Megaloceros sardus n. sp., a large deer from the Pleistocene of Sardinia*

J. Van der Made[1] & M.R. Palombo[1]

[1] *Museo Nacional de Ciencias Naturales, CSIC, c. José Gutiérrez Abascal 2, 28006 Madrid, Espa•a.*
[2] *Dipartimento di Scienze della Terra. Università degli Studi di Roma "La Sapienza". CNR, Istituto di Geologia Ambientale e Geoingegneria.*
P.le Aldo Moro, 5 - 00195 Roma, Italy.

ABSTRACT: Fossils from Sta. Lucia at Sardinia, include remains of a deer that is larger than *Megaloceros cazioti*, that is common from the Late Pleistocene and Holocene of Sardinia and Corsica. This material and remains of a similar large deer in the Forsyth Major collection from Capo Figari are described and assigned to a new species, *Megaloceros sardus*. A still larger deer from the Su Fossu de Cannas Cave near Sadali, *M. sardus* from Sta. Lucia and Capo Figari, and *M. cazioti* form a lineage, that is characterized by size decrease.

Key-words: *Late Pleistocene-Holocene, deer, Sardinia, lineage.*

ΠΕΡΙΛΗΨΗ: Τα απολιθωμένα ευρήματα από τη Sta. Lucia της Σαρδηνίας, περιλαμβάνουν τα λείψανα ενός ελαφιού μεγαλύτερου από το *Megaloceros cazioti*, το οποίο είναι κοινό στις ανωπλειστοκαινικές και ολοκαινικές αποθέσεις της Σαρδηνίας και Κορσικής. Το υλικό αυτό και τα λείψανα ενός παρόμοια μεγάλου ελαφιού της συλλογής Forsyth Major από το Capo Figari, περιγράφονται στη παρούσα εργασία και αποδίδονται στο νέο είδος *Megaloceros sardus*. Ένα ακόμη μεγαλύτερο ελάφι από το σπήλαιο Su Fossu de Cannas κοντά στο Sadali, το *M. sardus* από τη Sta. Lucia και Capo Figari, και το M. *cazioti* αποτελούν μία εξελικτική γραμμή, η οποία χαρακτηρίζεται από τη μείωση του μεγέθους.

Λέξεις-κλειδιά: *Αν. Πλειστόκαινο-Ολόκαινο, ελάφι, Σαρδηνία, εξελικτική γραμμή.*

INTRODUCTION

Sardinia has a long and complex history as an island and its sequence of endemic faunas is becoming increasingly well known (e.g. Kotsakis & Palombo, 1979; Kotsakis, 1980, 1986; Gliozzi *et al*., 1984; Sondaar *et al*., 1984, 1986; Sondaar, 2000; Van der Made, 1988, 1999; Palombo, in press; etc.). The Messinian Salinity Crisis when the Mediterranean became disconnected from the Atlantic and when sea level dropped several thousand metres (Hsü *et al*., 1977), was a key event in the faunal history of Sardinia and other Mediterranean islands, which allowed mammals from the continent to reach the island, including the ancestor of *Nesogoral* and *Myotragus*, the endemic bovids from Sardinia and the Balearic's. The subsequent Pliocene flooding of the Mediterranean around 5 Ma ago, isolated Sardinia from the continent. Corsica had a similar history and, due to eustatic sea level changes, was probably frequently connected to Sardinia. The Corsican faunal record is more modest, but its Pleistocene fauna is similar to that of Sardinia, and includes also different forms (Pereira *et al*., 2003).

Of the Plio-Pleistocene faunas from Sardinia, the earlier faunas have been indicated as "*Nesogoral* faunas" and the later faunas as "*Tyrrhenicola* faunas", after common elements (Sondaar *et al*., 1984, 1986). The bovid *Nesogoral* and other elements of this "faunal complex" are assumed to have reached Sardinia during the Messinian Crisis. The arvicolid *Tyrrhenicola*,a cervid and the dog*Cynotherium* are assumed to have reached Sardinia during the earliest important glaciations around the Early-Middle Pleistocene transition, when sea levels were low, resulting in a shorter distance to the continent. A small caprine astragalus, assigned to *Nesogoral* aff. *melonii*,was reported from the locality Capo Figari II, which also yielded a primitive *Tyrrhenicola* (Van der Made, 1999). A caprine, clearly different from *Nesogoral* in association with a primitive *Tyrrhenicola* was also found at Monte Tuttavista, where a large number of fissure fillings gave rise to the recognition of four different "faunal complexes" (Abazzi *et al*., 2004; Palombo, unpublished data). These authors tentatively subdivide the "*Praemegaceros-Tyrrhenicola* complex" in two, the older third "faunal complex" with a primitive representatives of *Cynotherium* and *Praemegaceros* (here *Megaloceros*, see note on taxonomy), and the fourth "complex" with the more typical *C. sardous* and *M. cazioti*. According to Palombo (in

---

* *Megaloceros sardus* n. sp., ένα μεγάλο ελάφι από το Πλειστόκαινο της Σαρδηνίας.

press) two main faunal complexes can be recognised on Sardinia: the Pliocene/Early Pleistocene "*Nesogoral* faunal complex" (including Mandriola and Capo Figari/Orosei 1 subcomplexes) and the earliest? Middle Pleistocene/Holocene "*Microtus (Tyrrhenicola)* faunal complex" (including Orosei 2 and Dragonara subcomplexes), in which also endemic deer are represented.

The cervid remains from the Pleistocene of Sardinia are usually assigned to the species *Cervus cazioti* DEPÉRET, 1897. Though it has been suggested that the Sardinian deer is related to *Dama* (KLEIN HOFMEIJER, 1996), most recent authors place the species in one of the genera of giant deer. Here we will use the binomen *Megaloceros cazioti* (see note on generic taxonomy below).

Remains of *Megaloceros cazioti* are relatively common in Sardinia and Corsica and are mainly known from eolianites or cave deposits, most of which are attributed to the Late Pleistocene (DEHAUT, 1911; COMASCHI CARIA, 1955, 1956; AZZAROLI, 1961; CORDY & OZER, 1973; CALOI & MALATESTA, 1974; CALOI *et al.*, 1981; KLEIN HOFMEIJER, 1996; ANTONIOLI *et al.*, 1998; GINESU *et al.*, 1998; MELIS *et al.*, 2003; etc). The oldest cervid records from the Pleistocene of Sardinia are from some fissures at Monte Tutavista (Orosei, central-eastern Sardinia) (ABAZZI *et al.*, 2004). These Monte Tuttavista Specimens indicate a deer that is larger than the one from the Late Pleistocene. It was known already that also the deer in the F. MAJOR collection from Capo Figari is larger (SIGOGNEAU, 1960; KOTSAKIS, 1980; CALOI *et al.*, 1981, 1988; VAN DER MADE, 1999) than the average typical *M. cazioti* from the Late Pleistocene and early Holocene of Sardinia and Corsica (SIGOGNEAU, 1960; CALOI & MALATESTA, 1974; KLEIN HOFMEIJER, 1996; PEREIRA, 2000; PEREIRA & BONIFAY, 1998; etc.).

The FORSYTH MAJOR collection from Capo Figari is of unknown exact provenance, but includes taxa present in Capo Figari I and II and might include material from both localities, or of a single unknown locality of intermediate age. Capo Figari I was dated around 1,807.5 ± 361,5 ka BP and Capo Figari II around 366.950 ± 73.390 ka BP (ESR dates by Dr. Ikeya from Osaka University; pers. comm. D. Reese to JvdM). At present there are no indications to assume that the F. MAJOR collection is younger than Capo Figari II.

