) and Cynotherium sardous (d, e and f) from Corbeddu cave. The drawings of Xenocyon are based on the illustrations by Palmqvist et al. (1999).

Vergelijking van de schedels van Xenocyon lycaonoides (a, b en c) van Venta Micena (Spanje) en Cynotherium sardous (d, e en f) uit de grot Corbeddu, Sardinië. De tekeningen van Xenocyon zijn gebaseerd op de illustraties van Palmqvist et al. (1999).
ments, large-sized carnivores prey on large animals (near predator’s mass) while smaller carnivores feed on small prey (less than half of predator’s mass). As we noted in Lyras et al. (in press), the cranial characters of Cynotherium (weak zygomatic arch, low sagittal crest, thin mandible; fig. 3) suggest that it was not able to hunt big game. From the diagrams of Carbone et al. (1999), it appears that carnivores smaller than 21 kg hunt prey smaller than half their own size. The body mass of 10 kg for Cynotherium falls well within the range of Carbone et al.’s (1999) small prey hunters.

**Locomotor adaptations**

Most morphological features that can be observed in Cynotherium can be found also in one or more living canids; in other words, they fall within the morphospace of the living canids. As there is no significant substantial diversity in locomotor patterns present in the living canids (Van Valkenburgh, 1985; Andersson, 2003), the pattern in Cynotherium could not have been much different from those seen in the living canids. There are, however, some unique morphological features in the neck and anterior limb of Cynotherium that are not seen in other canids. These features are the only ones that, in our view, could shed some light on particular adaptations of Cynotherium.

**Neck mobility and position**

Apart from the unusual combination of cranial and dental characters, the skull of Cynotherium has another peculiarity: its mastoid process is much enlarged and is situated laterally, being more or less a continuation of the nuchal crest (Lyras et al., in press). The mastoid process is the place of insertion for several muscles. Most of the surface of the process is occupied by the insertion of the M. obliquus capitis cranialis, and lateral to this area are the insertions for M. splenius, and two other neck muscles.

The M. obliquus capitis cranialis continues its insertion further upward on the dorsal nuchal line. The function of this muscle is to extend the insertion further upward on the dorsal nuchal line; its other insertion is situated on the spinous processes of the first thoracic vertebra. Its function is raising the head and entire neck.

The overall picture indicates that Cynotherium had stronger neck movements than any of the living canids. This includes rotation, extension and flexion of the atlanto-occipital joint and raising and lowering of the head.

**Anterior limb**

The very tip of the atlas is sharp and prominent in Cynotherium (fig. 4). It is the insertion point for the tendon of the M. omotransversarius. This muscle draws the limb forward; it is only a flat narrow muscle in Canis and Vulpes, but it appeared to have been stronger and more important in Cynotherium. The other insertion point of this muscles lies on the scapular spine just proximal to the acromion (figs. 4 and 5). This area is enlarged in Cynotherium, though this may equally be due to a larger insertion area for the M. deltoideus (see below).

The large, high and rugose scar for the M. deltoideus at the caudal surface of the posterior end of the deltoid ridge of the humerus indicates that this muscle was important; the same can be inferred from its insertion on the scapula. Its action is lifting of the humerus and flexion of the shoulder (fig. 5). Another shoulder flexor is the M. teres minor. The scar for this muscle insertion is well-developed in Cynotherium.

The well-developed attachment areas for the triceps on the scapula, humerus and ulna indicate that this muscle was important in Cynotherium, more so than in any other canid (fig. 5). Its...
function was assisted by an equally well-developed *M. anconeus*, which is also an extensor of the elbow. In view of the pronounced tubercles, the two main extensors of the elbow are stronger in *Cynotherium* than in *Canis* and *Cuon*. To sum up, flexion of the shoulder and extension of the elbow was very powerful in *Cynotherium*. The forward motion of the anterior limb may also have been more developed than in living canids. If we take into account that the elbow joint of *Cynotherium* has a higher maximal flexion than observed in *Canis*, *Cuon* and *Vulpes* (Lyra et al., in press), it is clear that the elbow extensors needed to work more for the same end result.

