

THE FOSSIL ENDEMIC GOAT *NESOGORAL CENISAE* N.SP.  
FROM CAMPIDANO, SARDINIA - CURSORIAL  
ADAPTATIONS IN INSULAR ENVIRONMENT

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**Resum**

Es descriu el bòvid de Campidano i s'assigna a *Nesogoral cenisae* n.sp. Se suposa que alguns dels seus caràcters, com ara la possessió d'un metacarp llarg i gràcil, són una adaptació cursorial que ha modificat la seva morfologia caprina original.

Els ungulats insulars es coneixen per la seva "locomoció de marxes curtes" d'eficient energia. Una comparació dels artiodàctils fòssils insulars mostra com el seu tipus de locomoció depèn de la presència de carnívors a les illes, i se situa entre una locomoció de marxes curtes extrema als ambients lliures de carnívors i unes habilitats cursorials incrementades en presència de carnívors. Un nanisme moderat pot ocórrer quan hi ha carnívors.

Es discuteix l'evolució faunística de Sardenya. *Nesogoral* va arribar a l'illa durant la Crisi Messiniana. Rere l'aïllament de l'illa fa uns 5 Ma, va coexistir amb el hiènid *Chasmaporthetes*, i des de fa 0,9 Ma va conviure amb el cànid *Cynotherium*. O bé l'ocupació d'un nínxol obert a les planes de l'illa va donar origen a una segona espècie, més cursorial, abans de l'arribada de *Cynotherium* (model de dos llinatges evolutius) o bé l'arribada d'aquest cànid va fer que *Nesogoral* es tornés més corredor.

**Paraules clau:** Bovidae, Caprinae, nova espècie, endemisme, Sardenya, Pliocè, Pleistocè, locomoció, adaptacions cursorials, ambients insulars, paleoecologia.

**Abstract**

The bovid from Campidano (Sardinia) is described and assigned to *Nesogoral cenisae* n. sp. Some of its characters, such as a long and gracile metacarpal, are assumed to be a cursorial adaptation which modified its original caprine morphology.

Insular ungulates are known for their energy efficient "low gear locomotion". A comparison of endemic insular artiodactyls shows that the type of their locomotion depends on the carnivores on the island, and ranges between extreme low gear locomotion in carnivore free environment and an increase in cursorial abilities in the presence of carnivores. Moderate dwarfing may occur even when carnivores are present.

The faunal evolution of Sardinia is discussed. *Nesogoral* arrived to the island during the Messinian Crisis. After isolation of the island some 5 Ma ago, it coexisted with the hyaenid *Chasmaporthetes* and from some 0.9 Ma ago it coexisted with the canid *Cynotherium*. Either the occupation of an open niche on the plains of the island resulted in a second and more cursorial species already before the arrival of *Cynotherium* (two lineage model), or the arrival of this canid caused *Nesogoral* to become more cursorial (single lineage model).

**Keywords:** Bovidae, Caprinae, new species, endemic, Sardinia, Pliocene, Pleistocene, locomotion, cursorial adaptations, insular environment, paleoecology.

**INTRODUCTION**

A number of well fossilised bovid remains were collected by Paul Sondaar at Campidano in Sardinia from sediments that came from a well that was being dug. There were no remains of other animals. There were no means to know the age of the deposits or fossils. When I studied these fossils, they were in the Instituut voor Aardwetenschappen of the University of Utrecht (IVAU).

The known bovids of Sardinia are the Holocene/Recent *Capra* and *Ovis* and the Plio-Pleistocene *Nesogoral*. Sondaar (1987) and Sondaar *et al.* (1984, 1986) recognised two Plio-Pleistocene faunal associa-

tions in Sardinia, the earlier *Nesogoral* and the later *Tyrrenicola* faunas. The earlier faunas are still not well known and *Nesogoral* is in fact known from only few localities. *Nesogoral melonii* was described by Dehaut on the basis of material he collected from Capo Figari. At present there are various fissure fillings known at Capo Figari, but it is not well known from which ones the older collections of Dehaut and Major come, which both contain this species. At the top of the hill there are two fissures, which are known as Capo Figari 1 and Capo Figari 2 and which have different faunas (Van der Made, 1988, 1999a). Gliozzi & Malatesta (1980) collected *Nesogoral* from Capo Figari 1 and stated that they believe that this

is the place where the material described by Dehaut comes from. If this is correct, it is the type locality of the species. Capo Figari 2 has the arvicolid *Tyrrhenicola* and was believed to have no *Nesogoral*, but an astragalus from that locality was assigned to *Nesogoral* aff. *melonii* (Van der Made, 1999a). The material collected by Forsyth Major, either is homogeneous and comes from still another locality, or is a mixture of materials from Capo Figari 1 and 2. Thaler and a team of the IVAU also collected at Capo Figari. Pecorrini *et al.* (1973) mentioned, but did not describe, material from the earliest Pliocene of Capo Mannu as “Caprinae?”. Some fossils from that locality were described and figured as “*Nesogoral* sp.” (Van der Made, 1999a). A second species of *Nesogoral* and an indeterminate caprine have been reported from Monte Tutavista near Orosei, but have not been described (Sondaar, 2000; Abazzi *et al.*, 2004). In view of the still scarce record of the Plio-Pleistocene bovids from Sardinia, the material from Campidano is interesting.

*Nesogoral* is widely considered to be a caprine, and it is assumed to be particularly close to *Gallogoral*, *Nemorhaedus* and *Myotragus* (Gliozzi & Malatesta, 1980). *Nesogoral* and *Myotragus* were endemic to Sardinia (and Corsica) and the Eastern Balearics respectively. They are believed to have evolved from *Pachygazella*, an Asian bovid that reached these islands when they became connected to the continent during the Messinian Crisis (Gliozzi & Malatesta, 1980), when the Mediterranean became disconnected from the Atlantic Ocean and its sea level dropped several thousand meters (Hsü *et al.*, 1977). Gliozzi & Malatesta (1980) suggested that besides *Nesogoral* also *Myotragus*, *Gallogoral* and *Procamptocebras* form a branch that evolved from *Pachygazella*. DNA recovered from *Myotragus* fossils, situates this bovid within the Caprinae and suggests a closer relationship with *Budorcas*, *Ovis*, *Oreamnos* and *Rupicapra*, than with other caprines like *Capra*, *Hemitragus*, or *Ovibos*, *Capricornis* and *Nemorhaedus* (Lalueza-Fox *et al.*, 2000). After Lalueza-Fox *et al.* (this volume), *Myotragus* is closely related to the *Budorcas-Ovis* clade.

Whereas *Myotragus* is known by many fossils from many localities through studies that deal with a wide

range of aspects of this animal and its ecology (Alcover *et al.*, 1981, 1999; Bover & Alcover, 1999; Köhler & Moyà-Solà, 2001, 2004; Lalueza-Fox *et al.*, 2000; Leinders & Sondaar, 1974; Spoor, 1988a, 1988b; *et c.*), *Nesogoral* is still not well known. Though all Sardinian bovids are considered to be Caprinae, we will see in the descriptions, that some morphological features do not fit normal caprines. For this, three relatively simple explanations will be discussed:

1) The bovid from Campidano is no caprine and does not belong to *Nesogoral*.

2) The bovid from Campidano belongs to *Nesogoral*, but this genus is not a caprine and became similar to caprines through convergent evolution.

3) The original caprine morphology of *Nesogoral* became modified due to the particular environment of Sardinia. This explanation implies the discussion of the ecology of insular environments.

## MEASUREMENTS AND THEIR ABBREVIATIONS

Measurements are given in mm and are taken as indicated by Van der Made (1989, 1996).

DAP = Antero-posterior diameter, often length.

DAPd = DAP of the distal part of a bone.

DAPb = DAP at the base of the crown of the teeth.

DAPh = DAP of the “head” of a bone (eg. calcaneum, ulna).

DAPm = Minimal DAP of a bone.

DAPmax = maximal DAP of a bone.

DAPn = DAP of the “neck” of a bone (eg. in calcaneum, ulna).

DAPo = Occlusal DAP in teeth.

DAPp = DAP of the proximal part of a bone.

DAPpf = DAP of the proximal articular facet of a bone.

DAPsf = DAP of the calcaneum, measured at the level of the sustentacular facet.

DAPIII, DAPIV, DAPI or DAPr = DAP of the distal articular surfaces of a metapodial, r/l indicates left or right of the axis of the bone, when it is not known whether the bone

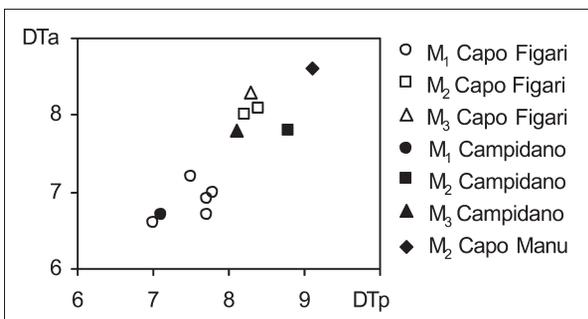


Fig. 1. Bivariate diagram of the lower cheek teeth of *Nesogoral* sp. from Capo Mannu (IVA), *Nesogoral melonii* from Capo Figari 1 (IVA; M<sub>2</sub>, M<sub>3</sub>), *Nesogoral* sp. from Capo Figari FM (NMB; M<sub>1</sub>, M<sub>2</sub>), and *Nesogoral cenisae* n. sp. from Campidano.

Fig. 1. Diagrama bivariat dels queixals de *Nesogoral* sp. De Capo Mannu (IVA), *Nesogoral melonii* de Capo Figari (IVA; M<sub>2</sub>, M<sub>3</sub>), *Nesogoral* sp. from Capo Figari FM (NMB; M<sub>1</sub>, M<sub>2</sub>), and *Nesogoral cenisae* n. sp. from Campidano.

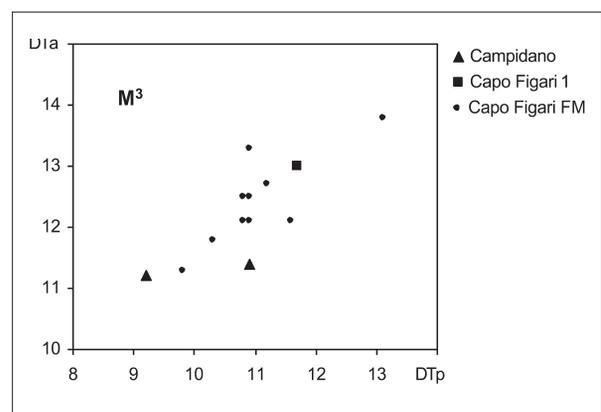


Fig. 2. Bivariate diagram of the M<sup>3</sup> of *Nesogoral* from Capo Figari 1 (IVA) and Capo Figari FM (NMB) and from Campidano (IVA; M<sub>2</sub>, M<sub>3</sub>).

Fig. 2. Diagrama bivariat del M<sup>3</sup> de *Nesogoral* de Capo Figari 1 (IVA), Capo Figari FM (NMB) i de Campidano (IVA; M<sub>2</sub>, M<sub>3</sub>).

itself is right or left.

DT = Transverse diameter.

DTa = DT of the anterior lobe of a tooth.

DTd = DT of the distal part of a bone.

DTfast = DT of the facet for the astragalus in the tibia or navicuboid.

DTfu = DT of the upper part of the facet for the humerus of the ulna.

DTh = DT of the "head" of a bone (eg. in the calcaneum and ulna).

DTm = Minimal DT of a bone.

DTmax = Maximal DT of a bone.

DTn = DT of the "neck" of a bone.

DTp = DT of the proximal part of a bone, or DT of the posterior lobe of a tooth.

DTpf = DT of the proximal articular surface of a bone.

DTpp = DT of the third lobe of a M<sub>3</sub>.

DTsf = DT of the calcaneum, measured at the level of the sustentacular facet.

H = Height.

h = Alternative height. In the magnum it is the minimal height of the elevated posterior structure at the posterior side of the bone.

Ha = H of the anterior lobe of a tooth.

L = length.

Lext = Length of the astragalus, measured at the lateral side. Length of the second phalanx, measured at the side that is not close to the axis of the foot.

Lint = Length of the astragalus, measured at the medial side. Length of the second phalanx, measured at the side that is close to the axis of the foot.

Lm = Length of the astragalus, measured in the middle of the bone.

Lu = Length of the upper part of a bone.

T1 = Thickness of the enamel measured at the first or anterior lobe of a tooth (also Ta).

## COLLECTIONS AND THEIR ABBREVIATIONS

The material from Campidano is compared to recent and fossil material which I studied or which is kept in the following institutions:

AUT	Aristotle University of Thessaloniki.
CIAG	Centre d'Investigacions Arquelògiques de Girona.
FASMN	Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied (Römisches-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte).
FBFSU	Forschungstelle Bilzingsleben, Friedrich Schiller Universität Jena.
HMV	Historisches Museum, Verden.
HUJ	The Hebrew University of Jerusalem.
IGF	Istituto di Geologia, Firenze.
IPH	Institut de Paléontologie Humaine, Paris.
IPS	Institut de Paleontologia, Sabadell.
IPUW	Institut für Paläontologie der Universität, Wien.
IQW	Institut für Quartärpaläontologie, Weimar.
IVAU	Instituut Voor Aardwetenschappen, Utrecht.
LAUT	Laboratori d'Arqueologia, Universitat Rovira i Virgili de Tarragona.

LPTUP	Laboratoire de Préhistoire de Tautavel, Université de Perpignan.
LVH	Landesmuseum für Vorgeschichte, Halle.
MAC	Museo de Arqueología de Cartagena.
MB	Museo de Burgos, Burgos.
MCP	Musee Crozatier, Le Puy-en-Velay.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MNHN	Muséum National d'Histoire Naturelle, Paris.
MRA	Musée Requien, Avignon.
NHCV	Natural History Collection of Vriza.
NHM	Natural History Museum, London.
NMB	Naturhistorisches Museum, Basel.
NMM	Naturhistorisches Museum, Mainz.
NMMa	Naturhistorisch Museum, Maastricht.
NMW	Naturhistorisches Museum, Wien.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.
ZMA	Zoologisch Museum, Amsterdam.

## DESCRIPTION AND COMPARISON

The M<sub>3</sub> (Plate 1, fig. 5) is well worn, but what is left of the crown is still high. The enamel has a very fine crenulation. The lingual wall is relatively flat with a slight depression between the two anterior lobes and a third lobe that recedes a little, but with a well marked antero-lingual styloid. The third lobe does not have a fossid. There is no interlobular column at the buccal side. A caprine fold is present, but it is not very strongly developed. The specimen is close in size to a specimen from Capo Figari (Fig. 1).

The M<sub>1/2</sub> (Plate 1, fig. 1) have a morphology that is similar to that of the M<sub>3</sub>, but of course, they lack the third lobe. These molars are close in size to their homologues in Capo Figari, while a specimen from Capo Mannu is a little bit larger (Fig. 1).

The P<sub>4</sub> (Plate 1, fig. 3) has finely crenelated enamel and a high crown. The metaconid is well developed, placed far forward and the metapreocrisid (terminology of Van der Made, 1996) extends forward to close the anterior fossid. The lingual wall is smoothly undulating, but the buccal wall has a deep groove separating the anterior and posterior lobe. In size the specimen is close to the P<sub>4</sub> from Capo Figari.

The M<sub>3</sub> (Plate 1, figs. 2 & 4) has smooth enamel and a high crown. The buccal wall has three well marked styles with relatively flat areas between them (the exocristas are thus not well developed). The postero-buccal style extends also a little more distally than the rest of the tooth. There is no lingual interlobular column. The morphology is essentially similar to that of the specimens from Capo Figari (Pl. 1, fig. 6). The specimens are relatively small and one of them is even just outside the ranges of the Capo Figari sample (Fig. 2).

The M<sup>1/2</sup> have morphologies that are largely similar to the M<sup>3</sup>.

The **ulna** (Plate 2, fig. 5) has a facet for the humerus, which is rather wide in its upper part. In this it is like in Caprinae, but unlike other ruminants, where this facet tends to be narrower. The facet for the humerus meets

the facets for the radius, forming little more or less horizontal crests. This is the widest part of the bone. The bone is not very wide here and there is no important lateral extension of the lateral facet for the radius. At this place, Caprinae tend to be wider and *Capra* has the ulna reaching even further medially than the radius. Besides, in *Capra*, the radius and ulna tend to be fused at this place, which evidently, is not the case here.

The **radius** (Plate 4, figs. 6-7) has a distal articular surface that has a relatively narrow appearance. The proximal facet sticks out medially over the shaft in a very pronounced way (Pl. 4, fig7a, 7c), which is typical in Caprinae, but not in most other Bovidae, including gazellas.

The **magnum** has a morphology that is common among ruminants. If seen from the back, the highest point of the bone is where the facets for the scaphoid and lunar meet; immediately laterally the surface slopes down. In Caprinae and *Nesogoral* from Capo Figari (Plate 4, fig. 5), this slope is steeper and there seems to be more difference in height between these two points than in other ruminants. In this respect, the magnum is not very caprine-like.

