

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 Pleistoceen. 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 energiebehoeften, 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 besluipen 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.

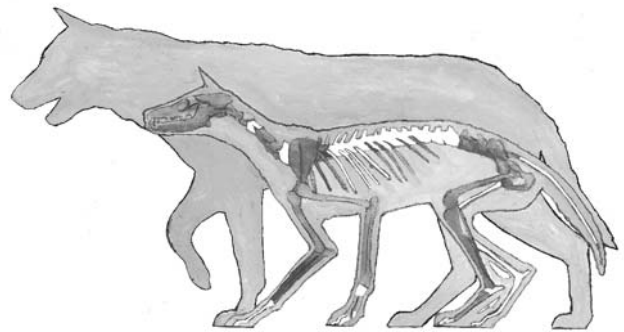


Fig 1 The studied skeleton of *Cynotherium sardous* (missing parts in white). The background outline represents the size of its ancestor *Xenocyon lycaonoides* (based on data from Sotnikova, 2001).

Het bestudeerde skelet van *Cynotherium sardous* (ontbrekende delen in wit). Het achtergrondprofiel stelt de grootte van zijn voorouder, *Xenocyon lycaonoides*, voor (gebaseerd op data uit Sotnikova, 2001).

The most promising place to study an insular mammalian predator is provided by the islands of Sardinia (Italy) and Corsica (France). From the Late Miocene to the Late Pleistocene, these two islands, which were for most of their geological history connected with each other, were repeatedly colonized by mammals (Sondaar & Van der Geer, 2005), and as a consequence, the fossil record of Sardinia-Corsica is

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*, *Enhydriactis galictoides*, *Megalenhydriactis 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 Cobeddu 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