The powerful shoulder flexion and elbow extension, together with the relatively flexed elbow,
points to stalking behavior with a lowered body and a lowered neck and head.

**Interpretation**

The increased extension power of the elbow joint and flexion of the humero-scapular joint of *Cynotherium* fits a stalker. When we take the lowered neck and the more flexed elbow into account, the picture arises of a canid which with...
its body and neck held low to the ground followed his prey. The strong flexors of the shoulder point to powerful, sudden forward thrusts to grab the prey. The increased power of the neck musculature indicates fast or strong movements of the neck, which is needed in cases where the prey escapes with random movements or in zigzag-patterns. The dentition of *Cynotherium*, together with its cranial features, indicates specialization on small prey. At present, canids that hunt small terrestrial animals use stalking to approach their prey. This is well-known for foxes (Ewer, 1973), but has also been reported for the Simenian wolf (Sillero-Zubiri & Gottelli, 1995, see also fig. 6) and occasionally coyotes (Fox, 1969). Most canids catch birds from time to time (Ewer, 1973), but a canid which mainly fed on birds was the Falkland wolf *Dusicyon australis* (Mivart, 1890), a recently extinct island canid. This species had strongly developed mastoid processes comparable to those of *Cynotherium*. As it became extinct before the turn of the 19th century (Nowak & Paradiso, 1999) unfortunately almost nothing is known about its hunting behavior.

As already noted above, none of the living canids has a truly specialized locomotion or neck mobility. This means that when we observe that some of the anatomical features of the anterior limb and neck of *Cynotherium* are beyond the degree seen in the living canids, it is likely that its behaviour was more specialized than that of any living canid. Based on the skeleton of *Cynotherium sardous*, we conclude that this species performed a similar stalking with lowered body while hunting small, swift animals and the same fast lateral head movements as living canids do, but to a much higher degree. *Cynotherium sardous* was a small-sized highly specialized hunter of small, swift prey (fig. 7).

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Table 1. Fauna list of Pleistocene of Sardinia. Cava 6, 7 and 10 are fissure deposits at Monte Tuttavista near Orosei, Nuoro (after Sondaar, 1998; added are species names for *Chasmaportheses melei* and *Sus sondaari*).

| Faunalijst van het Pleistoceen van Sardinia. Cava 6, 7 en 10 zijn spleetopvullingen in de berg Mone Tuttavista dichtbij Orosei, Nuoro (naar Sondaar, 1998; toegevoegd zijn de soortnamen voor *Chasmaportheses melei* en *Sus sondaari*). |
|---|---|---|
| **Pleistocene** | **Early** | **Middle** | **Late** |
| Cava 6 | Cava 10 | Cava 7 and Corbeddu |
| *Cynotherium* sp. | X | ? |
| *Cynotherium sardous* | X | X |
| *Macaca majori* | X | X |
| *Talpa tyrrenica* | X | X |
| *Nesiotes similis* | X | X | X |
| *Prolagus figari* | X |
| *Prolagus sardus* | X | X |
| Leporidae | X |
| *Tyrhenicola sondaari* | X |
| *Tyrhenicola henseli* | X | X |
| *Rhabapodemus minor* | X | X |
| *Rhabamys orthodon* | X |
| *Chasmaportheses melei* | X |
| Mustelidae sp.1 | X |
| Mustelidae sp.2 | X | X |
| *Nesogoral melonii* | X |
| *Nesogoral sp.2* | X |
| *Sus sondaari* | X |
| “*Megaloceros* cazioti” | X |
| Caprinae | X |
Table 2. List of extant canid skeletons used in this study. Note: *Dusicyon australis* is represented only by skulls, no postcranials have been preserved.

Lijst van skeletten van tegenwoordige hondachtigen die gebruikt zijn in deze studie. Opmerking: van *Dusicyon australis* zijn alleen schedels bewaard gebleven.

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