The **metacarpal** (Plate 2, fig. 1) is a surprisingly long and slender bone. The shaft widens gently towards the distal articulations, not abruptly as in most Caprinae.

The distal articular surface has some interesting features. When seen from distal, the outline is more or less trapezoidal, and in most bovids and cervids, the lateral sides of the “trapezium” are more or less straight and clearly convergent. In some bovids, including Caprinae, these sides are more or less parallel, or are parallel in their plantar half and convergent in their dorsal half. This is also the case in this metapodial and in a specimen from Capo Figari 1 (Plate 2, fig. 6), which might be a metacarpal. But in the metatarsal, the sides seem to be predominantly straight and convergent.

Each of the two distal articular surfaces is composed of two half cylinders, the smaller one having a much smaller diameter than the larger one in many Caprinae. In the specimen from Campidano, the difference is not so great and in this it is more like other bovids and like cervids. In Caprinae, the dorsal surface of the smaller cylinder tends to be horizontal, or even slightly dipping towards the larger cylinder, whereas in other bovids and cervids, this surface tends to slope away from the larger cylinder. In this, the Campidano metapodial is more like most bovids and cervids.

In most bovids and cervids, when seen from the side, the cylindrical distal articular surface is about half of a cylinder, but in Caprinae, it is a larger section, permitting thus a wider range of dorso-plantar movement of the first phalanx. In Campidano, the morphology is more like in cervidae and most bovidae that are no Caprinae.

Between the two cylinders of each of the two distal articular surfaces, there is a crest, which is often more marked on the plantar side than on the dorsal side. This crest is very well developed at any place in Caprinae, and in particular in *Capra*, but not in so much in other bovids, cervids and in the specimens from Campidano and Capo Figari. The two crests of the two articular surfaces converge usually dorsally, but tend to be parallel or converging plantarly in Caprinae. In this character, the specimen from Campidano is more like cervids and most bovids.

As said above, the metacarpal is surprisingly long and gracile. That is, compared to Caprinae and bearing in mind the common shortening of metapodials in insular environments. The specimen is more elongate than in other recent and fossil Caprinae (Fig. 3). There is a very clear difference with *Myotragus*, which is assumed to be closely related and which is also an insular endemic. While *Myotragus* has (together with *Budorcas*) the most robust metapodials of the Caprinae, *Nesogoral* has the most gracile or elongate ones (Fig. 4). Size and proportions of the metapodial are close to that of the continental Late Miocene *Gazella*.

The **tibia** is poorly preserved.

The **calcaneum** (Plate 4, fig. 4) has a head, that, when seen from the side, has a pointed shape that overhangs the tuber. This shape is unlike in *Capra*, but occurs in other Caprinae.

The **astragalus** (Plate 4, figs. 1-3, 8) has a short and wide appearance as in Caprinae, whereas in most other bovids and in cervids this bone has a more elongate appearance. The specimens from Campidano have the same size as those of *Nesogoral melonii* from Capo Figari (FM collection), but are larger than the one of *Nesogoral* sp. from Capo Figari 2. All these specimens are clearly larger than that of the smallest cervid from Sardinia, which is *M. cazioti* (Fig. 5).

The **metatarsal** (Plate 2, figs. 2 & 4) is represented by proximal and distal fragments. The proximal end is wide and has a short antero-posterior diameter. The posterior facet with the navico-cuboid is directed transversely and its end that is in the middle of the bone is clearly elevated above the proximal surface of the bone forming a point that can be seen very well in anterior view (Plate 2, fig. 2a). This is a typical bovid morphology, cervids do not have this facet on a point-like elevation. In cervids, the proximal end of the bone is as wide at the posterior side as in the middle. In bovids, this is often not the case. In many bovids, the antero-posterior diameter of the bone is large compared to the transverse diameter. This is noted in the shaft, but even better in the the proximal surface of the bone, where the posterior facet for the cubo-navicular and the smaller cuneiform are placed further backwards on a narrow posterior extension of the proximal surface. Such a morphology is seen in for instance *Gazella*. The metatarsals of the Caprinae, and the specimen from Campidano, have a relatively large transverse diameter and have the two posterior facets, mentioned above, placed more anteriorly.

The distal end of the metatarsal has an open gully in the middle as in bovids, whereas cervids have this gully covered by a bony bridge. The shaft widens gently, and not abruptly, towards the distal end. The morphology of the distal articular surfaces is like in the metacarpal. There is one exception, and that is one of the two articulations of a distal metatarsal (Plate 2, figure 4b). There are no clear signs of deformation that could explain this otherwise atypical morphology. Otherwise the morphology is unlike in Caprinae as is also seen in a particularly well preserved distal metapodial (Plate 2, fig. 3).

Some of the phalanges appear to articulate with each other and with a distal metatarsal. These specimens are marked with an asterisk in the tables.

Fig. 3. Bivariate diagram of the metacarpal in selected Caprinae. The taxa included and the provenance of the data is indicated under Figure 4.

Fig. 3. Diagrama bivariat del metacarpia de Caprinae seleccionats. Els taxa inclòs i la seva procedència, com a la figura 4.

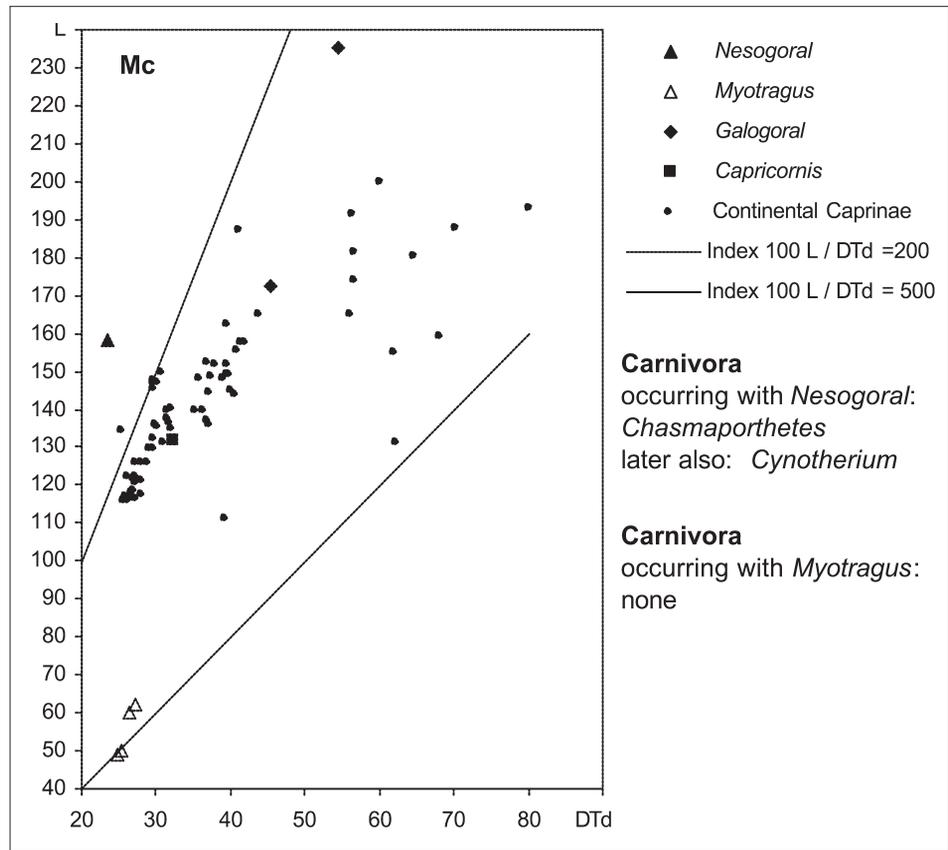


Fig. 4. Metacarpal index 100 L / DTd in selected Caprinae. *Myotragus* from Son Maiol (IVAU), recent *Budorcas taxicolor* (NHM), *Praeovibos priscus* from Bad Frankenhausen (IQW; estimated), recent *Ovibos moschatus* (NML), *Ovibos suessenbornensis* from Süßenborn (IQW), recent *Oreamnos americanus* (NMW), *Soergelia elisabethae* from Süßenborn (IQW) and Apollonia 1 (AUT), *Megalovis* from Senèze (NMB) and Nihowan (MNHN), *Gallogoral* from Senèze (NMB) and (?) *Olivola* (IGF), *Hemitragus bonali* from Hundsheim (NMB), *Capra ibex* from Petralona (AUT), recent *Capra ibex* (LPTUP), *Capricornis sumatrensis* (NML), recent *Capra pyrenaica* (MNCN), *Ovis antiqua* from Cueva Victoria (MAC), *Capra alba* from Quibas (MNCN), recent *Pseudois nayaur* (NHM), recent *Rupicapra* (LPTUP), *Nesogoral* from Campidano (IVAU).

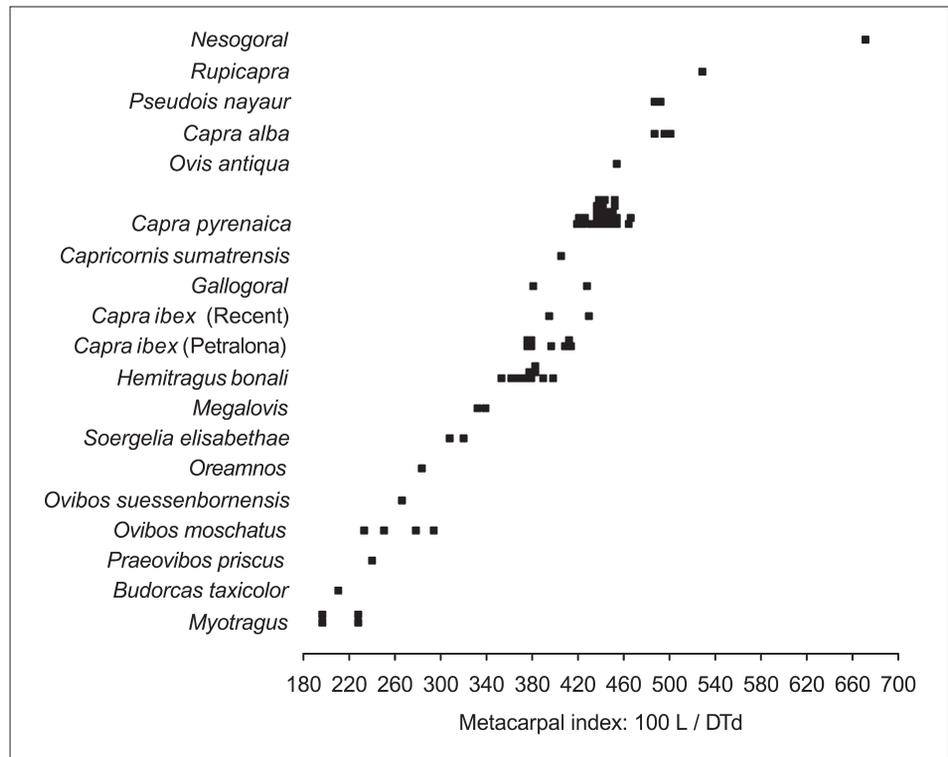


Fig. 4. Index metacarpia, 100 L / DTd, a Caprinae seleccionats. *Myotragus* de Son Maiol (IVAU), *Budorcas taxicolor* recent (NHM), *Praeovibos priscus* de Bad Frankenhausen (IQW; estimat), *Ovibos moschatus* recent (NML), *Ovibos suessenbornensis* de Süßenborn (IQW), *Oreamnos americanus* recent (NMW), *Soergelia elisabethae* de Süßenborn (IQW) i Apollonia 1 (AUT), *Megalovis* de Senèze (NMB) i Nihowan (MNHN), *Gallogoral* de Senèze (NMB) i (?) *Olivola* (IGF), *Hemitragus bonali* de Hundsheim (NMB), *Capra ibex* de Petralona (AUT), *Capra ibex* recent (LPTUP), *Capricornis sumatrensis* (NML), *Capra pyrenaica* recent (MNCN), *Ovis antiqua* de Cueva Victoria (MAC), *Capra alba* de Quibas (MNCN), *Pseudois nayaur* recent (NHM), *Rupicapra* recent (LPTUP), *Nesogoral* de Campidano (IVAU).

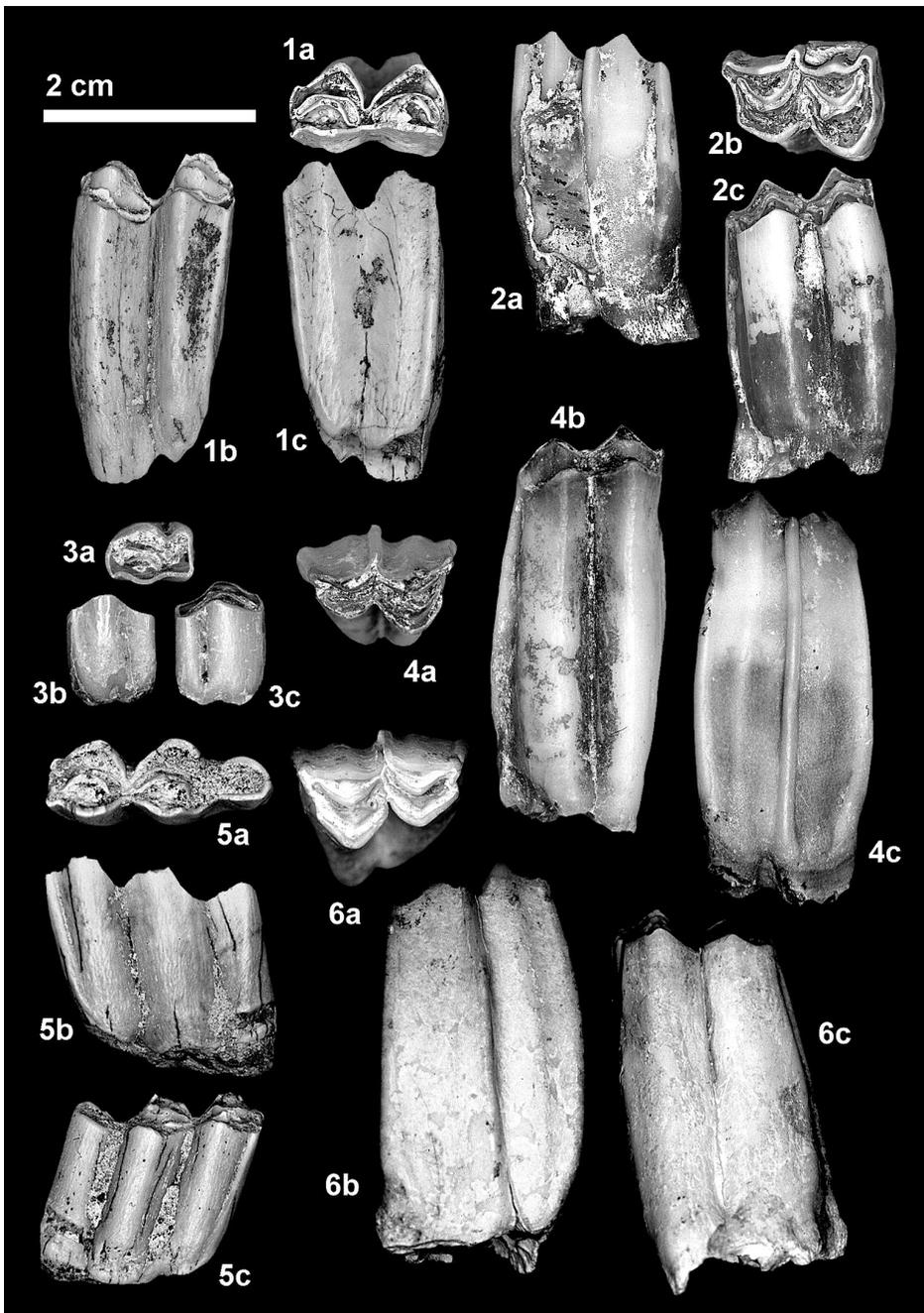


Plate 1. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral* from Capo Figari FM (fig. 6; NMB).

Figure 1. Right M2: a) occlusal view, b) buccal view, c) lingual view.

Figure 2. Right M<sup>3</sup>: a) buccal view, b) occlusal view, c) lingual view.

Figure 3. Right P4: a) occlusal view, b) lingual view, c) buccal view.

Figure 4. Right M3: a) occlusal view, b) lingual view, c) buccal view.

Figure 5. Right M3: a) occlusal view, b) lingual view, c) buccal view.

Figure 6. Ty 5439 - left M<sup>3</sup>: a) occlusal view, b) buccal view, c) lingual view.

*Lâmina 1. Nesogoral cenisae* n.sp. de Campidano (figs. 1-5) i *Nesogoral* de Capo Figari FM (fig. 6; NMB).

Figura 1. M<sub>2</sub> Dret: a) norma oclusal, b) norma bucal, c) norma lingual.

Figura 2. M<sup>3</sup> Dret: a) norma bucal, b) norma oclusal, c) norma lingual.

Figura 3. P<sub>4</sub> Dret: a) norma oclusal, b) norma lingual, c) norma bucal.

Figura 4. M<sub>3</sub> Dret: a) norma oclusal, b) norma lingual, c) norma bucal.