More recently, various large cervid remains have been discovered in Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia) (PALOMBO *et al.*, 2003; PALOMBO & MELIS, in press). The specimens analysed so far show close morphological affinities with the endemic Sardinian megacerine but differ in their larger size, in some morphological features, as well as in its proportionally smaller teeth and slender metacarpal (PALOMBO *et al.*, 2003) The peculiar features of the Sadali specimens suggest its attribution to a new species, which so far has not been described pending the recuperation of specimens and the paucity of chronological information (PALOMBO & MELIS, in press).

PAUL SONDAAR and HANS BRINKERINK made a small collection of fossils from the Sta Lucia quarry. This collection mainly includes well preserved remains of a large cervid, but also *Cynotherium*, *Prolagus* (large), a small mustelid, *Tyrrhenicola*, *Rhagamys* and Amphibia. The fossils are accompanied by a hand written note, stating that this is one (Sta. Lucia 1) of two fossiliferous points in the quarry. Tooth enamel from this locality was dated by Dr. MOTOJI IKEYA (Department of Earth and Space Science, Osaka University) by ESR, and gave a date of 450 ± 90 ka BP (pers. comm. to JvdM by D.S. REESE).

The deer from Sta. Lucia is interesting because the well preserved remains: 1) shed light on the origin of the endemic deer (giant deer versus *Dama*), 2) increase our knowledge of the larger form and permit to describe a new species, and 3) provide chronological information on the passage from a large to a smaller deer, and thus 4) provide a maximum age for the transition of the Orosei 2 and Dragonara "faunal sub complexes". It is the aim of this paper to describe the deer from Sta. Lucia and of the FORSYTH MAJOR collection from Capo Figari, with reference to these points. Also attention will be paid to the deer from Sadali.

NOMENCLATURE, MEASUREMENTS AND COLLECTIONS AND THEIR ABBREVIATIONS

The common anatomical nomenclature is used in the descriptions, occasionally a dental nomenclature by VAN DER MADE (1996) is used. Measurements are given in mm. The teeth were measured as indicated by VAN DER MADE (1989) and the bones as indicated for the suoids by VAN DER MADE (1996), as far as morphologies are comparable, and VAN DER MADE (in press).

The abbreviations used for the measurements are:

Dbu	Depth of the mandible, measured below each cheek tooth from P_2 to M_3. Normally the depth is measured at the lingual side (D; VAN DER MADE, 1989), but this is not possible here.
DAP	Antero posterior diametre (or length in a tooth).
DAPb	DAP measured at the base of a tooth.
DAPd	DAP of the distal end of a bone.
DAPdf	DAP of the distal facet of a bone.
DAPn	DAP of the "neck" of a bone; the minimal DAP.
DAPp	DAP of the proximal end of a bone.
DAPpf	DAP of the proximal facet of a bone.
DAP3 (DAP4)	DAP of the distal articulation of the third (fourth) metapodial.
DT	Transeverse diametre or width.
DTa	DT of the anterior lobe of a tooth.
DTd	DT of the distal end of a bone.
DTdf	DT of the distal facet of a bone.
DTm	DT of the middle lobe of the D_4, or minimal DT of a bone, generally near the middle.
DTn	DT of the "neck" of a bone; the minimal DT.
DTp	DT of the anterior lobe of a tooth.
DTpf	DT of the proximal facet of a bone.
DTpp	DT of the third lobe in a M_3.

DT3 (DT4)	DT of the distal articulation of the third (fourth) metapodial.
H	Height of a bone or tooth.
h	Alternative value for H.
Ha	Anterior height in a bone, height of the metaconid or paracone in a molar.
Hp	Height of the entoconid or metacone in a molar
L	Length of a bone; Lext, Lm and Lint = L of an astragalus, measured at different places; L3 and L4 lengths of metapodials measured at different places.
l	Alternative value for L.
R	Diameter of the distal articulation of the humerus, measured at various places (R1-5).
Ta	Thickness of the enamel measured at the metaconid or paracone.
Tp	Thickness of the enamel measured at the entoconid or metacone.

Whenever data are used in this text, either the bibliographical reference to these data is given, or the acronym of the institute where the material was studied by us. Occasionally, material was studied that was on loan or that was not kept in its "permanent" institute.

AUT	Aristotle University of Thessaloniki.
GSMT	Georgian State Museum, Tbilisi.
HMV	Historisches Museum, Verden.
HUJ	Hebrew University of Jerusalem.
IGF	Museo di Storia Naturale, sez. Geo-Paleontologica (ex Istituto di Geologia), Università degli Studi di Firenze, Florence.
IPH	Institut de Paleontologie Humaine, Paris.
IQW	Institut für Quartärpaläontologie, Weimar.
IVAU	Instituut Voor Aardwetenschappen, Utrecht.
LVH	Landesmuseum für Vorgeschichte, Halle.
MB	Museo de Burgos.
MCP	Musée Crozatier, Le Puy-en-Velay.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MCZR	Museo Civico di Zoologia, Roma
MPC	Museo di Paleontologia, Università degli Studi di Cagliari, Cagliari.
MPUSR	Museo di Paleontologia, Università degli Studi di Roma "La Sapienza", Rome.
MRA	Musee Requien, Avignon.
NHM	Natural History Museum, London.
NMB	Naturhistorisches Museum, Basel.
NMM	Naturhistorisches Museum, Mainz.
NMMa	Natuurhistorisch Museum, Maastricht.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
SBASN	Soprintendenza ai Beni Archeologici delle province di Sassari e Nuoro, Nuoro.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.

TAXONOMY

Megaloceros BROOKES, 1828

Note

AZZAROLI (1952) pointed out that the giant deer of the genus *Megaceros* (= *Megaloceros*) belong to two different groups, which he called the "*verticornis*" group and "*giganteus*" group. This was widely accepted and many, but not all, authors suggested to place members of the "*verticornis*" group in a different genus or subgenus: *Megaceroides*, *Praemegaceros*, *Ortogonoceros, Psekupceros, Nesoleipoceros* and *Notomegaceros*, the latter being a subgenus restricted to Sardinia. Most authors assume a close relationship between the Sardinian "giant" deer and the mainland species "*verticornis*", and "*cazioti*" has been placed in all the (sub)generic names mentioned above. In earlier papers we have either included "*verticornis*" with reservation in the genus *Megaceroides* as *"M." verticornis*, in *Praemegaceros* as *"P." verticornis* and in the species *Megaloceros solilhacus* and assigned the species "*cazioti*" to the same genus (e.g. PALOMBO *et al*., 2003; ABAZZI *et al*., 2004; VAN DER MADE, 1999, 2001). We both consider that the "*verticornis*" and "*giganteus*" groups are different. One of us (JvdM) thinks the two groups should be placed in different genera if they have different origins (to avoid that *Megaloceros* would be polyphyletic), but is at present not convinced of a separate origin and follows LISTER (1993) in placing the giant deer in *Megaloceros.* The other (MRP) favours placing the two groups in different genera. The problem is the name that should be applied to the members of the "*verticornis*" group.

JOLEAUD (1914) proposed the name *Megaceroides* as a subgenus of *Cervus*, with the type species *"Cervus" algericus,* which has as a type a maxillary fragment. Subsequently, ARAMBOURG (1932, 1938) ascribed a skull from the Late Pleistocene of Algeria and Morocco to this species. Mean similarities in skull characters between specimens from the Magreb and the megalocerine from Europe, first pointed out by AZZAROLI (1952), have subsequently been widely debated (see e.g. HADJOUDIS, 1990; AZZAROLI & MAZZA, 1992; ABAZZI *et al*., 2004), who favour using the name *Megaceroides* only for the North African species

The name "*Praemegaceros*", though not formally correct (see e.g. AZZAROLI, 1979; CALOI & PALOMBO, 1996), was frequently employed, whereas other names, such as "*Ortogonoceros*" or "*Psekupsoceros*", have not been *de facto* utilised in more recent times.