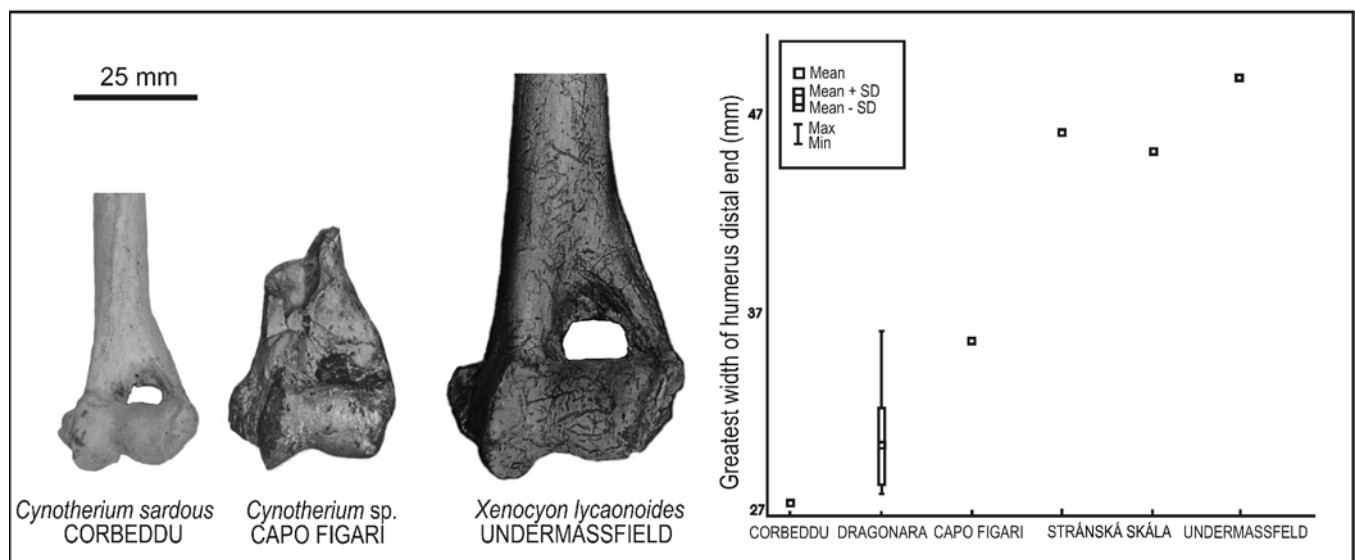


Fig 2 Greatest width of the distal end of the humerus of *Xenocyon lycaonoides* from Stránska Skála, Czech Republic, and Undermassfeld, Germany (data from Sotnikova, 2001), compared with *Cynotherium* spp. from Sardinia: *C. sp.* NMB Ty-5362 from Capo Figari (data and photograph from van der Made, 1999),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

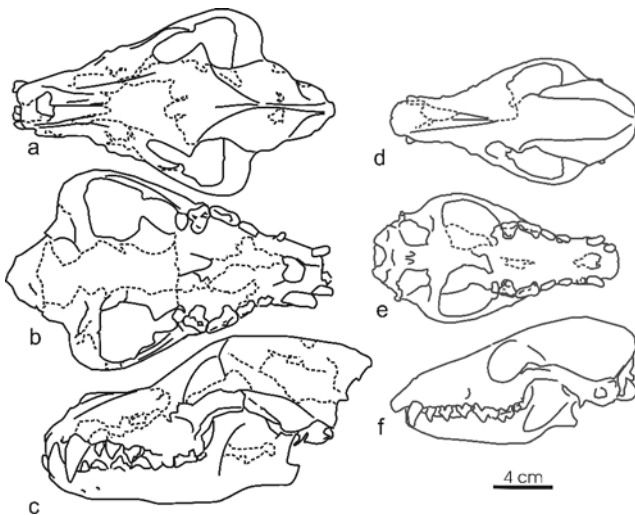


Fig 3 Comparison of the skulls of *Xenocyon lycaonoides* (a, b and c) from Venta Micena (Spain) and *Cynotherium sardous* (d, e and f) from Corbeddu cave. The drawings of *Xenocyon* are based on the illustrations by Palmqvist *et al.* (1999).

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 atlanto-occipital joint, while its caudal counterpart rotates the atlas, and thus the head on the axis. The anterior parts of the atlas wings are reduced (fig. 4), therefore, the fibres of the complementary muscle, the *M. obliquus capitis caudalis*, were oriented more ventrolaterally in *Cynotherium*, which is suggestive of a stronger rotational component. The *M. splenius* insertion

also continues with an aponeurosis 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 ventral surface of the basioccipital of *Cynotherium* is broader than in similar sized living canids and the two rugose fossae for neck muscle attachment are deep and wide (Lyras *et al.*, in press). These fossae are the scars for the *Mm rectus capitis ventralis*, *rectus capitis lateralis* and *longus capitis*. Their principal action is flexion of the atlanto-occipital joint; the latter also draws the neck downwards.

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.

In addition to the stronger neck musculature, the neck as a whole was held lower than in *Canis*, as already noted and figured by Malatesta (1970). Furthermore, it appears that C3 already bears a prominent spinous process, as in *Vulpes*, whereas this is in general the case for C4 in *Canis* and for C5 in *Cuon*.

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* (Lyras *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,