Figura 5. M<sub>3</sub> Dret: a) norma oclusal, b) norma lingual, c) norma bucal.

Figura 6. Ty 5439 - M<sup>3</sup> esquerre: a) norma oclusal, b) norma bucal, c) norma lingual.

The **first phalanx** is represented by specimens from the fore limb (Plate 3, fig. 1) and hind limb (Plate 3, figs. 3 & 4). Whereas in most Bovidae and in Cervidae, the bone is laterally compressed, in Caprinae the phalanx is wide. The specimens from Campidano are not very wide. When seen from proximal, not much bone can be seen below (or plantar) of the facet, as in most Caprinae. The upper border of the proximal facet is not flat (as in Caprinae), but slopes away from the axis of the foot. In one of the specimens there is a little bump on the dorsal surface (Plate 2, fig. 2c) that is elevated above the facet, which is common in cervids, but usually absent in Caprinae. The proximal facet has a vertical furrow in the middle (that articulates with a crest on the metapodials). The part of the facet on the external side of the furrow is rela-

tively wide in Caprinae, but not so in the specimens from Campidano. In Caprinae, the two little facets for the sesamoids, are lower and relatively wider than in other Bovidae, in Cervidae and in the phalanges from Campidano. All these characters contribute to the wide aspect in Caprinae and the more narrow appearance in other ruminants and Campidano.

In the specimens from Campidano, the distal end of the first phalanx is relatively high, but not as high as in cervids and most bovids. The plantar surface is rather flat, as is the case as in Caprinae.

The **second phalanx** (Plate 3, fig. 2) has a small "facet post-articulaire" (sensu Heintz, 1970) on the proximal surface. Not only does it extend only a little in plantar direction, but its surface slopes plantarly and is placed

**Plate 2.** *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral melonii* from Capo Figari 1 (fig. 6; IVAU).

Figure 1. Right metacarpal: a) anterior view, b) posterior view, c) distal view, d) proximal view.

Figure 2. Left metatarsal: a) anterior view, b) proximal view.

Figure 3. Distal metapodial: distal view (not to scale).

Figure 4. Distal metatarsal: a) anterior view, b) distal view.

Figure 5. Right ulna: a) lateral view, b) anterior view.

Figure 6. Distal metapodial: a) distal view, b) view from the side, c) dorsal view.

**Làmina 2.** *Nesogoral cenisae* n.sp. de Campidano (figs. 1-5) i *Nesogoral melonii* de Capo Figari 1 (fig. 6; IVAU).

Figura 1. Metacarpia dret: a) norma anterior, b) norma posterior, c) norma distal, d) norma proximal.

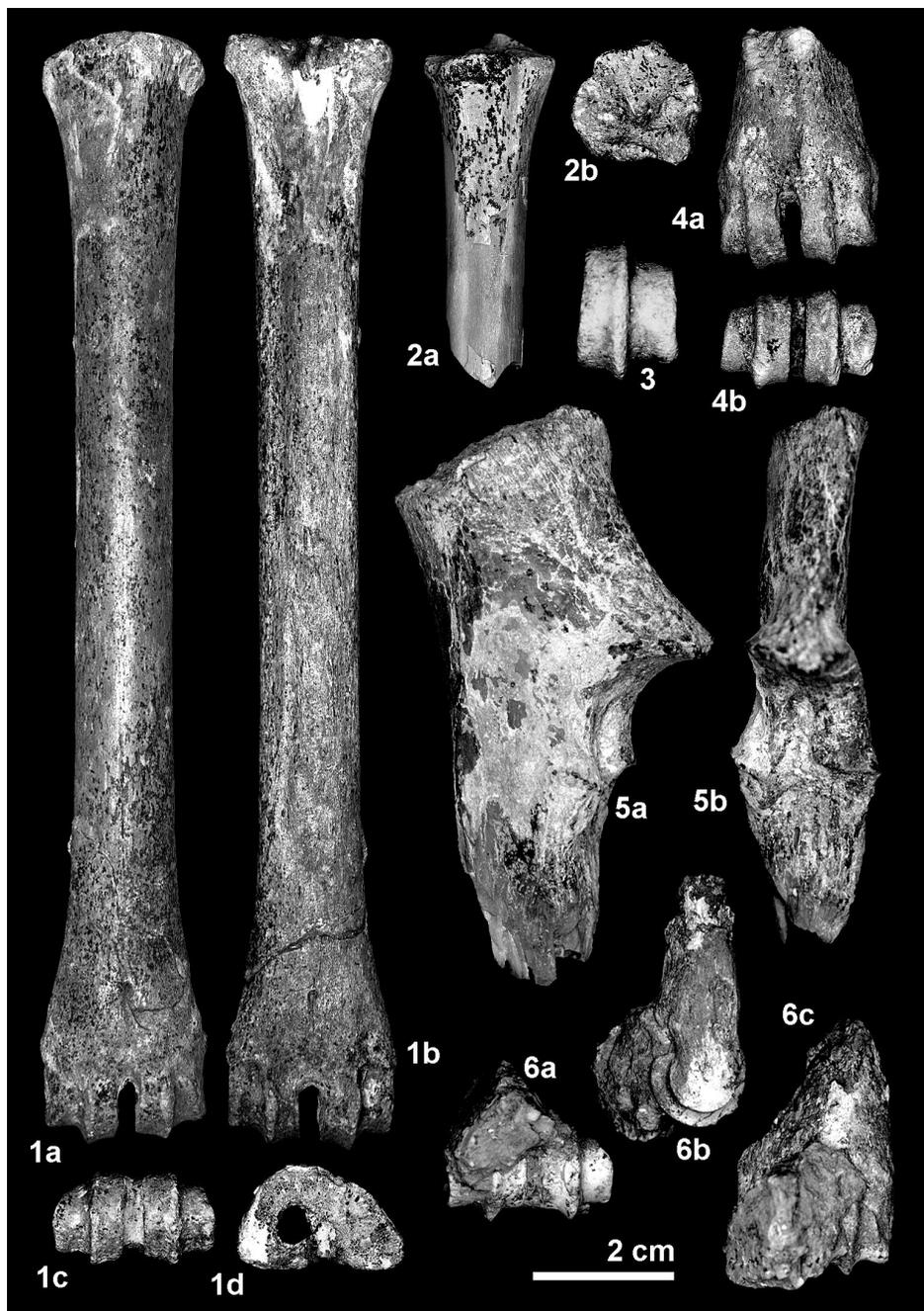
Figura 2. Metatarsia esquerra: a) norma anterior, b) norma proximal.

Figura 3. Detàpode distal: norma distal (no a escala).

Figura 4. Metatarsia distal: a) norma anterior, b) norma distal.

Figura 5. Ulna dreta: a) norma lateral, b) norma anterior.

Figura 6. Metàpode distal: a) norma distal, b) visió des del costat, c) norma dorsal.



more distally than the proximal articulation surface. This morphology is typical of Caprinae, and occurs also in Antilopinae like *Gazella* and *Madoqua*, but most other bovids and all cervids have this “facet post-articulaire” developed as a massive proximally and plantarly projecting bump.

The proximal facet is wide, as is common in Caprinae, but unlike in most other Bovidae and in Cervidae. When seen from the side with the plantar side horizontal, the plantar part of the facet is approximately vertical and the dorsal part overhangs and is the most proximal part of the bone. This is common in Caprinae, whereas in most other Bovidae and in Cervidae, the plantar part of the facet is dipping proximally and not even the dorsal part of the facet is vertical. As a result, the plantar part of

the facet extends more in proximal direction. Seen from the side, the curvature of the facet is like a small section of a circle, as common in Caprinae, but a much smaller section than in cervids and most other bovids.

The distal facet is wide, as is typical in most Caprinae, whereas most other bovids and cervids have narrower facets. This is shown very well with an index 100 DAPd / DTd, which has low values in wide facets and high values in narrow facets. Most Caprinae tend to have values between 100 and 125, while Cervidae and many bovids, including *Gazella*, have values between 120 and 155 (Fig. 6). Some Caprinae, like *Capricornis* and *Gallogoral* may have relatively high values, while other bovids, like *Cephalophus* and *Gazellospira* may have relatively low values. The large Bovini are expected to have low

Teeth	DAP	DAPb	DTa	DTp	DTpp	Ha	DAPmax	T1
M3	dext	21.7	20.3	7.8	8.1	5.1		
M1/2	sin	10.6	>10.6	6.7	7.1			
M1/2	dext	13.9	10.0	—	—			
M1/2	dext	14.4	13.4	7.8	8.8		>>25.6	0.6
P4	dext	8.3	8.4	5.6	5.8			
M <sup>3</sup>	dext	14.1	15.3	16.4	10.9		>33.5	16.8
M <sup>3</sup>	sin	15.0	14.6	—	—			15.4
M <sup>3</sup>	sin	16.7	15.8	—	—			
M <sup>3</sup>	dext	14.3	14.6	11.2	9.2		>>22.9	15.5
M <sup>1/2</sup>	dext	≥13.7	—	—	10.4			
M <sup>1/2</sup>	sin	12.8	11.8					
M <sup>1/2</sup>	dext	13.1	12.0	—	—		>28.4	
Ulna	DTh	DAPn	DTn	DTfu	DTmax	DAPmax	DAPf	Lu
dext	—	20.1	7.9	—	16.9	24.7	16.9	—
dext	—	20.7	8.8	11.2	15.5	26.8	17.9	—
dext	10.6	21.3	8.0	10.7	—	21.9	—	42.9
Radius	DAPp	DTp	L	DAPd	DTd	DAPdf	DTdf	
dext	>13.5	>26.8	—	—	—	—	—	
dext	14.9	—	—	—	—	—	—	
sin	—	—	—	20.1	29.8	15.8	26.1	
dext	—	—	—	20.5	29.3	15.9	25.7	
Magnum	DAP	DT	H	h				
sin	14.9	14.3	10.5	7.7				

Table 1

values, like Caprinae, but then they also tend to have robust metapodials, which is another similarity. In insular cervids, the phalanges may become shortened and more robust like the metapodials (eg. De Vos, 1979). Some specimens of *Cervus* aff. *cerigensis*, which has extremely shortened metapodials, do not show an increase in width of the distal facet of the second phalanx (Fig. 6), suggesting that the shortening of the phalanges, as an adaptation to insular environment, does not affect the relative width of the distal facets.

The distal facet of the second phalanx consists of two parts, separated by a furrow. The part that is closest to the axis of the foot is low, but not as low as in *Capra* and many other Caprinae. This part of the facet does not project much more forward beyond the other part of the distal facet. This is as in most ruminants, including *Gazella*, but unlike in most Caprinae, including *Capricornis*. *Nesogoral* from Capo Figari has the axial part of the facet low and a little more protruding than in Campidano, but not so much as in most Caprinae (Plate 3, fig. 6).

The **third phalanx** (Plate 3, fig. 5) is short and high. Caprinae like *Capricornis*, and many other Bovidae and Cervidae, have much more elongate phalanges, that end in a sharper distal “point”, but *Ovis*, *Capra*, *Hemitragus* etc. have short and high phalanges.

Seen from lateral, the dorsal profile of the anterior part is relatively steep and convex. The extensory

apophysis is large and, when seen from lateral, does not show up as a separate elevation, but forms part of this convex profile. However, behind the apophysis there is a relatively large depressed area. The proximal facet ends dorsally much below the apex of the extensory apophysis. A large elevated extensory apophysis is common in many Caprinae, but not in other Bovidae and in Cervidae.

When seen from the side, the proximal facet is vertical in its dorsal part and horizontal in its plantar part and forms more or less a quarter of a circle. This is common in many Caprinae, but some Caprinae (eg. *Capricornis*), Cervidae and other Bovidae have less curvature. The plantar part of the facet extends far proximally and forms a relatively large horizontal surface. *Myotragus* has this facet with a similar morphology (Spoor, 1988, Pl. 2, fig 12) or with less curvature and lacking an extensive horizontal part (Köhler & Moyà-Solà, 2001, Fig. 3).

## DISCUSSION

### The morphology of the Campidano bovid compared to the Caprinae

The first and second explanations mentioned in the introduction for some morphologies in the Campidano

Some values moved one or more columns, which was not detected in the print proofs.

<b>Ulna</b>	DTh	DAPn	DTn	DTfu	DTmax	DAPmax	DAPf	Lu
dext	--	20.1	7.9	--	16.9	24.7	16.9	--
dext	--	20.7	8.8	11.2	15.5	26.8	17.9	--
dext	10.6	21.3	8.0	10.7	--	21.9	--	42.9

<b>Radius</b>	DAPp	DTp	L	DAPd	DTd	DAPdf	DTdf
dext	>13.5	>26.8	--	--	--	--	--
dext	14.9	--	--	--	--	--	--
sin	--	--	--	20.1	29.8	15.8	26.1
dext	--	--	--	20.5	29.3	15.9	25.7

<b>Magnum DAP</b>	DT	H	h
sin	14.9	14.3	10.5
			7.7

<b>Metapodial</b>	Mc dext	Mc ?	Mc right	Mt sin	Mt dext	Mt ?	Mt* ?	Mp left
DAPp	15.0	--	--	18.6	>17.7	--	--	--
DTp	23.8	--	--	18.7	--	--	--	--
DAPpf	≥14.4	--	--	17.3	--	--	--	--
DTpf	22.9	--	--	17.6	--	--	--	--
DAPm	10.1	--	--	--	--	≤11.4	--	--
DTm	14.5	--	--	--	12.0	--	--	--
DTd	23.5	23.4	--	--	--	≥21.9	22.5	--
DAP <sub>III</sub> / DAPI	13.6	15.6	--	--	--	13.7	14.3	14.3
DT <sub>III</sub> / DTI	10.3	10.3	--	--	--	9.8	10.5	9.9
DAP <sub>IV</sub> / DAPr	13.8	14.8	--	15.4	--	13.9	14.3	--
DT <sub>IV</sub> / DTr	10.0	10.1	--	11.1	--	- 10.3	9.7	--
L	158.0							
L3	153.7							
L4	154.5							

<b>Phalanx</b>			DAPp	DAPpf	DTp	L	DAPd	DTd	Lint	Lext
phalanx 1		right	14.2	12.6	9.6	36.8	8.2	9.7		
phalanx 1		left	--	--	--	--	8.2	8.4		
phalanx 1	manus?	right	15.6	14.2	12.1	34.2	>9.4	11.3		
phalanx 1	pes?	left	14.2	13.3	11.2	34.2	8.6	9.7		
phalanx 1	pes?	right	14.1	13.1	11.1	34.4	8.4	9.6		
phalanx 1	manus	lleft	--	--	12.7	33.8	--	--		
phalanx 2		right	--	--	--	>18.3	≥8.5	--		
phalanx 1*	pes	left	14.9	14.4	11.6	32.2	8.5	9.8		
phalanx 1*	pes	right	14.9	13.7	11.4	33.2	8.5	9.6		
phalanx 2*	pes	left	12.6		10.5	19.2	9.2	8.2	21.7	21.7
phalanx 2*	pes	right	12.8		10.6	19.9	9.2	8.5	--	--
phalanx 3*	pes	left	13.8		8.5	23.3				
phalanx 3*	pes	right	13.4		8.6	22.6				

<b>Tibia</b>	DAPd	DTd	DTfast
dext	17.6	22.2	15.9

<b>Calcaneum</b>	DAPh	DTh	DAPn	DTn	DAPsf	DTsf	Lu
dext	--	--	15.1	7.0	18.4	16.0	
dext	15.5	14.8	14.3	8.1	--	--	- 37.4

<b>Astragalus</b>	Lext	Lm	Lint	DTp	DTd
sin	29.5	24.2	27.5	18.8	18.0
sin	--	22.9	26.2	16.2	--
sin	≥25.1	21.8	25.2	16.1	16.1
dext	30.6	24.8	>27.7	--	18.9

Metapodial	Mc	Mc	Mc	Mt	Mt	Mt	Mt*	Mp
	dext	?	right	sin	dext	?	?	left
DAPp	15.0	—	—	18.6	>17.7	—	—	—
DTp	23.8	—	—	18.7	—	—	—	—
DAPpf	≥14.4	—	—	17.3	—	—	—	—
DTpf	22.9	—	—	17.6	—	—	—	—
DAPm	10.1	—	—	—	—	≤11.4	—	—
DTm	14.5	—	—	—	12.0	—	—	—
DTd	23.5	23.4	—	—	—	≥21.9	22.5	—
DAPIII/ DAPI	13.6	15.6	—	—	—	13.7	14.3	14.3
DTIII / DTI	10.3	10.3	—	—	—	9.8	10.5	9.9
DAPIV/ DAPr	13.8	14.8	—	15.4	—	13.9	14.3	—
DTIV /DTr	10.0	10.1	—	11.1	—	-10.3	9.7	—
L			158.0					
L3			153.7					
L4			154.5					
<b>Phalanx</b>	DAPp	DAPpf	DTp	L	DAPd	DTd	Lint	Lext
phalanx 1		right	14.2	12.6	9.6	36.8	8.2	9.7
phalanx 1		left	—	—	—	—	8.2	8.4
phalanx 1	manus?	right	15.6	14.2	12.1	34.2	>9.4	11.3
phalanx 1	pes?	left	14.2	13.3	11.2	34.2	8.6	9.7
phalanx 1	pes?	right	14.1	13.1	11.1	34.4	8.4	9.6
phalanx 1	manus	left	—	—	12.7	33.8	—	—
phalanx 2		right	—	—	—	>18.3	≥8.5	—
phalanx 1*	pes	left	14.9	14.4	11.6	32.2	8.5	9.8
phalanx 1*	pes	right	14.9	13.7	11.4	33.2	8.5	9.6
phalanx 2*	pes	left	12.6	10.5	19.2	9.2	8.2	21.7
phalanx 2*	pes	right	12.8	10.6	19.9	9.2	8.5	—
phalanx 3*	pes	left	13.8	—	8.5	23.3	—	—
phalanx 3*	pes	right	13.4	—	8.6	22.6	—	—
<b>Tibia</b>	DAPd	DTd	DTfast					
dext	17.6	22.2	15.9					
<b>Calcaneum</b>	DAPh	DTh	DAPn	DTn	DAPsf	DTsf	Lu	
dext		—	—	15.1	7.0	18.4	16.0	
dext		15.5	14.8	14.3	8.1	—	—	-37.4
<b>Astragalus</b>	Lext	Lm	Lint	DTp	DTd			
sin	29.5	24.2	27.5	18.8	18.0			
sin	—	22.9	26.2	16.2	—			
sin	≥25.1	21.8	25.2	16.1	16.1			
dext	30.6	24.8	>27.7	—	18.9			

**Table 1.** Measurements of the teeth and bones of the bovid from Campidano. All measurements are in mm. The metapodial and phalanges marked with \* belong to the same foot. Where "sin" and "dext" are indicated, this refers to the side of the body. In phalanges and fragments of metapodials, it is often not known whether they belonged to a right or left limb, and where "right" and "left" is indicated, this refers to the position relative to the axis of the foot.