The debate is certainly not ended and for pragmatic reasons we apply the name *Megaloceros* here for both "*verticornis*" and the Sardinian deer.

Megaloceros sardus n. sp.

Holotype:

The metacarpal figured here on Plate 3, figure 1.

Paratypes:

All other specimens from Sta. Lucia described here. All types were studied and, are kept at present, in the IVAU.

Type locality:

Sta. Lucia 1, south western Sardinia.

Age of the type locality:

Middle Pleistocene, approximately 450 ka.

Diagnosis:

Species of *Megaloceros* with robust metapodials and phalanges, premolars with a simple morphology, and with a small size for the genus, but still some 25-40 % larger than *M. cazioti* (linear measurements).

DESCRIPTION AND COMPARISON OF THE STA. LUCIA AND CAPO FIGARI MATERIAL

The specimens studied are listed in the tables. Besides there are some vertebrae from Sta. Lucia, which are not included here.

The **P²** (Pl. 1, Figs. 1 & 4) has a rounded lingual side with only a faint grove suggesting two lobes. If seen from mesially, the lingual wall is high, but not completely convex (Pl. 1, Figs. 4a & 1d), it is more concavo-convex, and is intermediate between the states in *Cervus* and *Dama* (character 3 for the P⁴ of LISTER, 1996).

The **P³** (Pl. 1, Fig. 1) has a simple shape and does not have the very marked folds or crests on the inside of the lingual crescent, that are so common in most cervids. There is no vertical grove on the lingual side of the tooth, that might suggest a separation into two lobes. Specimens figured by CALOI & MALATESTA (1974) show that specimens with a clear separation and without any may occur in the same sample. These specimens also tend to have crests inside the lingual crescent. If seen from the front the lingual wall is very steep and high; its profile is nearly straight (Pl. 1, Fig. 1d; compare with the description of the P²).

The **P⁴** (Pl. 1, Fig. 1) has a remarkably flat buccal wall. Like the P³, it has a very simple shape; its lingual wall is more inclined (Pl. 1, fig. 1d).

The **M¹** and **M²** (Pl. 1, Fig. 1) have similar morphologies. A lingual interlobular column is not present at al. The specimens are well worn, but what is left shows a simple morphology. There are no folds on the inner side of the crescents (character 2 of LISTER, 1996).

The **M³** (Pl. 1, Figs. 1 & 2) is similar to the anterior molars, but has a more vertical postero-lingual style and relatively narrow second lobe. There is a complete and

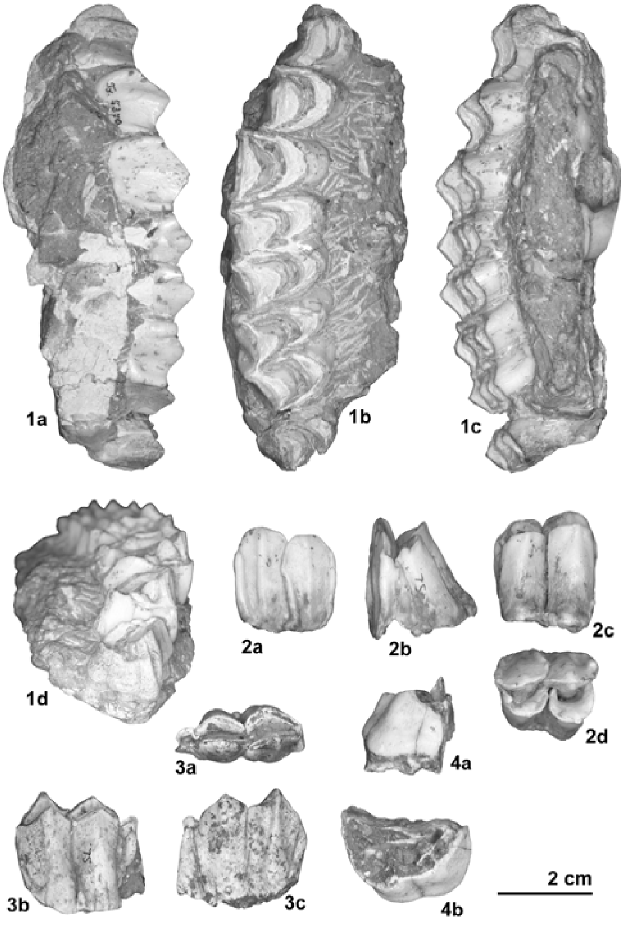

PLATE 1

Megaloceros sardus n.sp. from Capo Figari (FORSYTH MAJOR collection in NMB; figure 1) and Sta. Lucia (IVAU; figures 2-4).

Fig. 1. Ty 5370 - right maxilla with P^2-M^3; buccal (a), occlusal (b), lingual (c) and anterior (d) views.

Fig. 2. Right M^2; buccal (a), posterior (b), lingual (c) and occlusal (d) views.

Fig. 3. Left M_3; occlusal (a), buccal (b) and lingual (c) views.

Fig. 4. Lingual fragment of right P^2; anterior (a) and occlusal (b) views.

The scale bar represents 2 cm for Figures 1-3; Figure 4 is not to scale.

TABLE 1

Measurements (in mm) of the upper dentition of *Megaloceros sardus* n.sp.

Locality	coll.	number			DAP	DAPlo	DTa	DTp	Ha	Hp
Capo Figari	NMB	Ty 5370	d	P^2	-	-	-	≥18.4		
				P^3	14.9	15		17.8		
				P^4	19.5	16.1		18.7		
				M^1	21.6	18.6	20.2	20		
				M^2	21.5	21.2	21.6	19.4		
				M^3	-	-	>20.0	-		
Capo Figari	NMB	Ty 5371	s	M^3	-	-	-	19.7		
Capo Figari	NMB		s	M^{1-2}	>20.1	-	-	-		
Sta Lucia I	IVAU		d	P^2	-	-	-	-		
Sta Lucia I	IVAU		d	M^3	21.8	20.7	20.7	18	21.9	20.6