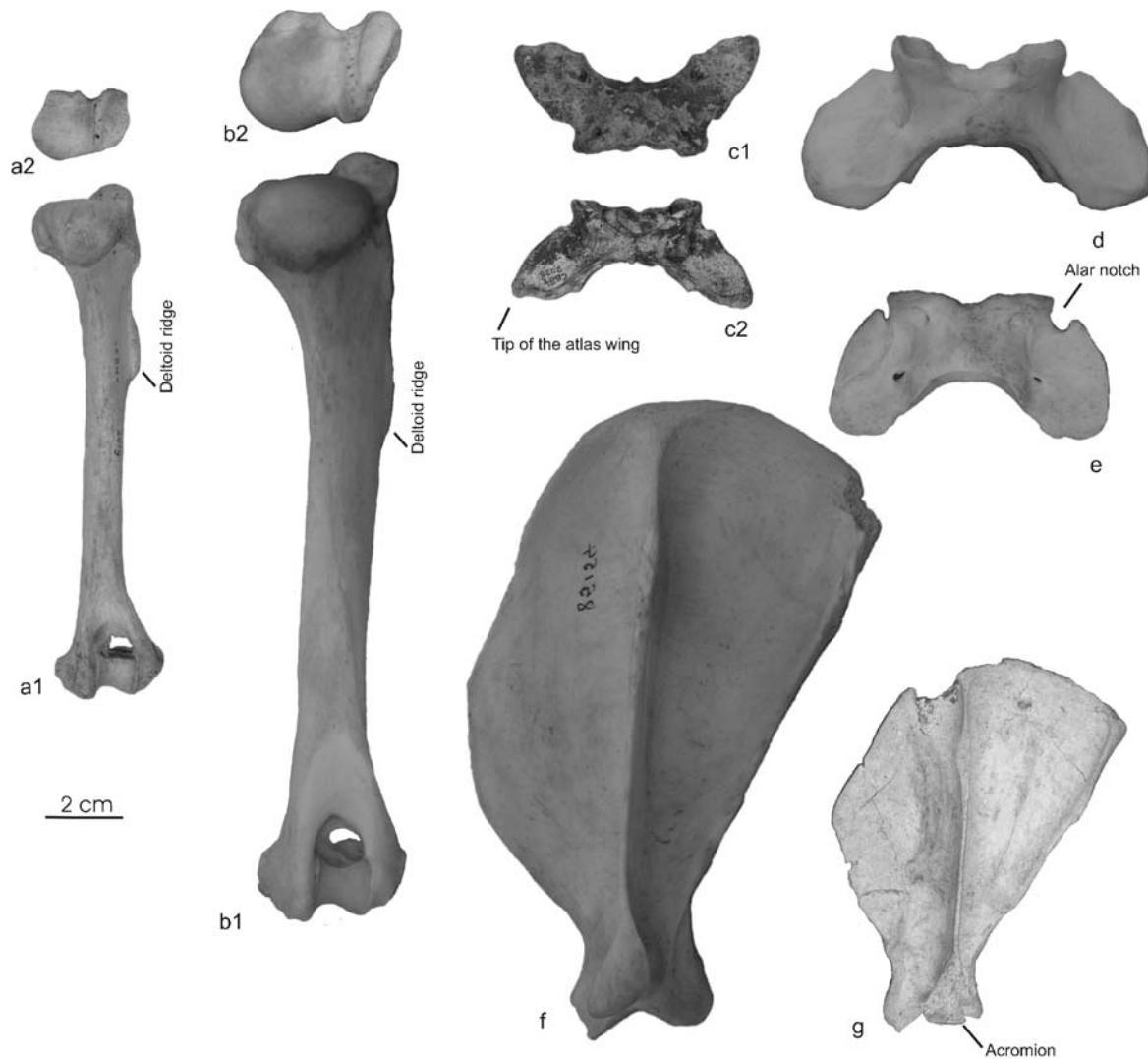


Fig 4 Postcranial elements of *Cynotherium*, *Lycaon* and *Canis*. a: *Cynotherium sardous* CB 84-8022 humerus, (a1) caudal, (a2) dorsal view; *Lycaon pictus* AMNH(M) 81853 humerus, (b1) dorsal and (b2) caudal view; *Cynotherium sardous* CB 84-8022 atlas, (c1) dorsal and (c2) ventral view; d: *Lycaon pictus* AMNH(M) 81853 atlas ventral view; e: *Canis simensis* AMNH(M) 81081 atlas dorsal view; f: *Lycaon pictus* AMNH(M) 85154 scapula lateral view; g: *Cynotherium sardous* CB 84-8022 scapula lateral view.