**Taula 1.** Mesures de les dents i ossos del bòvid de Campidano. Totes, en mm. Els metàpodes i falanges marcats amb un asterisc (\*) pertanyen al mateix peu. On s'indiquen « sin » i « dext », es refereix al costat del cos. Les falanges i fragments de metàpodes sovint no se sap si pertanyen a un membre dret o esquerre, i on s'indica «right» i «left» es refereix a la posició respecte l'eix del peu.

material that do not seem to fit the Caprinae either imply that: the Campidano material is no *Nesogoral*, or *Nesogoral* is not a caprine, but became similar to caprines through convergent evolution. For this it is necessary to discuss the morphology of early Caprinae.

Caprinae appeared relatively late in the fossil record, but existed in Europe from the early Late Miocene onwards (Köhler *et al.*, 1995; Alcalá & Morales, 1997; Gentry *et al.*, 1999). The latter authors state that the Caprinae are a well defined group on the basis of DNA, but that there are few or no morphological characters that define the subfamily and proceed to discuss some cranial and dental characters. However, Caprinae have so many peculiar morphologies in the post cranial skeleton, that it should be possible to find characters that help to recognise most members of this subfamily. Though, as usual, the many typical morphologies may get fewer closer to the origin of the group.

Gliozzi & Malatesta (1980) indicated *Pachygazella* as the most likely ancestor of *Nesogoral*, but some Late Miocene Caprinae were described after their study. I have not had access to postcranial material of *Pachygazella* or to a publication describing it, but of at least some of the European Late Miocene caprines, phalanges and metapodials have been described and figured. *Norbertia* from the latest Miocene of Maramena is primitive in being still not very hypsodont and having a P<sub>4</sub> that may have the anterior fossid open or more or less closed, but already very typically caprine in having a wide second phalanx with a proximal facet that overhangs a little and has relatively little curvature, a reduced “plateau post-articulaire” and a low axial half of the distal facet that protrudes much distally, and in having a third phalanx with a very extended horizontal part of the proximal articular facet and a well developed extensor apophysis (Köhler *et al.*, 1995). These morphologies form part of foot type C of Köhler (1993).

Köhler (1993) described a number of characters that are typical of three foot types and interpreted these in terms of ecology (A wooded and humid, B open flat and dry, C mountainous habitats) and believed that these types do not reflect phylogeny. This is certainly true for most characters, but type C seems to be mainly restricted to Caprinae and Neotragini, and a number of characters related to the C type adaptation have probably evolved only in Caprinae. Köhler (1993) used *Gazella* as an example of foot type B, but also indicated that this type is of the open landscapes. *Bison* was common in open landscapes and has a large “plateau postarticulaire” and therefore a locomotion that is different from that of *Gazella*. Antilopinae, like *Gazella* and *Madoqua* have second phalanges with a reduced “plateau postarticulaire” and an overhanging proximal facet and third phalanges with a proximal facet with a well developed horizontal part. These morphologies indicate a posture that is necessary for the “pogostick effect” described by Leinders (1979).

This pogostick effect is known from horses and ruminants. This is an adaptation which involves the modification of several muscles, tendons and ligaments. One of them is the *musculus interosseus*. Contraction of this muscle causes volar flexion of the foot. When this muscle is replaced through tendofication by a tendon, the Tendo interosseus or suspensory ligament, the elas-

tic properties of the tendon cause volar flexion. Dorsal flexion of the phalanges causes this elastic tendon to become extended, and thus acts to absorb the shock of landing after jumping. If not constrained by the action of muscles, the extension of this tendon will automatically cause volar flexion as a reaction. This is a mechanism which preserves or re-uses energy in running.

For the pogostick effect to function, a particular posture in rest is necessary. While normally the metapodial and phalanges are approximately aligned, in animals with pogostick locomotion, the first phalanx tends to have some dorsal flexion with respect to the metapodial, the second phalanx has volar flexion with respect to the first phalanx, and the third phalanx has again dorsal flexion. This posture is seen in many morphologies, some of the easiest recognisable are:

- Distal articulations of the metapodials that permit more movement in dorso-plantar direction.
- A distal facet in the first phalanx that extends much on the plantar side.
- An “overhanging” proximal facet in the second phalanx.
- A reduced (or receding) plateau post articulaire in the second phalanx.
- A well developed extensor apophysis in the third phalanx.
- A proximal facet in the third phalanx with a relatively large horizontal part.

This “pogostick locomotion” is probably a necessary pre-adaptation to arrive at a C type of locomotion and starting with this morphology, the Caprinae, developed existing morphologies further and acquired a set of morphologies which are possibly a further adaptation to mountainous or rocky environments, like:

- A wide second phalanx having the axial part of the distal facet protruding much distally.
- Shorter and more robust metapodials with: a shaft that widens abruptly towards the distal articulations, and distal articulations with a particular shape (see under “description and comparison”).
- No elevated area of insertion of tendon of the lateral or medial digital extensor muscles on the proximal end of the dorsal surface of the first phalanx.
- Reduction of the “height” of the facets for the sesamoids on the first phalanx.
- Shorter third phalanges.

In addition, Caprinae have typical morphologies in the proximal metatarsal, ulna, and many carpal and tarsal bones. (Which possibly are also adaptations to a rocky or mountainous environment). The Antilopinae do not only share the pogostick locomotion (and corresponding morphologies) with the Caprinae, but also many dental characters, like: the loss of interlobular columns, flat lingual walls in the lower molars, the shape of the buccal wall of the upper molars, etc. Caprinae, have a dentition that is basically more hypsodont and usually with more reduced premolars. It is possible that Caprinae evolved from Antilopinae.

Bearing the foregoing in mind, the characters that suggest that the Campidano bovid may not be a caprine are:

- A long and gracile metacarpal.
- The gradual increase in width from the shaft of the metapodials to the distal end of the bone.

Fig. 5. Bivariate diagram of the astragalus: *Nesogoral* from Capo Figari FM (NMB), Campidano and Capo Figari 2 (IVAUI) and *Megaloceros cazioti* from Corbeddu (IVAUI).

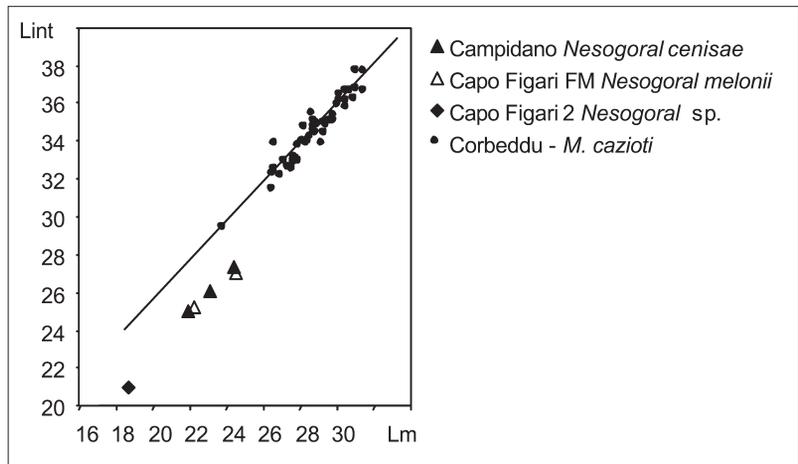


Fig. 5. Diagrama bivariat de l'astràgal de: *Nesogoral* de Capo Figari FM (NMB), Campidano i Capo Figari 2 (IVAUI), i *Megaloceros cazioti* de Corbeddu (IVAUI).

Fig. 6. The index 100 DAPd / DTd in the second phalanx in selected Bovidae and Cervidae.

- A) Bovidae with a second phalanx with a reduced facet post articulaire: *Nesogoral* from Capo Figari FM (NMB) and Campidano, *Myotragus* from Son Mayol (IVAUI), *Praeovibos* sp. from Quibas (MNCN), *Praeovibos/Ovibos* from the Olyorian (PIN), *Praeovibos priscus* from Atapuerca TD7 (MB) and Bad Frankenhausen, *Capra ibex* from Petralona (AUT), *Hemitragus bonali* from Hundsheim (IPUW), recent *Budorcas taxicolor* (NHM), *Gazellospira torticornis* from Pyrgos (IVAUI), *Gallogoral* from Senèze (NMB), recent *Capricornis sumatrensis* (NNML), recent *Madoqua saltiana* (NMW), *Gazella* from Pikermi (NMW), Gerakarou (AUT), Vátera (NHV), Ubeidiya (HUJ) and recent (LAUT).

- B) Bovidae and Cervidae with a second phalanx with large facet post articulaire: recent *Cephalophus niger* (NHM), recent *Anoa depressicornis* (ZMA, IVAUI), *Bison schoetensacki* from Bilzingsleben (FBFSU), *Bison menneri* from Untermassfeld (IQW), *Bos primigenius* from Miesenheim (FASMN), Torralba (MNCN), Neumark Nord (LVH), Lehringen (HMY), *Leptobos* from Montopoli (IGF), Olivola (IGF), Láchar (MNCN) and Pyrgos (IVAUI), *Megaloceros giganteus* Ireland (NHM), *Megaloceros* aff. *cazioti* from Santa Lucia 1 (IVAUI), Cervidae from Liko and Liko 2D on Crete (IVAUI), *Dama dama geiselana* from Neumark Nord (LVH), *Cervus elaphus spelaeus* from Neumark Nord (LVH), *Alces* from East Runton (NHM), Voigtstedt (IQW), Stissenborn (IQW) and Mauer (SMNK), and *Capreolus* from Can Rubau (CIAG).

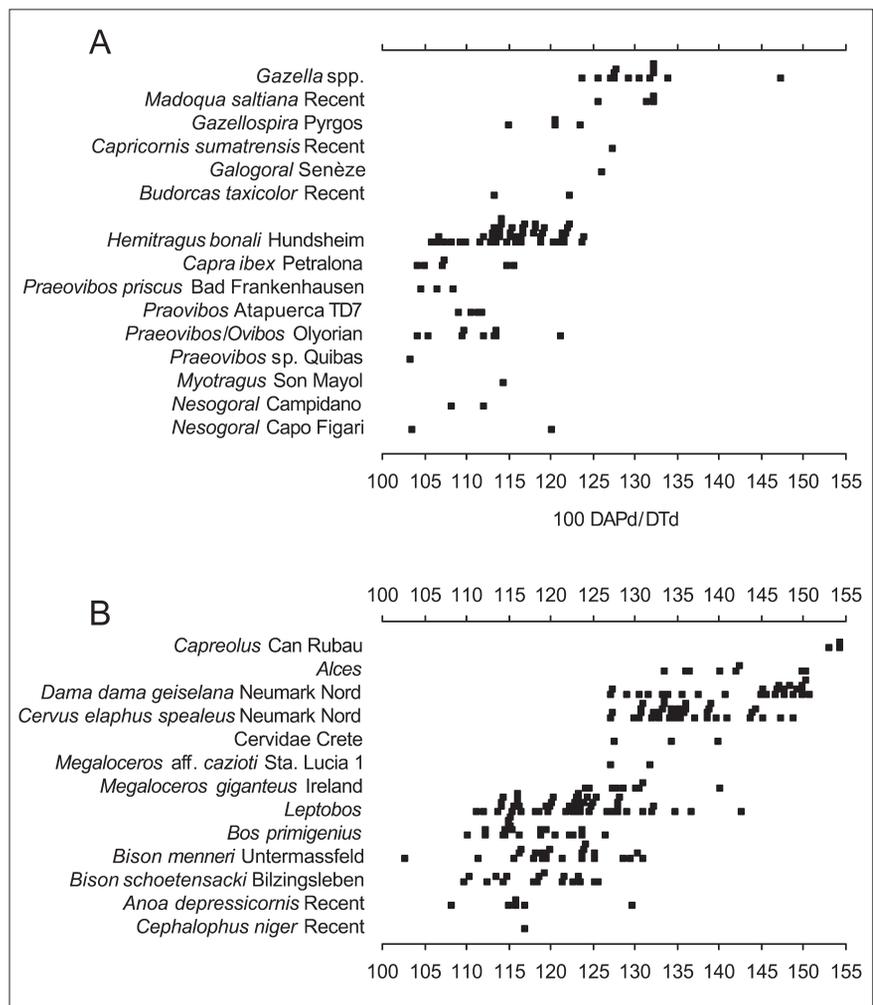


Fig. 6. L'index 100 DAPd / DTd a la segona falange de Bovidae i Cervidae seleccionats.

- A) Bovidae amb una segona falange amb una faceta post-articular reduïda: *Nesogoral* de Capo Figari FM (NMB) i Campidano, *Myotragus* de Son Maiol (IVAUI), *Praeovibos* sp. de Quibas (MNCN), *Praeovibos/Ovibos* de Olyorian (PIN), *Praeovibos priscus* d'Atapuerca TD7 (MB) i Bad Frankenhausen, *Capra ibex* de Petralona (AUT), *Hemitragus bonali* de Hundsheim (IPUW), *Budorcas taxicolor* recent (NHM), *Gazellospira torticornis* de Pyrgos (IVAUI), *Gallogoral* de Senèze (NMB), *Capricornis sumatrensis* recent (NNML), *Madoqua saltiana* recent (NMW), *Gazella* de Pikermi (NMW), Gerakarou (AUT), Vátera (NHV), Ubeidiya (HUJ) i recent (LAUT).

- B) Bovidae i Cervidae amb una segona falange amb una faceta post-articular grossa: *Cephalophus niger* recent (NHM), *Anoa depressicornis* recent (ZMA, IVAUI), *Bison schoetensacki* de Bilzingsleben (FBFSU), *Bison menneri* de Untermassfeld (IQW), *Bos primigenius* de Miesenheim (FASMN), Torralba (MNCN), Neumark Nord (LVH), Lehringen (HMY), *Leptobos* de Montopoli (IGF), Olivola (IGF), Láchar (MNCN) i Pyrgos (IVAUI), *Megaloceros giganteus* Irlanda (NHM), *Megaloceros* aff. *cazioti* de Santa Lucia 1 (IVAUI), Cervidae de Liko i Liko 2D a Creta (IVAUI), *Dama dama geiselana* de Neumark Nord (LVH), *Cervus elaphus spelaeus* de Neumark Nord (LVH), *Alces* d'East Runton (NHM), Voigtstedt (IQW), Stissenborn (IQW) i Mauer (SMNK), i *Capreolus* de Can Rubau (CIAG).