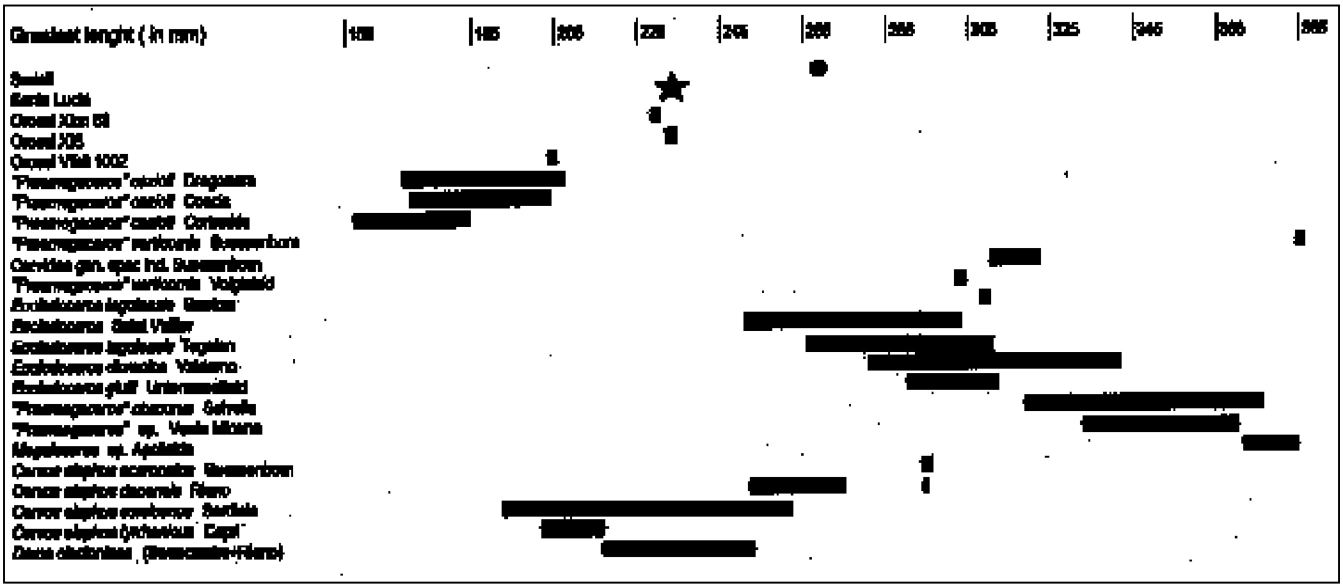

Fig. 1. Metacarpal length in the deer from Santa Lucia and Sadali compared to *Megaloceros cazioti* from Sardinia (Dragonara and Corbeddu Cave; KLEIN HOFMEIJER, 1996) and Corsica (Coscia Cave; PEREIRA & BONIFAY, 1998) and to other endemic insular deer and large main land cervids (AZZAROLI & MAZZA, 1992; KAHLKE, 1956-1959, 1958, 1969, 1997; KOSTOPOULOS, 1997; LEONARDI & PETRONIO, 1974, 1976; SPAAN, 1992; DI STEFANO, 1994; PALOMBO, unpublished data).

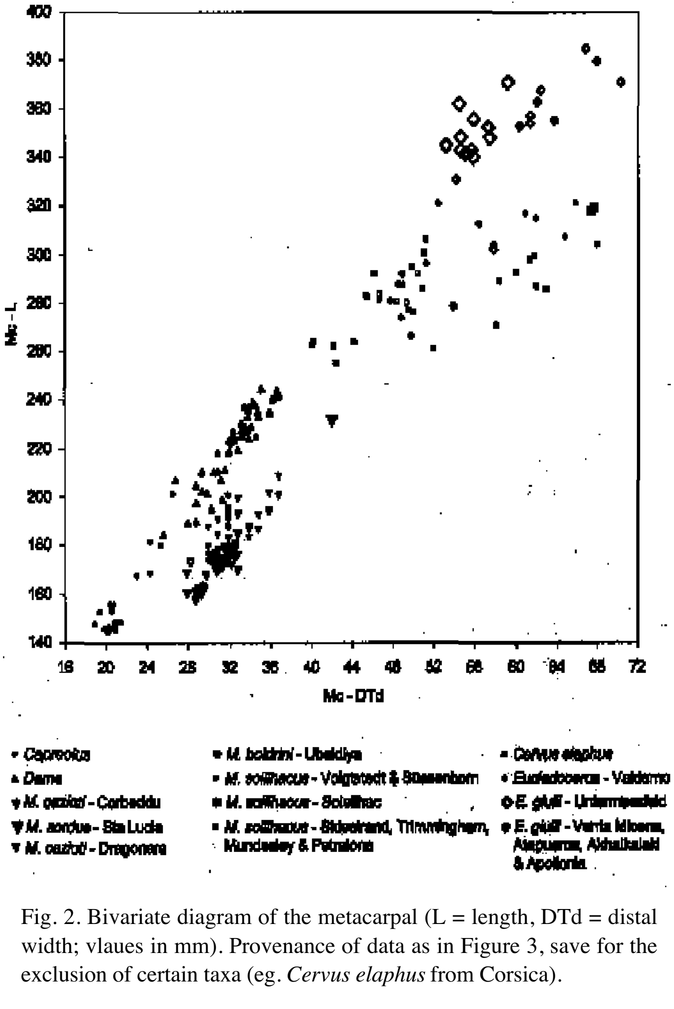

Fig. 2. Bivariate diagram of the metacarpal (L = length, DTd = distal width; vlaues in mm). Provenance of data as in Figure 3, save for the exclusion of certain taxa (eg. *Cervus elaphus* from Corsica).

unworn specimen from Sta. Lucia, which is not particularly high. In buccal view, the lower end of the anterior edge is not angled as in *Dama* (character 5 of LISTER, 1996).

There are some **incisors** from both localities, which have the common morphology of cervid incisors. Their main interest is that they do not show any increase in hypsodonty (a trait that might be expected in insular environment). They are not included in the tables.

The $\mathbf{P_2}$ (Pl. 2, Figs. 1c, 1d, 1i) has a well developed, but low, parastylid that turns lingually. There is a marked lingual valley between the parastylid and the massive base of the main cusp. In this character and in general, the tooth is more of the "*Dama* type" than of the "*Cervus* type" (sensu DI STEFANO, 1995 and LISTER, 1996). The morphology is highly modified in *Cervus*, but in *Dama* it is not unlike in *Megaloceros* and *Eucladoceros*. In many characters it resembles the P_2 in *M. cazioti* (PEREIRA, 2000).

The $\mathbf{P_3}$ (Pl. 2, Figs. 1c, 1d, 1e, 1i) was probably not a very high tooth. The metaconid is a low cusp that is placed far backward and appears more as a cuspule on the widely inflated base of the protoconid than as an individual cusp. The paraconid is only faintly indicated.

The $\mathbf{P_4}$ (Pl. 2, Figs. 1c, 1d, 1e, 1i) has a metaconid that is placed rather distally and which has an anterior surface that is rounded, without any development of the metaprecristid. The parastylid is well developed, but the paraconid is only faintly indicated. The anterior fossid is wide open on the lingual side. There is no clear vertical furrow on the buccal side between the protoconid and hypoconid. The long axis of the entoconid is transversely oriented. In most of its morphology, and in particular in the absence of a meta-