Postcraniale elementen van *Cynotherium*, *Lycaon* en *Canis*. a: *Cynotherium sardous* CB 84-8022 opperarmbeen, (a1) achteraanzicht, (a2) bovenaanzicht; *Lycaon pictus* AMNH(M) 81853 opperarmbeen, (b1) bovenaanzicht and (b2) achteraanzicht; *Cynotherium sardous* CB 84-8022 atlas, (c1) bovenaanzicht en (c2) onderaanzicht; d: *Lycaon pictus* AMNH(M) 81853 atlas onderaanzicht; e: *Canis simensis* AMNH(M) 81081 atlas bovenaanzicht; f: *Lycaon pictus* AMNH(M) 85154 schouderblad, zij-aanzicht; g: *Cynotherium sardous* CB 84-8022 schouderblad, zij-aanzicht.

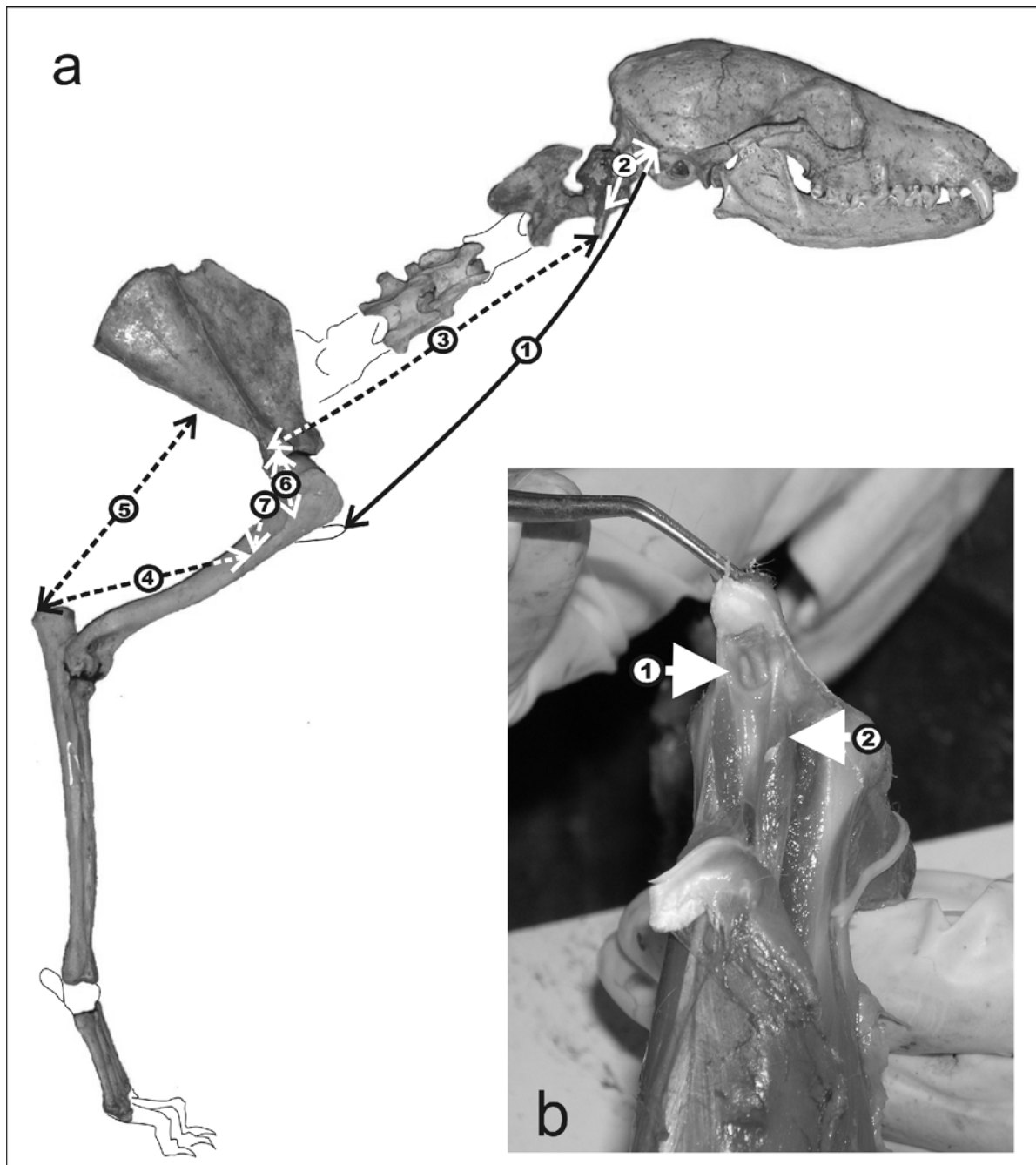


Fig 5 a: Directions of pull of the muscles of the neck (solid line) and anterior limb (dotted lines) of *Cynotherium sardous*. 1: *M. sternocephalicus*; 2: *M. obliquus capitis*; 3: *M. omotransversarius*; 4: *M. triceps caput laterale*; 5: *M. triceps caput logum*; 6: *M. teres minor*; 7: *M. deltoideus*. b: Dorsal view of the elbow of a dissected fox. 1: *M. anconeus*; 2: *M. triceps caput mediale*.