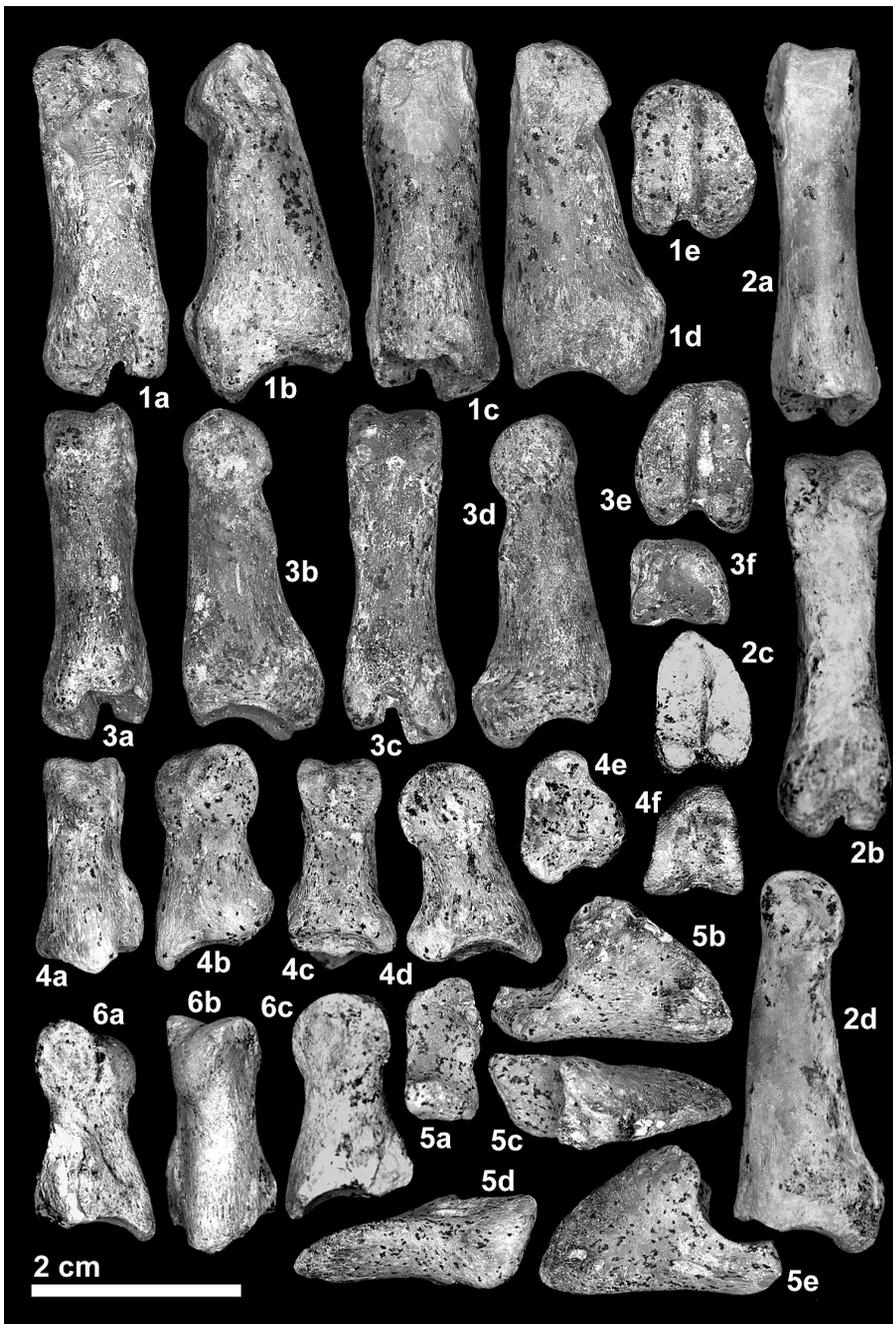


Plate 3. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral* from Capo Figari FM (Fig. 6; NMB).

Figure 1. First phalanx right of the axis of the manus: a) volar view, b) axial view, c) palmar view, d) anti-axial view, e) proximal view.

Figure 2. First phalanx right of the axis of the pes: a) dorsal view, b) plantar view, c) proximal view, d) anti-axial view.

Figure 2. First phalanx left of the axis of the pes: a) dorsal view, b) axial view, c) plantar view, d) anti-axial view, e) proximal view, f) distal view.

Figure 4. Second phalanx left of the axis of the pes: a) dorsal view, b) axial view, c) plantar view, d) anti-axial view, e) proximal view, f) distal view.

Figure 5. Third phalanx left of the axis of the pes: a) proximal view, b) axial view, c) dorsal view, d) anti-axial view, e) plantar view.

Figure 6. Second phalanx right of the axis of the pes (?): a) axial view, b) dorsal view, c) anti-axial view.

Làmina 3. *Nesogoral cenisae* n.sp. de Campidano (figs. 1-5) i *Nesogoral* de Capo Figari FM (Fig. 6; NMB).

Figura 1. Primera falange dreta de l'eix del peu anterior: a) norma volar, b) norma axial, c) norma palmar, d) norma anti-axial, e) norma proximal.

Figura 2. Primera falange dreta de l'eix del peu posterior: a) norma dorsal, b) norma plantar, c) norma proximal, d) norma anti-axial.

Figura 3. Primera falange esquerra de l'eix del peu posterior: a) norma dorsal, b) norma axial, c) norma plantar, d) norma anti-axial, e) norma proximal, f) norma distal.

Figura 4. Segona falange esquerra de l'eix del peu posterior: a) norma dorsal, b) norma axial, c) norma plantar, d) norma anti-axial, e) norma proximal, f) norma distal.

Figura 5. Tercera falange esquerra de l'eix del peu posterior: a) norma proximal, b) norma axial, c) norma dorsal, d) norma anti-axial, e) norma plantar.

Figura 6. Segona falange dreta de l'eix del peu posterior (?): a) norma axial, b) norma dorsal, c) norma anti-axial.

- The shape of the distal articulations of the metapodials.
- The narrow first phalanges, occasionally having an elevated area for insertion of the tendon of the digital extensor muscle.
- The second phalanx with a distal articulation that does not project more distally on the axial side.
- The ulna having a lateral facet or area of contact with the radius, that is not much extended in lateral direction.

All these characters are present in the Antilopinae. Some of the characters mentioned in the descriptions are like in Caprinae, but do not exclude other affinities:

- Hypsodont teeth. Increase in hypsodonty is common in insular environment.

- Tooth morphology: no interlobular column, caprine fold, flat lingual walls of the lower molars, flat buccal walls of the paracone and metacone, three pronounced buccal styles in the upper molars, P4 with meta-precrisid closing the anterior fossid.
  - First phalanx with facets for the sesamoids that have a very short dorso-plantar diameter.
  - Second phalanx with a reduced "plateau post-articulaire" and a overhanging proximal facet.
  - Third phalanx with a facet that has a proximal facet that has a long section that is parallel to the plantar surface of the bone.
  - Third phalanx with a well developed extensor apophysis.
- Again, all these characters are also found in some or

**Plate 4.** *Nesogoral cenisae* n.sp. from Campidano (figs. 1-4, 6-8) and *Nesogoral* from Capo Figari FM (Fig. 5; NMB).

Figure 1. Right astragalus: a) posterior view, b) lateral view.

Figure 2. Left astragalus: a) proximal view, b) posterior view, c) medial view, d) anterior view, e) lateral view, f) distal view.

Figure 3) Left astragalus: posterior view.

Figure 4) Right calcanaeum: a) upper view, b) lateral view, c) anterior view, d) medial view, e) posterior view.

Figure 5) Right magnum: posterior view (not to scale).

Figure 6) Left distal radius: a) distal view, b) posterior view, c) anterior view.

Figure 7) Right radius, proximo-medial part: a) anterior view, b) medial view, c) posterior view.

Figure 8) Left astragalus: posterior view.

**Làmina 4.** *Nesogoral cenisae* n.sp. de Campidano (figs. 1-4, 6-8) i *Nesogoral* de Capo Figari FM (Fig. 5; NMB).

Figura 1. Astràgal dret: a) norma posterior, b) norma latera.

Figura 2. Astràgal esquerre: a) norma proximal, b) norma posterior, c) norma medial, d) norma anterior, e) lateral, f) norma distal.

Figura 3) Astràgal esquerre: norma posterior.

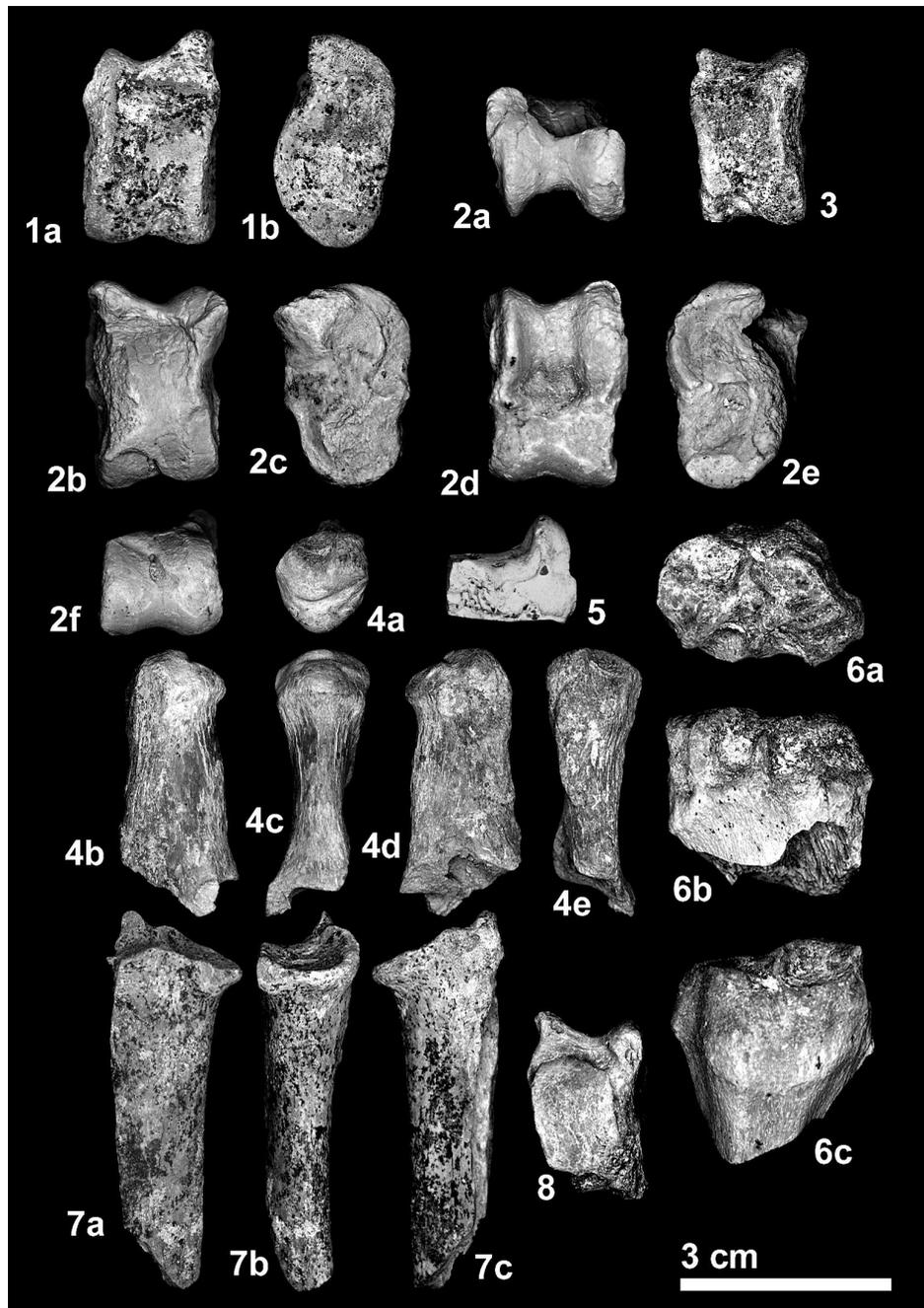
Figura 4) Calcani dret: a) norma superior, b) norma lateral, c) norma anterior, d) norma medial, e) norma posterior.

Figura 5) Capitatotrapezoide dret: norma posterior (no a escala).

Figura 6) Left distal radius: a) distal view, b) posterior view, c) anterior view.

Figura 7) Radi dret fragment distal, part proximo-medial: a) norma anterior, b) norma medial, c) norma posterior.

Figura 8) Astràgal esquerre: norma posterior.



all of the Antilopinae. Some characters or combination of characters seems to be typical for all or at least most of the Caprinae:

- Second phalanx that is wide, and in particular in combination with the reduced or receding “plateau post-articulaire” and the overhanging proximal facet.
- Ulna with wide facet for the humerus.
- The morphology of the proximal surface of the metatarsal.
- Wide astragalus.

Most of the differences between *Nesogoral* and the majority of the Caprinae are in the metapodials and in the phalanges and may well be related. Similarly, the caprine *Myotragus* changed the original morphology of its phalanges in response to insular environment, acquir-

ring a morphology and a locomotion type that are very different from those of all continental Caprinae (Köhler & Moyà-Solà, 2001). In the ulna from Campidano, a derived character of most Caprinae is absent (it is not very wide at its widest point); it is thus primitive. The maintenance of a primitive character in a caprine lineage that originated some 5 Ma ago is not surprising. The characters that are typical of the Caprinae, are from different parts of the skeleton (wide facet for the humerus in the ulna, metatarsal, second phalanx). It is difficult to see how these different characters, which are not directly related, may have evolved convergently. It is, however, possible to explain the differences from most Caprinae as a single adaptation, which is in favor of a placement of the bovid from Campidano within the Caprinae.

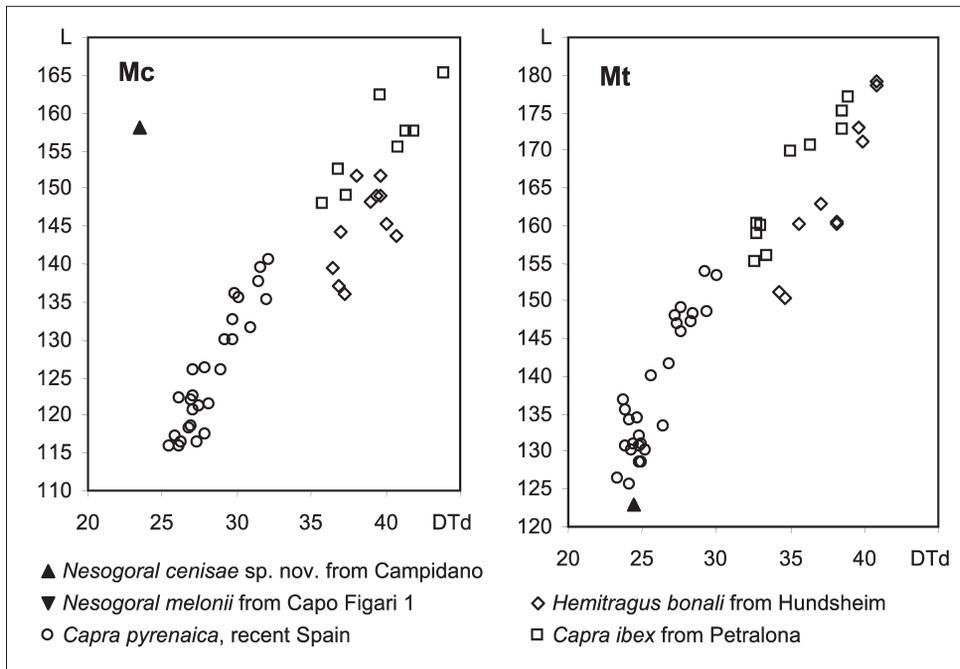
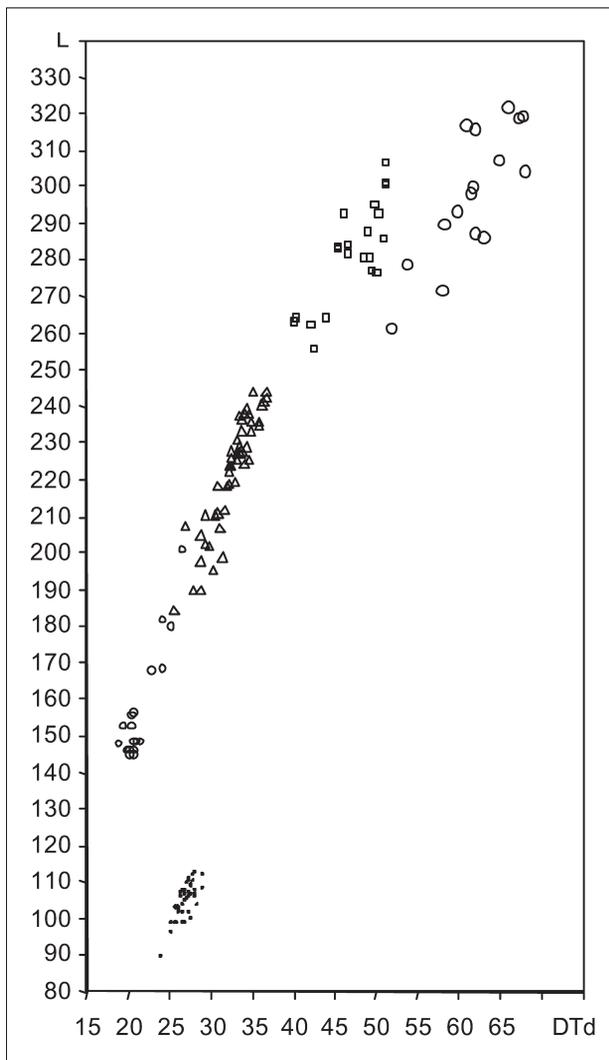


Fig. 7. Bivariate diagram of the metacarpals and metatarsals of selected caprines. Provenance of data as in Figure 4, and *Nesogoral melonii* from Capo Figari 1 (Gliozzi & Malatesta, 1980).