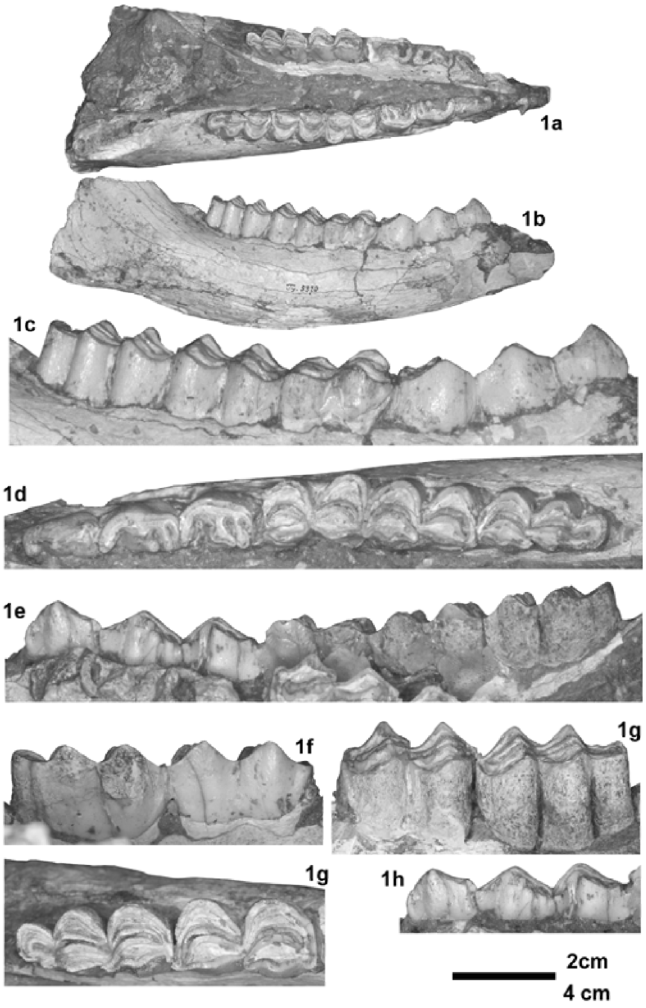

PLATE 2
Megaloceros sardus n.sp. from Capo Figari
(Forsyth Major collection in NMB).
Fig. 1. Ty 5370 - mandible with left M$_{2-3}$ and right P$_2$-M$_3$.
Figs a-b: occlusal and right buccal views of the complete specimen.
Figs c-e: detail of right P$_2$-M$_3$; buccal, occlusal and lingual views respectively.
Figs f-h: detail of left M$_{2-3}$; lingual, buccal and occlusal views respectively.
Fi. i: lingual view of the P$_{2-4}$ with crown base not hidden by left mandible.
The scale bar represents 4 cm for Figures 1a-1b and 2 cm for Figures 1c-1i.

precristid, the tooth resembles its homologue of *M. cazioti* (many specimens figured by CALOI & MALATESTA, 1974; PEREIRA, 2000). In *Cervus*, *Dama* and *Megaloceros giganteus*, the metaprecristid tends to be prominent as well as the paraconid and both close the anterior fossid on the lingual side, though occasionally the metaprecristid may be not well developed and the fossid opens lingually. In *M. savini*, *M. solilhacus* and the older *Eucladoceros* both morphologies are well represented. In many specimens of *E. giulii* from Untermassfeld (IQW) the metaprecristid is nearly never developed and the anterior fossid is open, save for in some heavily worn specimen. In the large deer from Akhalkalaki (= *Praemegaceros verticornis* of VEKUA, 1996) and Apollonia (= *Megaloceros* sp. of KOSTOPOULOS, 1997) the metaconids tend to be placed more foreward and the paraconid is more prominent, while in the large deer from Atapuerca TDW4 and Kuruksay this is less the case.

The **M$_1$** and **M$_2$** (Pl. 2, Figs. 1c-1h) have similar morphologies. Most of the lingual side is fairly flat: stylids or exocristids are not well marked and there is no marked depression between the two lobes. Near the occlusal surface the metapostcristid overlaps with the entoprecristid, interrupting the flat lingual surface. Unless wear is advanced (as is the case in the M$_1$), the two cristids do not fuse. There is no connecting element between the two cristids (metaendocristid or interlobular accessory cristid), as is common in *Cervus*, but not so in *Dama*. Both morphologies tend to occur in the various species of large deer. The interlobular collumn is low. The enamel is fairly thick. Thick enamel is common in insular artiodactyls (VAN DER MADE & RODRÍGUEZ, 2003; VAN DER MADE, 2004) and the Pleistocene cervids from Crete and Karpathos have much thicker enamel than their assumed ancestors. For the moment it is not possible to establish whether the deer from Capo Figari has thicker enamel than the taxa that might be ancestral.

The **M$_3$** (Pl. 1, Fig. 3; Pl. 2, Figs. 1c-1h) has basically the same structure as the M$_{1-2}$, but has a third lobe. The specimen from Sta. Lucia is not much worn, but does not have a high crown, unlike the homologues in the deer from Crete and Karpathos, where there is a moderate increase in hypsodonty.

There are several fragments of a **D$_4$** (Tab. 2) from Sta. Lucia.

The **mandible** (Pl. 2, Figs. 1a-b) does not seem much inflated (pachyostosis). The degree of robusticity or pachyostosis increases from *Dama*, which tends to have rather flat mandibles, to *Cervus*, *Eucladoceros* and *Megaloceros*, of which some species have particularly robust mandibles (e.g. *M. pachyosteus*). The specimen from Capo Figari is closer to *Dama* and *Cervus* in its degree of robusticity and to *M. cazioti* from Dragonara and Corbeddu, than to a *Megaloceros* with well developed pachyostosis. It has a long area behind the M$_3$ that is not much inclined before a more marked inclination marks the ascending ramus. In the deer from Sadali (Pl. 4, Fig. 1) the mandible is deeper and has a more curved ramus and the teeth are smaller in proportion to the mandible.

The **scapula** has a tuberosity with a downturned, but not hooked tuberosity (Character 1 of LISTER, 1996) and resembles *Cervus* rather than *Dama*.

The **humerus** (Pl. 3, Fig. 2) looks massive. It is slightly larger than the humeri of *Dama* from Neumark Nord.

There **radius** (Pl. 4, Fig. 3) does not have the posterior edge much elevated as is the case in *Cervus*.

There are fragments of the **ulna**, but these fragments do not present characters of great interest here.

There are several **carpals** of at least two individuals and one **cuneiform II+III**. These carpal bones and cuneiforms are usually not studied in detail, but in insular environment

TABLE 2

Measurements (in mm) of the lower dentition of *Megaloceros sardus* n.sp.

Locality	coll.	number			DAP	DAPb	DTa	DTp	DTpp	Ta	Tp	Dha
Capo Figari	NMB	Ty 5370	s	M_2	23.6	20.8	13.8	13.2		1.2	1.1	33
				M_3	27.1	26.2	12.5	11.8	6.7	1.1	0.9	
			d	P_2	15.8	14.8	7.2	9.4				28.5
				P_3	16.2	15.7	8.6	10.8				27.5
				P_4	14.7	16	11.6	10.9				28.6
				M_1	19.7	>19.7	13	13.9		0.9	0.9	34.8
				M_2	23.0	21.9	15.1	13.6		1.1	0.9	37.1
				M_3	27.3	26.4	12.5	11.7	6.5	0.9	0.9	36.5
Capo Figari	NMB	Ty 5372	d	P_3	17.0	16.0	9.2	-				
				P_4	17.1	16.5	10.5	10.3				
Sta Lucia I	IVAU		d	P_3	–	–	–	–				
Sta Lucia I	IVAU		d	D_4	–	–	–	11.8	–			
Sta Lucia I	IVAU		d	D_4	–	–	–	–	11.0			
Sta Lucia I	IVAU		d	D_2	–	–	–	–	11.2			
Sta Lucia I	IVAU		d	M_1	–	–	–	14.5				
Sta Lucia I	IVAU		d	M_1	–	–	–	12.9				
Sta Lucia I	IVAU		d	M_2	20.0	>20.0	13.7	12.6		0.8		
Sta Lucia I	IVAU		s	M_3	–	–	13.3	12.8	–			

occasionally fusions between the carpals or between the cuneiform and navicocuboid and metatarsal are reported (LEINDERS & SONDAAR, 1979; DE VOS 1979, 1984). The carpals and cuneiform from Sta. Lucia were are not fused and no particularities in their morphology were observed. Their size is slighly larger than in *Dama* from Neumark Nord.