a: richtingen van trekkracht van spieren van de nek (doorgetrokken lijn) en van de voorpoot (gestippelde lijnen) van *Cynotherium sardous*. b: de elleboog van een ontlede vos gezien van boven. Voor de spiernamen, zie overeenkomstige nummers in het Engelstalig onderschrift.

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

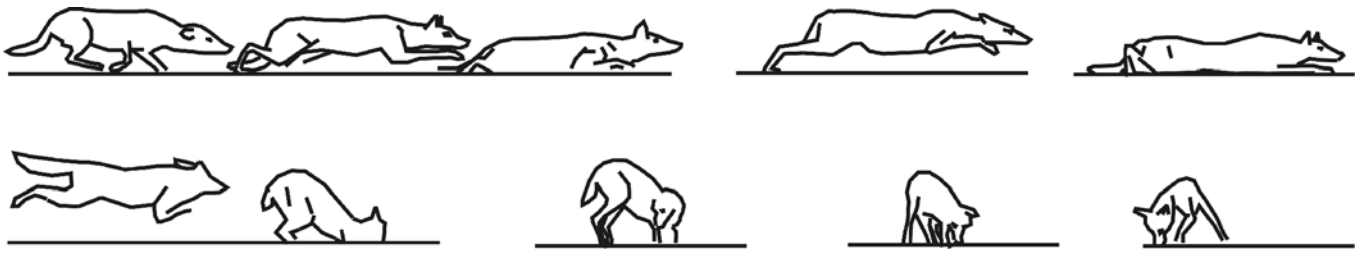


Fig 6 Lateral view of the Simenian wolf, *Canis simensis*, engaged in stalking locomotion while approaching its prey. Drawn from a fragment of a BBC film.

Zij-aanzicht van de Ethiopische wolf, *Canis simensis*, bezig met het besluipen van een prooi. Nagetekend naar een fragment uit een BBC film.

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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Fig 7 *Cynotherium*, which originates from the large, wolf-like *Xenocyon*, became specialized in hunting small prey instead of large animals. That is the subject of this cartoon: two *Xenocyons*, while hunting an ungulate, realize that the island is full of small *Prolagus* and decide to adapt.