Fig. 7. Diagrama bivariat dels metacarpians i metatarsians de caprins seleccionats. Dades de procedència, com a la figura 4, i *Nesogoral melonii* de Capo Figari 1 (Gliozzi & Malatesta, 1980).



**Carnivora**  
 occurring with the deer from  
 Karpathos:  
 none

- Karpathos
- *Cervus elaphus*
- *Capreolus*
- △ *Dama*
- *M. solilhacus*

Fig. 8. Bivariate diagram of the metacarpal of *Cervus cerigensis* from Kandilia Cave (Kuss, 1975) and *Cervus* aff. *cerigensis* from Karpathos I and II (IVAU) compared with *Cervus elaphus* from Voigtstedt (IQW), Petralona (AUT) and Neumark Nord (LVH). *Dama* from Montopoli (IGF), Ubeidiya (HUU), Tegelen (NHMM), Casa Frata (IGF), Il Tasso (IGF), Valdarno (IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMM), Gimbshheim (NMM), and recent *Dama mesopotamica* (HUU); *Capreolus* from Pirro Nord (?; cast IGF), Mosbach (NMM), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Lehringen (HMM) and recent from Spain (MNCN) and the Netherlands (NML); *Megaloceros solilhacus* and related forms from Ubeidiya (HUU), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCPV), Trimmingham (NHM), Sidestrand (NHM), Mundesley (NHM), and Petralona (AUT).

Fig. 8. Diagrama bivariat del metacarpà de *Cervus cerigensis* de la Cova Kandilia (Kuss, 1975) i *Cervus* aff. *cerigensis* de Karpathos I i II (IVAU) comparat amb *Cervus elaphus* de Voigtstedt (IQW), Petralona (AUT) i Neumark Nord (LVH). *Dama* de Montopoli (IGF), Ubeidiya (HUU), Tegelen (NHMM), Casa Frata (IGF), Il Tasso (IGF), Valdarno (IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMM), Gimbshheim (NMM), i *Dama mesopotamica* recent (HUU); *Capreolus* de Pirro Nord (?; motlle IGF), Mosbach (NMM), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Lehringen (HMM) i recent de la Península Ibèrica (MNCN) i dels Països Baixos (NML); *Megaloceros solilhacus* i formes relacionades de Ubeidiya (HUU), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCPV), Trimmingham (NHM), Sidestrand (NHM), Mundesley (NHM), i Petralona (AUT).

## The morphology of the Campidano bovid compared to *Nesogoral melonii*

In most cases when the morphology could be compared with *Nesogoral melonii* from Capo Figari 1 and the Forsyth Major collection, there are no great differences. A possible exception is the width or robusticity of the first phalanx, which might be more caprine-like in Capo Figari. However, the typical wide second phalanx which lacks the distal projection of part of the distal articular facet is similar in both. It has to be assumed that both bovids are closely related and there does not seem to be a good reason for not classifying the bovid from Campidano as *Nesogoral*.

However, fragments of two metatarsals of *Nesogoral* from Capo Figari (Gliozzi & Malatesta, 1980, p. 328, Pl. 4, figs. 1 & 4) seem to be relatively long and gracile within the Caprinae, but with lengths of 119 and 123 and a distal width of 24.4 mm, these bones seem to be shorter and more robust than what could be expected in the Campidano bovid. In bovids, the metatarsal is usually clearly longer and less robust than the metacarpal. However, the metacarpal from Campidano is nearly one third longer than the metatarsal from Capo Figari 1 and has a comparable distal width. It is thus much more gracile. A comparison of the *Nesogoral* metapodials with the metacarpals and metatarsals in *Hemitragus bonali* from Hundsheim, *Capra ibex* from Petralona and recent *Capra pyrenaica* shows that, the bovids from Campidano and Capo Figari 1 represent different species (Fig. 7). The bovid from Campidano is *Nesogoral*, but is not *Nesogoral melonii*. A new species is named here:

### *Nesogoral cenisae* nov. sp.

Holotype: the metacarpal figured in Plate 2, fig. 1.

Paratypes: the other specimens from Campidano described here.

Definition: *Nesogoral* close in size and morphology to *Nesogoral melonii*, but with longer and more gracile metapodials.

Derivatio nominis: the species is named in honour of Cenis Valdés.

Type locality: Campidano.

Age of the type locality: not exactly known, probably early Middle Pleistocene.

## CARNIVORES AND LOCOMOTORY ADAPTATIONS OF INSULAR ARTIODACTYLS

In the classic model of insular environment and evolution, typical insular faunas are characterised by a particular taxonomical composition, with Carnivora tending to be absent, which leads to a series of adaptations: size reduction in large mammals and size increase in small mammals, low gear locomotion, and particular visual and dental adaptations (Sondaar, 1977, 1986). However, predators are not always absent and low gear locomotion is not always developed to the same extreme. Low gear locomotion is more energy efficient and would thus be an advantage in any environment, if it were not for the

presence of predators. Low gear locomotion is seen in the morphology of the bones, fusions of bones, the proportions of the different segments of the limb, and the proportions of the individual bones (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; De Vos, 1979; Spoor, 1988a and b; Köhler & Moyà-Solà, 2001; and others). The metacarpal is probably the bone that most clearly reflects this adaptation.

The metacarpal of *Myotragus*, which lived in a carnivore-free environment, is very short and robust (Figs. 3 & 4).

The fossil endemic fauna from Karpathos included deer but no predators (Kuss, 1975; Dermitzakis & Sondaar 1979). Two species of deer have been described *Cervus cerigensis* and *C. pygadiensis*, which probably form a lineage. Antlers of the more primitive species have a crown as in *Cervus elaphus*, which is its probable ancestor. The metacarpals in Fig. 8 are from a form which is probably intermediate between the type material of the two species. *Cervus elaphus* changed much in size at various moments in the Pleistocene, and we do not know the size of the founder population on Karpathos. Nevertheless, the distal width (DTd), which is probably related to body weight, reflects an important decrease in size in comparison to any continental *Cervus*. But the length decreased relatively more and as a consequence the metapodials are more robust than in any continental deer. Such short and robust metapodials indicate low gear locomotion.

The fossil deer from Crete have been described by De Vos (1979, 1984). No Carnivora have been reported from the faunas that occurred with these deer. The ancestors of the deer are debated, but to me it seems likely that *Cervus elaphus* and *Dama* gave rise to at least some of these endemic deer. There were various contemporaneous species of deer which had different locomotory adaptations. Some of the deer may have had a giraffe-like appearance. Most deer however, were dwarfed and had robust metapodials that reflect low gear locomotion (Fig. 9).

The Pleistocene deer of Sardinia are usually assigned to *M. cazioti*, though there are of very different sizes. These deer are usually assumed to be descendants of *Megaloceros solilhacus* (or similar forms, referred to under a variety of names, including *Megaceroides*, *Praemegaceros* and “*verticornis*”). The metapodials of the Sardinian deer are much more gracile than those of *M. solilhacus* and it was noted that either we have to assume this deer became more cursorial, or we have to consider a possible descendance from species with more gracile metapodials such as: *Dama*-like deer, a form close to *Eucladoceros tetraceros*, *Eucladoceros giulii* and *Arverno-ceros* (Van der Made, 1999a). Palombo *et al.* (2003) suggested that Van der Made (1999a) believed that *Eucladoceros giulii* is ancestral to *M. cazioti*, derived *M. cazioti* from “slender-limbed megalocerines” (which includes material assigned by Van der Made, 1999b to *E. giulii*) and suggested a size decrease in a *M. cazioti* lineage and increase in robusticity of the metapodials. In addition to large material from Capo Figari FM (NMB) and Sadali, a particularly large metapodial from Santa Lucia 1 (the isolated dot in Fig. 10) is much larger than *M. cazioti* from Corbeddu and is wider and more robust than any continental *Dama*, suggesting that these authors may have

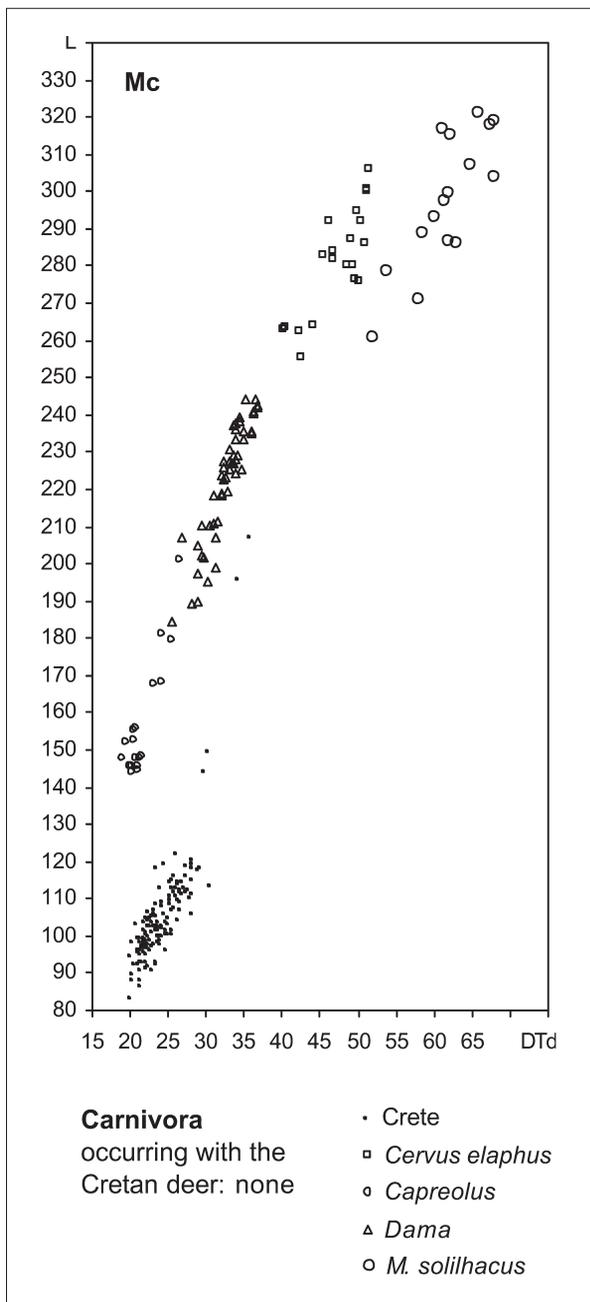


Fig. 9. Bivariate diagram of the metacarpal of the Pleistocene Cervidae from Crete (IUAU, SMNK) compared with *Cervus elaphus*, *Dama*, *Capreolus* and *Megaloceros solilhacus* and related forms (provenience of data as in Figure 10).

Fig. 9. Diagrama bivariat del metacarpia de Cervidae del Pleistocè de Crete (IUAU, SMNK) comparat amb *Cervus elaphus*, *Dama*, *Capreolus* and *Megaloceros solilhacus* i formes relacionades (procedència de les dades com a la Figura 10).

been correct in assuming a large species to be ancestral, and a size decrease in the Sardinian lineage. However, we have to note that the “slender-limbed megalocerines” of these authors also include the deer from Ubeidiya, which is related to *M. solilhacus* and which has a metacarpal with an index of 517, which is more robust than any of the *M. cazioti* from Corbeddu. If the Sardinian deer descended from *Dama*, this would imply an increase in size, which is not very likely in insular envi-

ronment. It is of importance here to note that *M. cazioti* became either: 1) much smaller with more gracile metapodials (if a descendant of a member of the *M. solilhacus* lineage) or 2) much smaller with very slightly more robust metapodials (if a descendant of *E. giulii* or “slender-limbed megalocerines”), but that in any case it did not greatly increase the robusticity of its metapodials. The Sardinian deer have always lived together with *Cynotherium*.

*Dama carburangelensis* and *Cervus elaphus siciliae* are endemic forms from the Pleistocene of Sicily (Gliozzi & Malatesta, 1982; Gliozzi *et al.*, 1983) have metacarpals which show dwarfing and which, in the case of *Dama* show only a minor increase in robusticity, and in the case of *Cervus* even a decrease in robusticity (Figs. 11-12). These forms lived together with large carnivores like *Panthera leo*, *Crocuta crocuta* and *Ursus arctos* (Di Maggio *et al.*, 1999; Marra, 2003).

From the same faunas of Sicily, also endemic *Bos* and *Bison* have been reported (Brugal, 1987; Di Maggio *et al.*, 1999). The metacarpals of *Bos* show clearly dwarfing and a moderate increase in robusticity (Fig. 13).

The Pleistocene fauna from Pianosa was discussed by Stehlin and includes *Ursus*, *Vulpes*, *Equus*, “short-legged deer”, deer of the size of *Cervus elaphus*, *Capreolus* and *Bos* (Stehlin, 1929; Brugal, 1987). The *Bos* shows dwarfing and a moderate increase in robusticity (Fig. 13). The short-legged deer has metapodials with indices 490 and 500 (calculated from the figures by Stehlin), while the larger deer is represented by a skull fragment that was reported to be similar in morphology to *C. elaphus*. If the “short-legged deer” is a descendant of *Cervus elaphus* or *Dama* it became smaller and more robust, but if it is a descendant of some *Megaloceros* species, it became smaller, but not more robust.

From Sardinia a dwarfed pig is known, *Sus sondaari*, which may have been more cursorial than its ancestor (Van der Made, 1999a). This suid was reported, along with *Chasmaporthetes* from Cava 6 near Orsei (Sondaar, 2000; Abazzi *et al.*, 2004).

From the foregoing it appears that Artiodactyla dwarfed and evolved “low gear locomotion” in predator free islands, but when predators were present they may have dwarfed but evolved little or nothing in the direction of “low gear locomotion” and may have even become more cursorial. It is proposed here that *Nesogoral* in the presence of predators became more cursorial (explanation 3 of the introduction). This resulted in longer and more gracile metapodials and first phalanges and different distal articulations in the metapodials and second phalanges. In terms of the classification of Köhler (1993) the animal changed towards locomotion type B, which is typical of open, flat and dry habitats.

*Nesogoral* may have lived during some 4 Ma together with *Chasmaporthetes* on Sardinia. The only other large mammals were *Sus* and *Macaca*. Sardinia may have had plains with an open niche for a large herbivore, which may have been occupied by *Nesogoral*. The more elongate metapodial in *Nesogoral cenisae* explained by various models, including the following:

- 1) *Nesogoral* moving into these plains and splitting up into two lineages, *N. melonii* in the mountains and the cursorial *N. cenisae* in the plains.

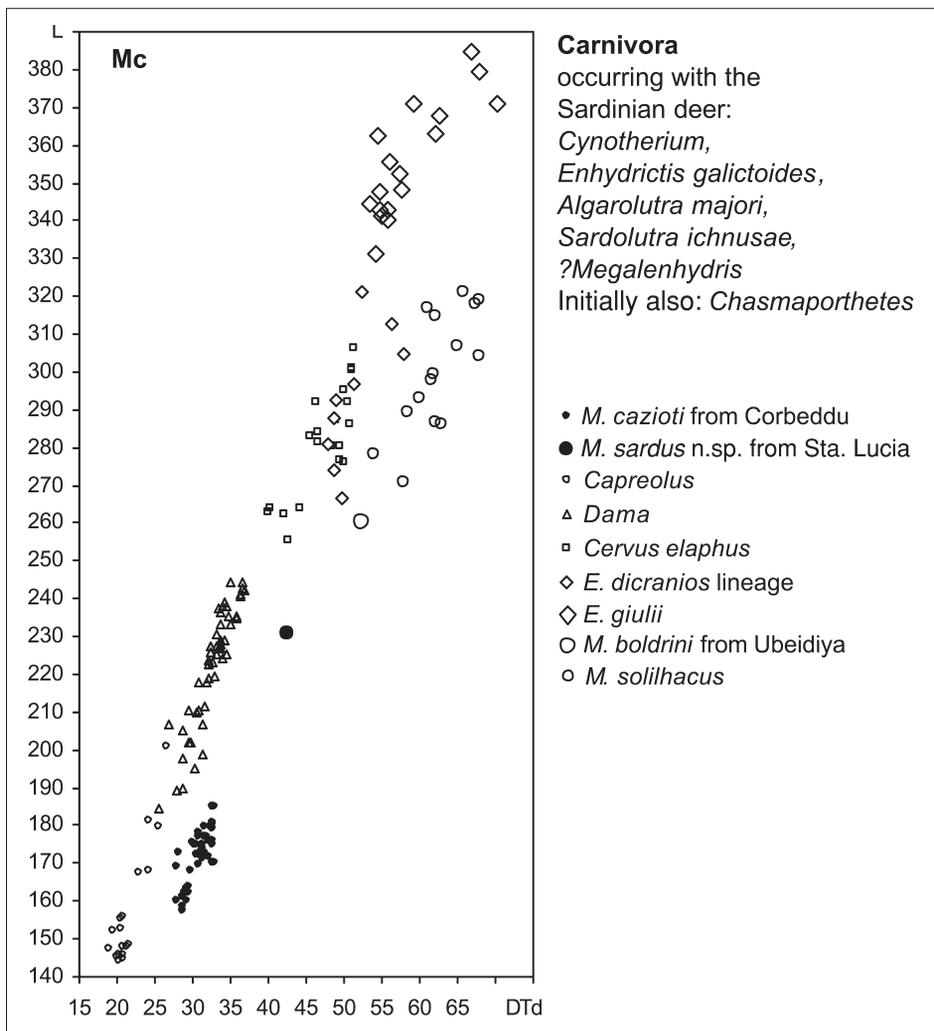


Fig. 10. Bivariate diagram of the metacarpal of *Megaloceros cazioti* and *M. aff. cazioti* from Corbeddu (Klein Hofmeijer, 1996) and Santa Lucia I (IVAUI) in Sardinia, compared with *Cervus elaphus*, *Dama*, *Capreolus*, *Eucladoceros dicranios* lineage from Valdarno (IGF), *Eucladoceros giulii* from Untermassfeld (IQW), Venta Micena (Menéndez, 1987), Atapuerca TD4 (MB) and Apollonia (AUT), and *Megaloceros solilhacus* and related forms (provenance of data as in Figure 10), including *Megaloceros boldrini* from Ubeidiya (HUI).