There is one complete **metacarpal** (Pl. 3, Fig. 1) and several fragments. The complete specimen has a rather thick shaft, giving it a massive appearance. The facets for the magnum and unciform do not meet at the posterior side (Pl. 3, Fig. 1d), which is as in *Cervus*, but unlike in *Dama* (character 1 of LISTER, 1996) and *M. cazioti*, where the facets meet. There is a split between the distal articulations (character 6 of LISTER, 1996), which is the common state in *Cervus* and unlike in *Dama*. The distal articular facets are rather wide dorsally, whereas normally in the Cervidae these articulations become narrower dorsally. The specimen is large (Figs 1 & 2), and its length and distal width are about 135 and 136% of the average of the same values of 47 specimens of *M. cazioti* from Corbeddu (data from KLEIN HOFMEIJER, 1996); 128 and 123 %, respectively, of 34-36 specimens from Dragonara (CALOI & MALATESTA, 1974). With a length of about 262 mm, the metacarpal from Sadali has about 153 % the length of the average of the Corbeddu. The specimen is close in length to material from Monte Tuttavista, fissures "XI canide" and "XI mar 2002" (Fig. 1; ABAZZI *et al.*, 2004; PALOMBO, ARCA & TUVERI, unpublished data). The specimen from Sta. Lucia has a robusticity index of 551, while this is on average 573 in Dragonara (n = 33; CALOI & MALATESTA, 1974) and 558 in Corbeddu (n = 47; KLEIN HOFMIJER, 1996). The metapodial from Sadali has a significantly more slender diaphysis, but a larger epihysis (Fig. 5). The specimen from Sta. Lucia is as long as the longest specimens of the *Dama*-like deer, and much wider than any of them (Figs 2 & 4), as a consequence it is much more robust (Figs 2 & 3). Its size and robusticity are less than in *Megaloceros giganteus* and *M. solilhacus* (and related or similar forms), while the size is less than in any species assigned to *Eucladoceros*. The metapodials of

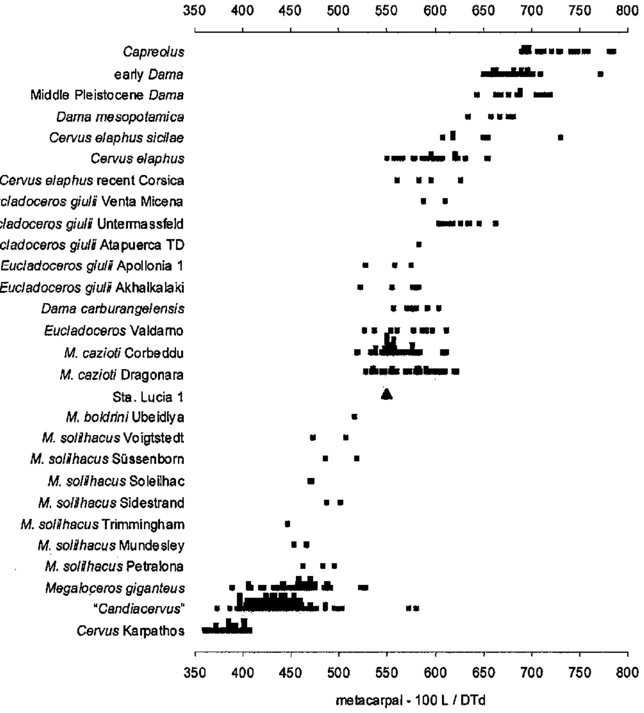

Fig. 3 . The metacarpal index 100 L / DTd in selected Cervidae. Sta. Lucia is indicated with a triangle. *Cervus cerigensis* from Kandilia Cave at Karpathos (Kuss, 1975) and *Cervus* aff. *cerigensis* from Karpathos I and II (IVAU); "*Candiacervus*" various species of Pleistocene Cervidae from Crete (IVAU, SMNK); *Megaloceros giganteus* (LISTER, 1994); *Megaloceros solilhacus* and related forms from Ubeidiya (HUJ), Voigtstedt (IQW), Süssenborn (IQW), Soleilhac (MCP), Trimmingham (NHM), Sidestrand (NHM), Mundesley (NHM), and Petralona (AUT); *M. cazioti* from Corbeddu (KLEIN HOFMEIJER, 1996); *M. sardus* n.sp. from Santa Lucia I (IVAU); *Eucladoceros dicranios* lineage from Valdarno (IGF); *Dama carburangelensis* from Capo Tindari (GLIOZZI & MALATESTA, 1982); *Eucladoceros giulii* and similar forms from Untermassfeld (IQW), Venta Micena (MENÉNDEZ, 1987), Atapuerca TD4 (MB), Apollonia 1 (AUT) and Akhalkalaki (GSMT); *Cervus elaphus* from Voigtstedt (IQW), Petralona (AUT) and Neumark Nord (LVH); recent *Cervus elaphus* from Corsica (IPH); *Cervus elaphus siciliae* from Puntali (GLIOZZI, MALATESTA & SCALONE, 1983); recent *Dama mesopotamica* (HUJ); *Dama*-like deer from Montopoli (IGF), Ubeidiya (HUJ), Tegelen (NMMa), Casa Frata (IGF), Il Tasso (IGF), Valdarno (IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMV), Gimbsheim (NMM); *Capreolus* from Pirro Nord (?; cast IGF), Mosbach (NMM), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Lehringen (HMV) and recent from Spain (MNCN) and the Netherlands (NNML).

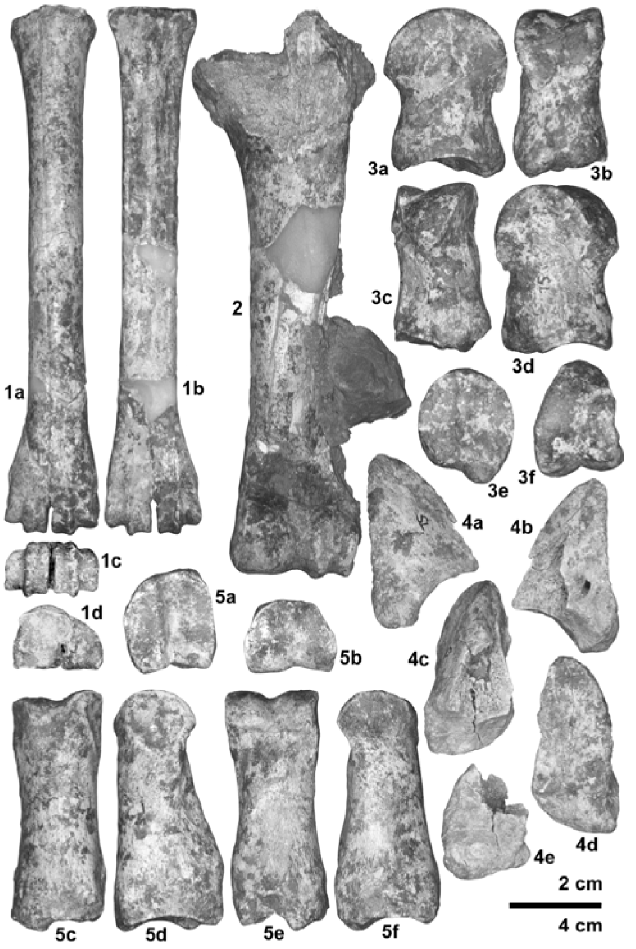

PLATE 3
Megaloceros sardus n.sp. from Sta. Lucia (IVAU).
Fig. 1. Right metacarpal; anterior (a), posterior (b), distal (c) and proximal (d) views.
Fig. 2. Left humerus; anterior view.
Fig. 3. Second phalanx; abaxial (a), plantar (b), dorsal (c), axial (d), proximal (e) and distal (f) views.
Fig. 4. Third phalanx; abaxial (a), axial (b), dorsal (c), plantar (d) and proximal (e) views.
Fig. 5. First phalanx; proximal (a), distal (b), dorsal (c), axial (d), plantar (e) and abaxial (f) views.
The scale bar represents 4 cm for Figures 1-2 and 2 cm for Figures 3-5.