Cynotherium, een afstammeling van de grote, wolf-achtige *Xenocyon*, specialiseerde zich in het jagen op kleine prooidieren in plaats van grote prooi. Dat is het onderwerp van deze cartoon: twee *Xenocyons*, jagend op een hoefdier, realiseren zich dat het eiland vol is met kleine *Prolagus* en besluiten zich aan te passen.

and Duncan Reeder (NNML), Bruce Patterson and Bill Stanley (FMNH), Jean Spence (AMNH), Michel Tranier and Géraldine Pothet (MNHN) for their assistance during the study of collections under their care. Finally, we thank Hans Brinkerink (Vista Natura, Baarn, the Netherlands) for making a cast of the *Cynotherium* skeleton. This project has been co-financed within Op. Education by the ESF (European Social Fund) and National Recourses.

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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 *Chasmaporthetes 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 *Chasmaporthetes melei* en *Sus sondaari*).

	Pleistocene		
	Early	Middle	Late
	Cava 6	Cava 10	Cava 7 and Corbeddu
<i>Cynotherium</i> sp.	X	?	
<i>Cynotherium sardous</i>		X	X
<i>Macaca majori</i>	X	x	
<i>Talpa tyrrhenica</i>	X	x	
<i>Nesiotites similis</i>	X	x	X
<i>Prolagus figari</i>	X		
<i>Prolagus sardus</i>		x	X
Leporidae	X		
<i>Tyrrhenicola sondaari</i>		X	
<i>Tyrrhenicola henseli</i>		X	X
<i>Rhagapodemus minor</i>	X	x	
<i>Rhagamys orthodon</i>			X
<i>Chasmaporthetes melei</i>	X		
Mustelidae sp.1	X		
Mustelidae sp.2	X	x	
<i>Nesogoral melonii</i>	X		
<i>Nesogoral</i> sp.2	X		
<i>Sus sondaari</i>	X		
" <i>Megaloceros</i> " <i>cazioti</i>			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.

Species	Number	Species	Number
<i>Alopex lagopus</i>	NNML cat b, NNML cat a, NNML 19797, NNML 3329	<i>Cuon alpinus</i>	NNML cat a, NNML cat b, NNML cat j, NNML 945
<i>Atelocynus microtus</i>	AMNH(M) 100095, FMNH 60675, FMNH 121286	<i>Dusicyon australis</i>	NNML 19111, NNML 19112
<i>Canis adustus</i>	NNML cat a, NNML cat b, NNML cat g, NNML cat j	<i>Lycaon pictus</i>	AMNH(M) 81853, AMNH(M) 164162, NNML cat a, NNML cat b, FMNH 12781, FMNH 12813
<i>Canis aureus</i>	NNML 1814, NNML 3217, NNML 39176, FMNH 105740	<i>Nyctereutes procyonoides</i>	NNML cat a
<i>Canis latrans</i>	NNML 1232, NNML 3400	<i>Otocyon megalotis</i>	MNHN 1960-480
<i>Canis lupus</i>	NNML cat a, FMNH 160107	<i>Pseudalopex culpaeus</i>	NNML cat a
<i>Canis lupus hodophylax</i>	NNML 39182	<i>Pseudalopex sechurae</i>	NNML 2381
<i>Canis mesomelas</i>	NNML cat a, NNML 2461	<i>Speothos venaticus</i>	NNML cat a, NNML 3224, AMNH(M) 167846, FMNH 121544
<i>Canis sinensis</i>	MNHN 1967-474, AMNH(M) 81081	<i>Urocyon cinereoargenteus</i>	MNHN c.q. 1880-1228, FMNH 129298
<i>Cerdocyon thous</i>	NNML cat b, FMNH 70758	<i>Vulpes vulpes</i>	NNML 9881, NNML 10934, NNML 9775, NNML 8889
<i>Chrysocyon brachyurus</i>	FMNH 150739	<i>Vulpes zerda</i>	AMNH(M) 90156
<i>Chrysocyon brachyurus</i>	AMNH(M) 133941	<i>Vulpes zerda</i>	MNHN 2000-666

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