Fig. 10. Diagrama bivariat del metacarpia de *Megaloceros cazioti* i *M. aff. cazioti* de Grotta Su Corbeddu (Klein Hofmeijer, 1996) i Santa Lucia I (IVAUI) a Sardinia, comparat amb *Cervus elaphus*, *Dama*, *Capreolus*, línia d'*Eucladoceros dicranios* de Valdarno (IGF), *Eucladoceros giulii* d'Unter-massfeld (IQW), Venta Micena (Menéndez, 1987), Atapuerca TD4 (MB) i Apollonia (AUT), anid *Megaloceros solilhacus* i formes relacionades (procedència de les dades com a la Figura 10), incloent-hi *Megaloceros boldrini* d'Ubeidiya (HUI).

2) The arrival of *Cynotherium* around the Early-Middle Pleistocene transition, which caused *N. melonii* to become more cursorial and thus evolve into *N. cenisae*.

The citation of two different species of *Nesogoral* in Orosei 6 (Sondaar, 2000; Abazzi *et al.*, 2004), seems to be in favour of the two lineage model, however, the indeterminate caprine in Orosei 10 hints of more important changes following the arrival of *Cynotherium* as in the single lineage model. We will have to await the description of this material.

### NESOGORAL AND THE FAUNAL HISTORY OF PLIO-PLEISTOCENE SARDINIA

Sondaar (1987) and Sondaar *et al.* (1984, 1986) recognised an earlier “*Nesogoral* fauna” and a later “*Tyrrhenicola* fauna” for the Plio-Pleistocene of Sardinia. This became more complex, when it was recognised that *Nesogoral* and *Tyrrhenicola* had overlapping ranges (Van der Made, 1999a; Sondaar, 2000). Abazzi *et al.* (2004) recognized up to 4 faunal units in the Monte Tuttavista faunas, but this does not even include all possible faunal units.

A selection of localities and their faunal associations are given in Fig. 14, which is based mainly on Fig. 1 of Van der Made (1999a), Fig. 5 of Sondaar (2000), information by Abazzi *et al.* (2004) and the literature cited by these authors. Six to eight tentative faunal units are indicated. The Capo Figari collection of Forsyth Major is placed here close to Capo Figari 2, and though this seems to fit unexpectedly well for most of the taxa, some taxa do not quite fit. The exact provenance of this material is not known, nor whether it is a mixture or whether it reflects a true faunal association that once lived on Sardinia. Its suid is more advanced than the one from Monte Tuttavista in the reduction of the premolars and diastemata. Only one of the possible *Nesogoral* evolutionary models is shown. Some localities are included because they are the only or one of the few localities with this taxon, but their position relative to the other localities is a problem. There might be a problem with the assignation of the *Prolagus* material. In spite of these and other problems, the figure gives an impression of the faunal evolution of the island that basically seems coherent and shows a pattern similar to that in other islands. Some localities have been dated. The ESR dates by Dr. M. Ikeya (Osaka Univ.) are: 1,807,500 ± 20 % BP for Capo Figari 1, 450,000 ± 20 % for Santa Lucia 1, 366,950 ± 20 % BP for Capo Figari 2, and 15,375 BP for Cor-

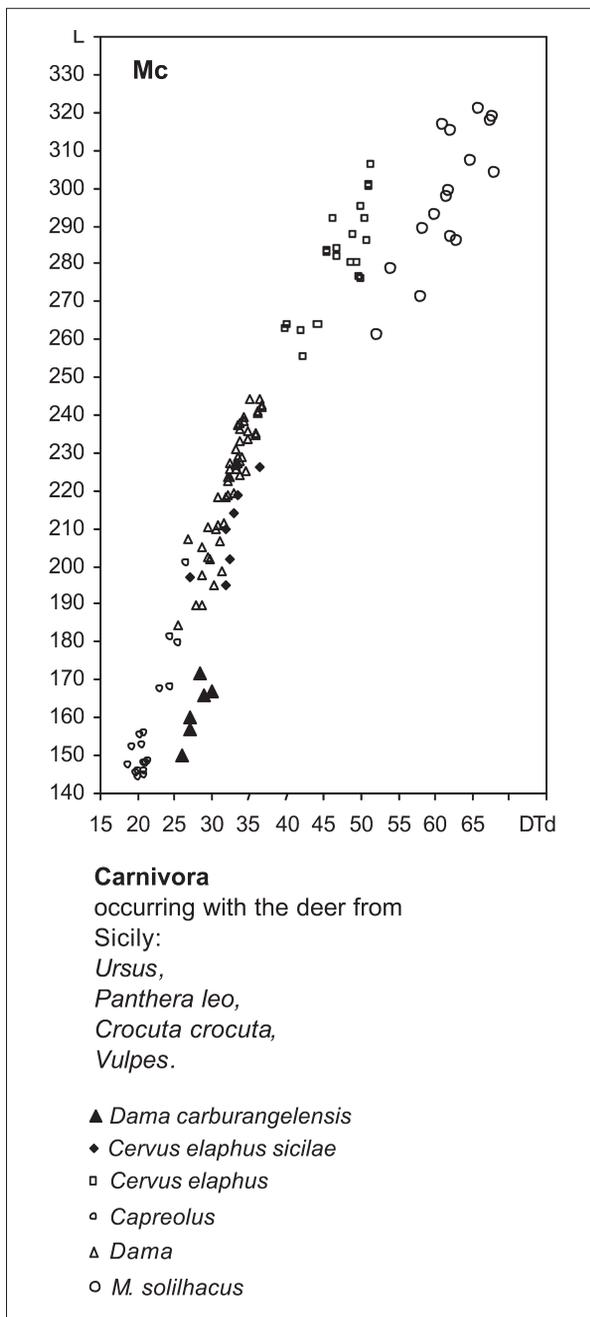


Fig. 11. Bivariate diagram of the metacarpal of *Dama carburangelensis* from Capo Tindari (Gliozzi & Malatesta, 1982) and *Cervus elaphus siciliae* from Puntali (Gliozzi, Malatesta & Scalone, 1983) in Sicily compared with *Cervus elaphus*, *Dama*, *Capreolus* and *Megaloceros solilhacus* and related forms (provenance of data as in Figure 10).

Fig. 11. Diagrama bivariat del metacarpà de *Dama carburangelensis* de Capo Tindari (Gliozzi & Malatesta, 1982) i *Cervus elaphus siciliae* de Puntali (Gliozzi, Malatesta & Scalone, 1983) a Sicília comparat amb *Cervus elaphus*, *Dama*, *Capreolus* i *Megaloceros solilhacus* i formes relacionades (procedència de les dades com a la Figura 10).

beddu (pers. comm. D. Reese to Van der Made, 1999a). These dates serve to situate the faunal associations approximately. One of the main faunal events in the sequence is the arrival of *Tyrrhenicola*, the dog and the deer on the island. This is usually assumed to have occurred during the sea level lowstand caused by the first severe glaciation.

That is OIS22, around 900 ka. This is an additional tentative date. It is not quite clear whether the arrival of *Oryctolagus* and the mustelids is a different and earlier event.

Sardinia is believed to have been populated by a continental fauna during the Messinian Crisis. This model is supported by the fact that the earliest faunas include forms that are not known from oceanic or very isolated islands, probably because they are not good in dispersing over sea. Bovids tend to be rare on islands, and when present these islands are usually known to have been connected to the mainland. *Nesogoral* is very probably among the animals that reached Sardinia during the Messinian Crisis. For the same reason, it seems unlikely that during the Middle Pleistocene Caprinae that are not related to *Nesogoral* appeared in Sardinia.

This continental fauna became isolated after the Pliocene flooding and subsequently became impoverished and altered by the insular environment which differs from the continental environment. Today Sardinia is rather far away from the mainland and the fact that that in Capo Figari 1 only lineages are recorded which were already present in the earlier faunas suggest that it remained isolated during all the Pliocene. Even though it is recorded only from one of the Monte Tuttavista sites, *Chasmaporthetes* must have entered Sardinia during the Messinian Crisis because: 1) there are no documented cases of hyaenids which have crossed wide sea barriers, 2) it was extinct on the mainland of Europe, when from 0.9 Ma onward, more severe glaciations caused very low sea levels, which might have permitted it to cross from the shelf near Elba to Corsica. The presence of this hyaenid is probably the reason why *Nesogoral* did not adapt in the same way as *Myotragus*; it did not develop low gear locomotion. *Nesogoral* may even have even given rise at this time to a more cursorial species (*N. cenisae*) inhabiting the plains (two lineage model). The presence of a predator probably limited herbivore population size and herbivore pressure on the environment. This again is probably the reason why *Nesogoral* did not evolve extreme dental adaptations as in *Myotragus*.

Close to the Early-Middle Pleistocene transition, the Sardinian fauna became enriched in one or several steps with the arrivals of *Oryctolagus*, mustelids, *Mammuthus*, *Tyrrhenicola*, canids and cervids. *Mammuthus lamarmorae* is known from several isolated finds and from San Giovanni in Sinis. Its morphology suggests that it is a descendant of *Mammuthus meridionalis*, which occurred in Europe from some 2.6 to 0.7 Ma. Judging from the isotope record, OIS 22 was a particularly cold stage, while 18 and 20 were much milder. OIS 16 is another cold stage, but by that time *M. meridionalis* was already replaced on the main land by another species. OIS 22 is thus the best candidate for several new arrivals as indicated in Fig. 14.

This enriched fauna had a very peculiar composition: a group of lineages which arrived to the island walking and which had become reduced selection for survival in insular environment (*Nesogoral*, *Chasmaporthetes*, *Sus*, *Talpa*) and a group of new arrivals, which were selected primarily on their ability to colonize islands (cervids, *Mammuthus*). There were two large predators, *Chasmaporthetes* and *Cynotherium*. On the long run, this may have been too much for the island, and *Casmaporthetes* went extinct, though it is not clear when. *Chasmaporthetes* was a true carnivore and *Cynotherium*, being a canid,

Fig. 12. The metacarpal index 100 L / DTd in selected Cervidae. Provenance of data as in Figures 8-11; in addition: recent *Cervus elaphus* from Corsica (IPH) and *Megaloceros giganteus* (Lister, 1994).

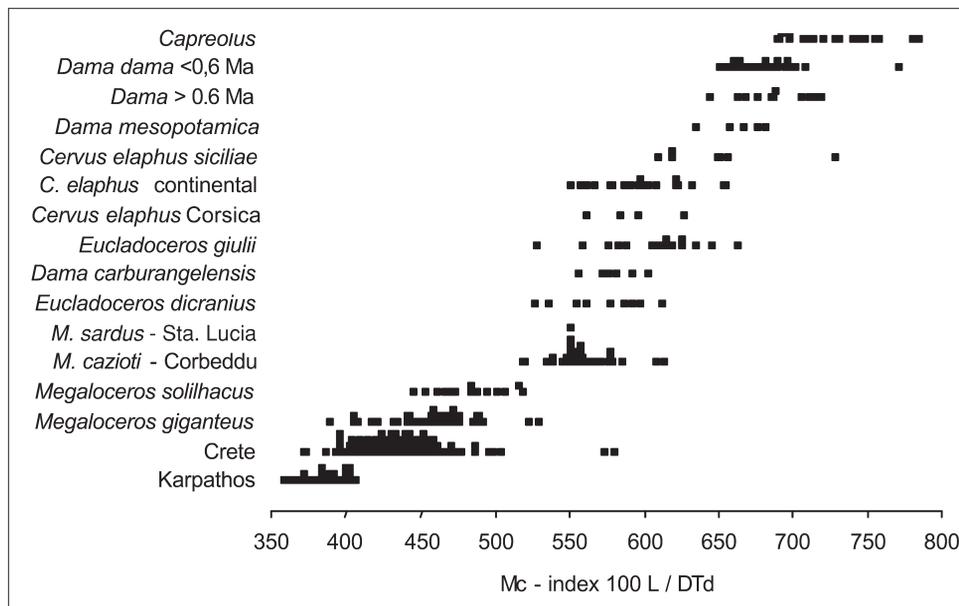


Fig. 12. L'index metacarpia 100 L / DTd a Cervidae seleccionats. Procedència de les dades com a les Figures 8-11; a més: *Cervus elaphus* recent de Còrsega (IPH) i *Megaloceros giganteus* (Lister, 1994).

Fig. 13. Bivariate diagram of the metacarpal of *Bos*: continental *Bos primigenius* from Miesenheim (FASMN) and Neumark Nord (LVH), insular *Bos* from Puntali in Sardinia (Brugal, 1987) and Pianosa (Brugal, 1987).

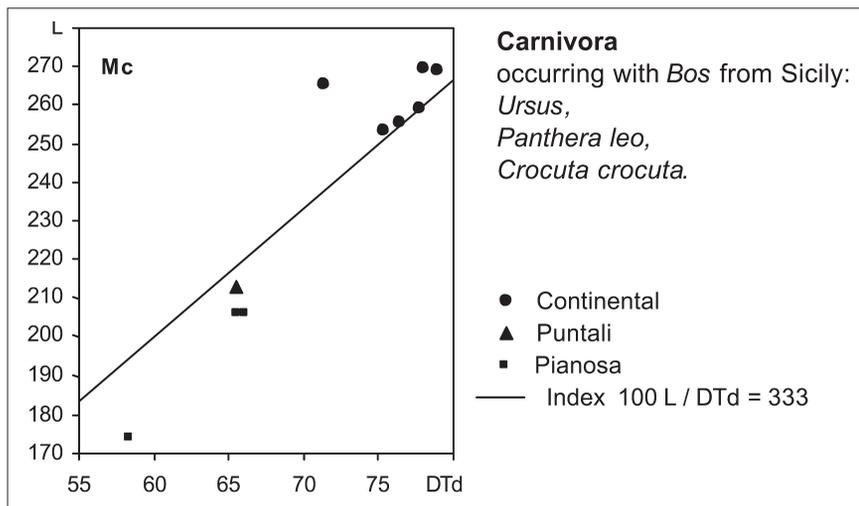


Fig. 13. Diagrama bivariat del metacarpia de *Bos*: *Bos primigenius* continental de Miesenheim (FASMN) i Neumark Nord (LVH), *Bos* insular de Puntali a Sardenya (Brugal, 1987) i Pianosa (Brugal, 1987).

had a more diverse diet. This may have allowed for greater population densities for this genus, which thus may have gradually replaced the hyaenid. The arrival of a new carnivore, may have caused *Nesogoral* to have become more cursorial (single lineage model). Also the deer may have become more cursorial or at least did not become less cursorial and initially remained relatively large. From this time on, the fauna of Sardinia gradually impoverished again and several lineages went extinct.

At some time or period in the middle of the Middle Pleistocene *Cynotherium* became smaller as well as the deer and bovid, *Prolagus* and *Rhagamys* increased in size. It is not known whether this occurred during a short or long period. However, these changes may well be related to the size decrease in *Cynotherium*, or to the extinction of *Chasmaporthetes*, or to both, and in that case, may have occurred in a short period. If these changes occurred in a short period, this may have been between some 450 ka (age of Santa Lucia, where still a large deer is found) and 367 ka (age of Capo Figari 2, where a very small *Nesogoral* was found).

The disappearance of *Eliomys*, *Nesogoral* and possibly *Macaca*, may have occurred shortly after this event, if this had not happened earlier. Maybe these disappearances are still consequences of the same cause that also provoked the size changes in the different lineages.

Later changes in the fauna of Sardinia concern mainly evolutionary changes in *Tyrrhenicola*, the arrival of *Homo sapiens* and the replacement of the Pleistocene fauna by the species from the mainland. Noteworthy is the apparent early extinction of *Talpa*.

## CONCLUSIONS

- The bovid from Campidano belongs to *Nesogoral*.
- *Nesogoral* from Campidano differs from *N. melonii* and is a new species: *N. cenisae*.
- *Nesogoral* belongs to the Caprinae, but *N. cenisae* lost some of the characters typical of this subfamily.