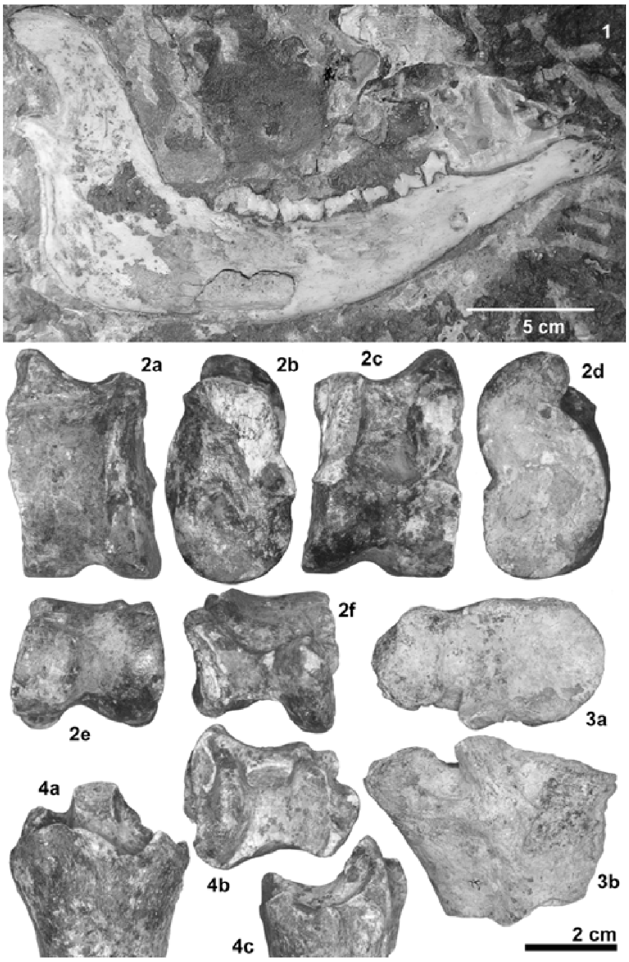

PLATE 4
Fig. 1. Left mandible of *Megaloceros* sp. from the Su Fossu de Cannas Cave, Sadali.
Fig. 2. Left astragalus of *Megaloceros sardus* n.sp. from Sta. Lucia (IVAU); posterior (a), medial (b), anterior (c), lateral (d), distal (e), and proximal (f) views.
Fig. 3. Left radius of *Megaloceros sardus* n.sp. from Sta. Lucia, proximal part; proximal (a) and posterior (b) views.
Fig. 4. Left tibia of *Megaloceros sardus* n.sp. from Sta. Lucia, distal part; anterior (a), distal (b), and lateral (c) views.
The 5 cm bar indicates the scale for the mandible, and the 2 cm bar indicates the scale for Figures 2-4.

the large deer from Apollonia, Akhalkalaki and Atapuerca TD are of a similar robusticity but are much larger than the specimen from Sta. Lucia.

The **tibia** (Pl. 4, Fig. 4) has the distal part of the anterior facet for the maleolar down turned (character 4 of LISTER, 1996).

The **astragalus** (Pl. 4, Fig. 2) has the lateral extension of the lateral ridge of the proximal articulation greater in its proximal part as in *Cervus* and unlike in *Dama* and the medial bulge does not seem to be very pronounced (Characters 4 and 5 of LISTER, 1996). The specimen from Sta. Lucia is much larger than its homologue from Corbeddu (Fig. 6). The external length (Lext) of the specimen from Sta. Lucia, expressed as a percentage of the average Lext of other samples is: 137% of Corbeddu (n=51; IVAU), 127% of Dragonara (n=42; CALOI & MALATESTA, 1974), 141% of Corte (n=2; PEREIRA, 2000) and 126% of Coscia NW (n=15; PEREIRA, 2000).

There are several **metatarsal** fragments. The distal articulation is as in the metacarpal, it does not become much narrower dorsally.

The **first phalanx** is represented by several specimens, both from the manus and pes. An anterior specimen is figured here (Pl. 3, Fig. 5). The specimen has a massive

TABLE 3

Measurments (in mm) of various bones of *Megaloceros sardus* n.sp. from Sta Lucia I (IVAU).

Bone		DAPd	DTd	DAPdf	DAPa	DTa					
Scapula	d	57.2	38.9	43.9	–	–					
Scapula	d	55.1	39.3	44.4	38.7	24.9					
Bone		DAPp	DAPpf	DTp	DTpf	L	l	DAPd	DAPdf	DTd	DTdf
Radius	s	≥31.3	–	52.1	48.1	–	–	–	–	–	–
Radius	d	–	–	–	–	–	–	35.1	27.3	≥48.8	45.3
Radius	s	31.7	26.6	54.3	48.9	–	–	–	–	–	–
Radius	d	–	–	–	–	–	–	33.1	27.5	≥49.5	45.2
Bone		DAPd	DTd								
Ulna	d	15.2	15.1								
Bone		DAPd	DTd	DTdf							
Tibia	s	31.6	39.4	29.3							
Bone		Lmi	Lm	Lmt	DTp	DTd					
Astragalus	s	38.5	39.5	–	–	31.5					

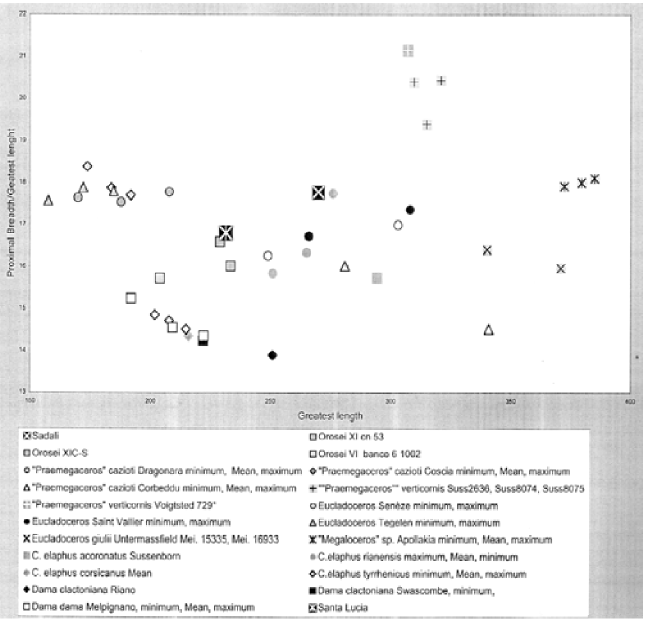

Fig. 4. Bivariate diagram of the ratio proximal width/greatest length against greatest length of the metacarpus. Provenance of data as in Figure 1.

appearance. As in the metacarpal, the specimens are about as long as their homologues in *Dama*, but they are clearly wider (Fig. 7). There is much variation in the robusticity of the first phalanges in the Cervidae (Fig. 8), the specimens from Sta. Lucia being intermediate between *Dama* and *M. giganteus* and close to *Eucladoceros*. The distal articulation appears to be relatively wide (Pl. 3, Fig. 5e) and this is confirmed by the measurements (Fig. 9). In this the phalanges from Sta. Lucia are unlike those of *Dama*, but more similar to *Cervus* and the large deer from Atapuerca and Apollonia.