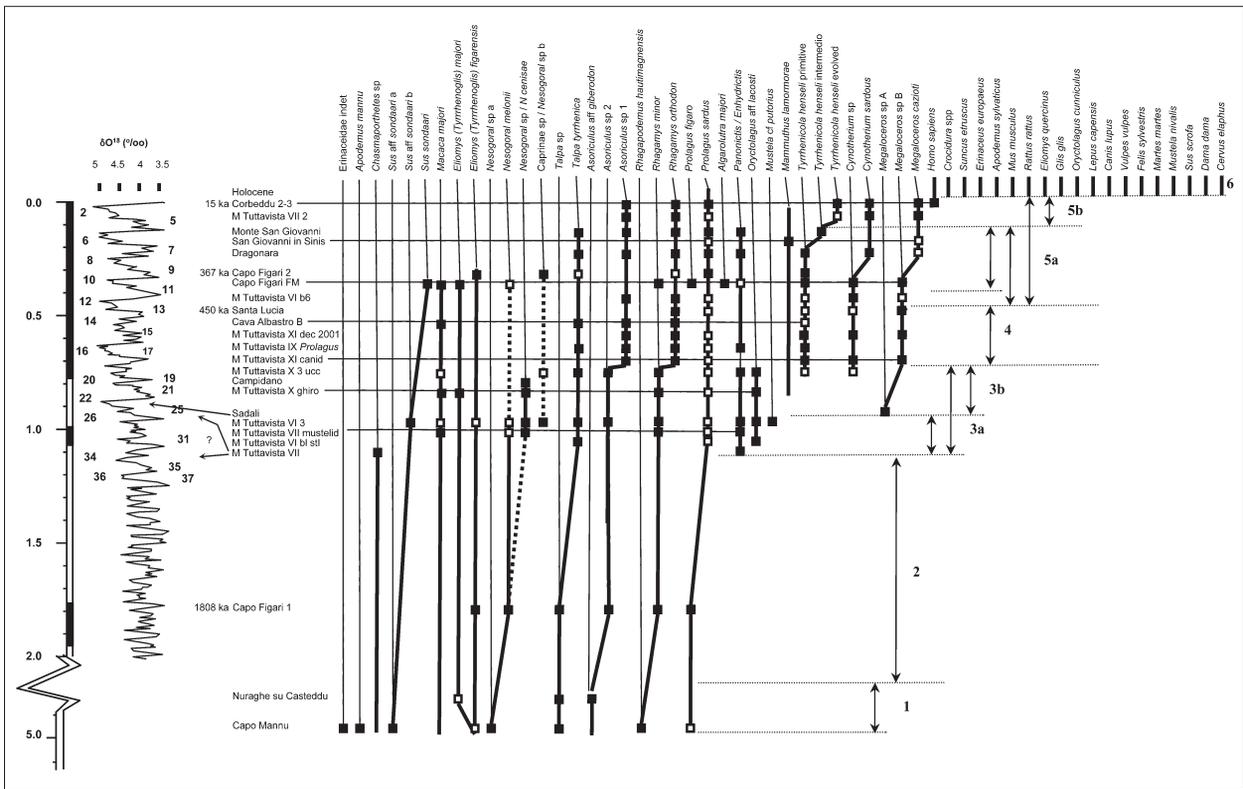


Fig. 14. The faunal evolution of Sardinia. On the left the palaeomagnetic and time scale in Ma and the oxygen isotope record (Shackleton, 1995). The localities are in approximate position, dates are ESR dates on tooth enamel by Dr. Ikeya (Osaka Univ.). Solid squares indicate presence of taxa in localities, open squares indicate doubts (sp., cf., aff. or ?), usually on the species, not on the presence of the genus. Thick lines indicate assumed temporal distribution, oblique lines indicate assumed ancestor-descendant relationships of species and the time range in which the transition occurred. Faunal events are indicated with arrows, and faunal complexes are indicated on the right. For *Nesogoral* only one of several possibilities is indicated (multi and single lineage models). Data and interpretations from Van der Made, 1999a, using data from Kotsakis (1980, 1986), Kotsakis & Palombo (1979), Gliozzi et al. (1984), and others, Abazzi et al. (2004), in addition Sondaar (2000).

Fig. 14. L'evolució faunística de Sardenya. A l'esquerra, l'escala paleomagnètica i temporal, en Ma, i el registre d'isòtops d'oxigen (Shackleton, 1995). Les localitats es presenten en una posició aproximada, i les dates són dates ESR sobre esmalt dentari subministrades pel Dr Ikeya (Universitat d'Osaka). Els quadrats sòlids indiquen la presència de taxa a les localitats, els quadrats oberts indiquen dubtes (sp., cf., aff. o ?), normalment sobre l'espècie, no sobre la presència del gènere. Les línies gruixades indiquen la distribució temporal suposada, les línies obliques indiquen una relació ancestre-descendent de l'espècie i l'espectre temporal en el qual la transició hauria esdevingut. Els esdeveniments faunístics s'indiquen amb flexes, i els complexes faunístics s'indiquen a la dreta. Per a *Nesogoral* només s'indica una de les diferents possibilitats (models d'una o múltiples línies evolutives). Dades i interpretacions de Van der Made (1999a), emprant dades de Kotsakis (1980, 1986), Kotsakis & Palombo (1979), Gliozzi et al. (1984); Abazzi et al. (2004); Sondaar (2000) i altres.

- *Nesogoral cenisae* lost characters by adapting to a different and more rapid locomotion.
- The cursorial adaptation in *Nesogoral* may have been the result of either the entry of *Cynotherium* in Sardinia (single lineage model), or the occupation of an empty niche on the plains before the arrival of this canid (two lineage model).
- The absence of predators, or the types of predators present on an island, determine in large part the environment and thus the evolution of the prey species.
- Ungulates may evolve energy efficient "low gear locomotion" on predator free islands, may evolve a little in this way, not at all, or even may become more cursorial, depending on predator pressure.
- Size decrease in large mammals may occur in insular environment, even in the presence of carnivores, but becomes more pronounced when predator pressure is less.

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## REFERENCES

- Abbazzi, L., Angelone, C., Arca, M., Barisone, G., Bedetti, C., Delfino, M., Kotsakis, T., Marcolini, F., Palombo, M.R., Pavia, M., Piras, P., Rook, L., Torre, D., Tuveri, C., Valli, A.M.F. & Wilkens, B. 2004. Plio-Pleistocene fossil vertebrata of Monte Tuttavista (Orosei, Eastern Sardinia, Italy), an overview. *Rivista Italiana di Paleontologia e Stratigrafia*, 110 (3): 603-628.
- Alcalá, L. & Morales, J. 1997. A primitive caprine from the Upper Vallesian of La Roma 2 (Alfambra, Teruel, Aragón, Spain). *Comptes Rendus de l'Académie des Sciences Paris, série IIa*, 324: 947-953.
- Alcover, J.A., Campillo, X., Macias, M. & Sans, A. 1998. Mammal species of the world: additional data on insular mammals. *American Museum Novitates*, 3248: 1-29.
- Alcover, J.A., Moyà-Solà, S. & Pons, J. 1981. *Les Quimeres del Passat. Els Vertebrats Fòssils del Plio-Quaternari de les Balears i Pitiüses*. Editorial Moll. Ciutat de Mallorca. *Monografies Científiques*, 1: 1-260.
- Alcover, J.A., Pérez-Obiol, R., Yll, E.I. & Bover, P. 1998. The diet of *Myotragus balearicus* Bate 1909 (Artiodactyla: Caprinae), and extinct bovid from the Balearic Islands: evidence from coprolites. *Biological Journal of the Linnean Society*, 66: 57-74.
- Bover, P. & Alcover, J.A. 1999. The evolution and ontogeny of the dentition of *Myotragus balearicus* Bate, 1909 (Artiodactyla Caprinae): evidence from new fossil data. *Biological Journal of the Linnean Society*, 68: 401-428.
- Brugal, J.P. 1987. Cas de "nanisme" insulaire chez l'aurochs. In *112<sup>e</sup> Congrès national des Sociétés savantes, Lyon, 1987. Sciences*, 2: 53-66.
- Dermitzakis, M.D. & Sondaar, P.Y. 1979. The importance of fossil mammals in reconstructing paleogeography with special reference to the Pleistocene Aegean Archipelago. *Annales Géologiques de Pays Helléniques*, 29: 808-840.
- Di Maggio, C., Incandela, A., Masini, F., Petruso, D., Renda, P., Simonelli, C. & Boschian, G. 1999. Oscillazioni eustatiche, biochronologia dei depositi continentali Quaternari e neotettonica nella Sicilia nord-occidentale (Penisola di San Vito lo Capo - Trapani). *Il Quaternario*, 12 (1): 25-50.
- Gentry, A.W., Rössner, G.E. & Heizmann, P.J. 1999. Suborder Ruminantia. In Rössner, G. & Heissig, K. (eds.), *The Miocene land mammals of Europe*. 225-258. Verlag Dr. Friedrich Pfeil. München.
- Gliozzi, E. & Malatesta, A. 1980. The Quaternary goat of Capo Figari (Northeastern Sardinia). *Geologica Romana*, 19: 295-347.
- Gliozzi, E. & Malatesta, A. 1982. A megacerine in the Pleistocene of Sicily. *Geologica Romana*, 21: 311-389.
- Gliozzi, E., Malatesta, A. & Scalone, E. 1983. Revision of *Cervus elaphus siciliae* Pohlrig, 1893, Late Pleistocene endemic deer of the Siculo-Maltese district. *Geologica Romana*, 29: 307-353.
- Gliozzi, E., Malatesta, A. & Palombo, M.R. 1984. Upper Pleistocene small mammal associations in the Is Orlis area (Iglesiente, SE Sardinia). *Geologica Romana*, 23: 121-129.
- Heintz, E. 1970. Les cervidés Villafranchiens de France et d'Espagne. *Mémoires du Muséum National d'Histoire Naturelle, nouv. sér., série C, Sciences de la Terre*, 22: 1-303.
- Hsü, K.J., Montadert, L., Bernouilli, D., Cita, M.B., Erkison, A., Garrison, R.E., Kidd, R.B., Mèlierés, F., Müller, C. & Wright, R. 1977. History of the Mediterranean Salinity Crisis. *Nature*, 267: 399-403.
- Klein Hofmeijer, G. 1996. *Late Pleistocene deer fossils from Corbeddu cave - implications for human colonization of the island of Sardinia*. PhD Thesis. University of Utrecht. 437 pp.
- Köhler, M. 1993. Skeleton and habitat of recent and fossil ruminants. *Münchener Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie*, 25: 1-88.
- Köhler, M. & Moyà-Solà, S. 2001. Phalangeal adaptations in the fossil insular goat *Myotragus*. *Journal of Vertebrate Paleontology*, 21 (3): 621-624.
- Köhler, M., Moyà-Solà, S. & Morales, J. 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 15. Bovidae and Giraffidae (Artiodactyla, Mammalia). *Münchener Geowissenschaftliche Abhandlungen A*, 28: 167-180.
- Kotsakis, T. 1980. Osservazioni sui vertebrati Quaternari della Sardegna. *Bolletino della Società Geologica Italiana*, 99: 151-165.
- Kotsakis, T. 1986. Elementi di paleobiogeografia dei mammiferi Terziari dell'Italia. *Hystrix*, 1 (1): 25-68.
- Kotsakis, T. & Palombo, M.R. 1979. Vertebrati continentali e paleogeografia della Sardegna durante il Neogene. *Annales Géologiques des Pays Helléniques, tome hors serie*, 2: 621-630.
- Kuss, S.E. 1975. Die pleistozäne Hirsche des ostmediterranen Insel Kreta, Kasos, Karpantos und Rhodos (Griechenland). *Ber. Naturf. Gesellschaft Freiburg in Br.*, 65: 25-79.
- Lalueza-Fox, C., Bertranpetit, J., Alcover, J.A., Shailer, N. & Hagelberg, E. 2000. Mitochondrial DNA from *Myotragus balearicus*, an extinct bovid from the Balearic Islands. *Journal of Experimental Zoology (Mol. Dev. Evol.)*, 288: 56-62.
- Lalueza-Fox, C., Sampietro, L., Marquès, T., Alcover, J.A. & Bertranpetit, J. 2005. Mitochondrial and nuclear genes from the extinct Balearic bovid *Myotragus balearicus*. In Alcover, J.A. & Bover, P. (eds.), *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach"*. *Monografies de la Societat d'Història Natural de les Balears*, 12: 145-154.
- Leinders, J.J.M. 1979. On the osteology and function of the digits of some ruminants and their bearing on taxonomy. *Zeitschrift für Säugetierkunde*, 44: 305-318.
- Leinders, J.J.M. & Sondaar, P.Y. 1979. On functional fusions in the footbones of ungulates. *Zeitschrift für Säugetierkunde*, 39: 109-115.
- Lister, A.M. 1994. The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zoological Journal of the Linnean Society*, 112: 65-100.
- Marra, A.C. 2003. *Ursus arctos* from selected Pleistocene sites of Eastern Sicily. *Bolletino della Società Paleontologica Italiana*, 42 (1-2): 145-150.
- Mezzabotta, C., Masini, F. & Torre, D. 1996. Evolution of the first lower molar in the endemic vole *Microtus (Tyrrhenicola) henseli* (Arvicolidae, Rodentia, Mammalia) from Pleistocene and Holocene localities of Sardinia and Corsica. *Acta Zoologica Cracoviense*, 39 (1): 357-372.
- Palombo, M.R., Melis, R., Meloni, S. & Tuveri, C. 2003. A new cervid in the Pleistocene of Sardinia: preliminary report. *Bolletino della Società Paleontologica Italiana*, 42 (1-2): 157-162.
- Pecorini, G., Rage, J.C. & Thaler, L. 1973. La formation continentale de Capo Mannu, sa faune de vertébrés Pliocènes et la question du Messinien en Sardaigne. *Rend. Sem. Fac. Sci. Univ. Cagliari*, 43 (suppl.): 305-319.
- Shackleton, N. 1995. New data on the evolution of Pliocene climatic variability. In Vrba, E.S., Denton, G.H., Partridge, T.C. & Buckle, L.H. (eds.), *Palaeoclimate and evolution with emphasis on human evolution*: 242-248. Yale University Press. New Haven and London.
- Sondaar, P.Y. 1977. Insularity and its effects on mammal evolution. In Hecht, M.K., Goody, M.C. & Hecht, B.M. (eds.), *Major patterns in vertebrate evolution*: 671-707. Plenum Press. New York.

- Sondaar, P.Y. 1986. The Island Sweepstakes. Why did pygmy elephants, dwarf deer, and large mice once populate the Mediterranean?. *Natural History*, 9: 50-57.
- Sondaar, P.Y. 1987. Pleistocene man and extinctions of island endemics. *Mémoires de la Société Géologique de France, N.S.*, 150: 159-165.
- Sondaar, P.Y. 2000. Early human exploration and exploitation of islands. *Tropics*, 10 (1): 203-230.
- Sondaar, P.Y., de Boer, P.L., Sanges, M., Kotsakis, T. & Esu, D. 1984. First report on a Palaeolithic culture in Sardinia. In Waldren, W.H., Chapman, R., Lewthwaite, J. & Kennard, R.C. (eds.), *The Deya Conference of Prehistory - Early settlement in the western Mediterranean islands and the peripheral areas. BAR International Series*, 229: 29-47.
- Sondaar, P.Y., Sanges, M., Kotsakis, T. & de Boer, P.L. 1986. The Pleistocene deer hunter of Sardinia. *Geobios*, 19 (1): 17-25.
- Spoor, C.F. 1988a. The body proportions in *Myotragus balearicus* Bate, 1909. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B*, 91 (3): 285-293.
- Spoor, C.F. 1988b. The limb bones of *Myotragus balearicus* Bate, 1909. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B*, 91 (3): 295-309.
- Stehlin, H.G. 1929. Ueber eine altpleistozäne Säugetierfauna von der Insel Pianosa. *Schweizerische Paläontologische Gesellschaft*: 433-460.
- van der Made, J. 1988. *Sus nanus* nov. sp. a Pliocene dwarf pig from Capo Figari (Sardinia). *Bolletino della Società Paleontologica Italiana*, 27 (3): 367-378.
- van der Made, J. 1989. The bovid *Pseudoeotragus seegrabensis* nov. gen. nov. sp. from the Aragonian (Miocene) of Seegraben near Leoben (Austria). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, serie B*, 92 (3): 215-240.
- van der Made, J. 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology*, 33 (1-4): 3-254.
- van der Made, J. 1999a. Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. *Deinsea*, 7: 337-360.
- van der Made, J. 1999b. Ungulates from Atapuerca-TD6. *Journal of Human Evolution*, 37: 389-413.
- Vos, J. de. 1979. The endemic Pleistocene deer of Crete. *Proceedings of the Koninklijke Nedrlandse Akademie van Wetenschappen, Series B*, 82 (1): 59-90.
- Vos, J. de. 1984. The endemic Pleistocene deer of Crete. *Verhandelingen der Koninklijke Nedrlandse Akademie van Wetenschappen, afd. Naturkunde, eerste reeks*, 31: 1-110.