The **second phalanx** (Plate 3, Fig. 3) looks rather massive and this is probably related to the wide distal articulation of the first phalanx. The shape of the plantar

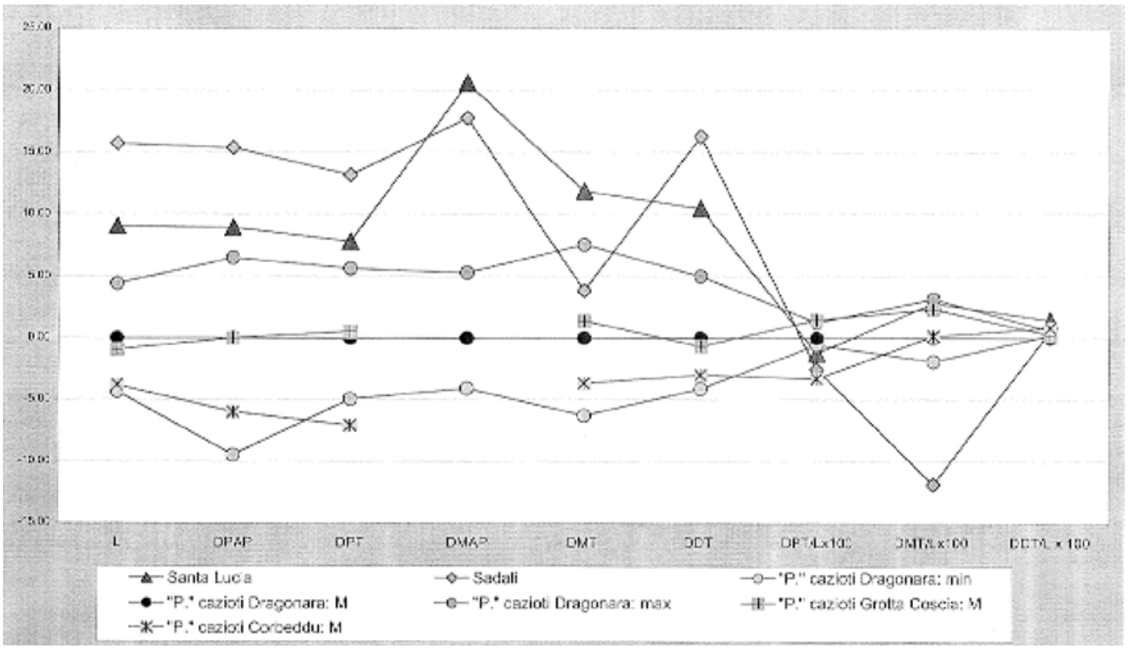

Fig. 5. Logarithmic distances of the measurements of the metacarpals of Sta. Lucia, the Su Fossu de Cannas Cave and Corbeddu compared to Dragonara (standard). Provenance of data as in Fig. 1.

TABLE 4

Measurments (in mm) of the humerus and metapodials of *Megaloceros sardus* n.sp. from Sta Lucia I (IVAU).

Bone		DAPp	DAPpf	DTp	DTpf	L	l	DAPd	DTd	DTdf	H1	H2	H3	H4	H5
Humerus	s	≥81.0	72.0	–	54.4	–	216.5	54.0	52.0	47.9	35.9	37.1	32.0	28.1	26.1
Humerus	d									47.5	36.1	37.0	32.9	24.7	27.8
Bone		DAPp	DTp	DAPpf	DTpf	DAPm	DTm	DTd	DAP3	DT3	DAP4	DT4	L	L3	L4
Mc III+IV	s	±32.2	–	±36.1	–	–	–	–	–	–	–	–	–	–	–
Mc III+IV	d	27.5	38.9	24.6	36.9	28.6	24.5	42.0	23.6	19.7	25.9	19.4	231.5	228.2	226.1
Mc III+IV	d	26.6	38.7	25.5	36.8	–	–	–	–	–	–	–	–	–	–
Mt III+IV	s	32.7	30.3	28.0	27.4										
Mt III+IV	?	–	–	–	–	15.9	–	–	–	–	–	–	–	–	–
Mt III+IV	?	–	–	–	–	–	–	≤44.8	26.4	30.0	25.3	19.5	–	–	–
Mt III+IV	s	36.2	32.7	33.5	31.0	–	–	–	–	–	–	–	–	–	–

TABLE 5

Measurements (in mm) of the carpals, cuneiform and sesamoid of *Megaloceros sardus* n.sp. from Sta Lucia I (IVAU).

Bone		DAP	DT	H	h	DTp	DTd	Hs
magnum	s	25.5	24.2	16.9	13.9			
magnum	d	25.3	24.9	17.4	13.8			
unciform	s	23.7	19.2	16.7				
cuneiform	s	22.4	18.5	15.9				
ulnar	s	27.3	17.5	30.8	20.9			
lunar	s	26.9				20.1	14.5	21.1
lunar	d	27.3				19.9	21.3	14
scaphoid	s	33.5	17.5					22.6
scaphoid	s	31.8	26.1					21.3
sesamoid		21.6	8.6	19.1	19.1			
cuneiform II + III	s	21.8	12.9					

TABLE 6

Measurements (in mm) of the phalanges of *Megaloceros sardus* n.sp. from Sta Lucia I (IVAU).

Bone			DAPp	DAPp	DTp	L	DAPd	DTd
Phalanx 1	r	ant	24.0	22.1	19.7	53.8	16.4	20.2
Phalanx 1	l	ant	22.7	21.8	19.9	53.2	16.3	20.2
Phalanx 1	r	post	23.5	22.5	≥19.6	51.4	14.8	17.6
Phalanx 1	r	ant	23.5	22.9	20.5	53.3	16.2	20.2
Phalanx 1	l	ant	23.3	22.1	20.9	52.8	16.3	19.9
Phalanx 1	l	post	–	–	20.6	>53.9	16.3	18.4
Phalanx 1	r	?	juv				±11.8	±14.3
Phalanx 1	r	?	juv				–	–
Phalanx 2	r	?	24.9	22.2	20.5	38.5	25.2	19.1
Phalanx 2	r	?	>24.5	23.1	20.2	41	22.4	17.6
Phalanx 3	l	?	–	–	17.9	38.6		

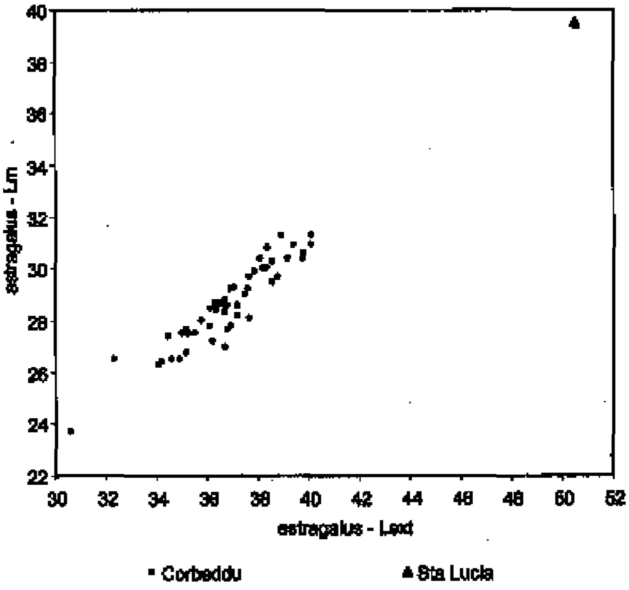

Fig. 6. Bivariate diagram of the astragalus (Lext against Lm; values in mm). *M. cazioti* from Corbeddu (when studied in IVAU) and *Megaloceros sardus* n.sp. from Sta. Lucia (IVAU).

part of the distal articulation suggests that the specimen figured might be from the hind foot. The proximal articulation has a nearly circular outline and the "postarticular process" is small. As in the first phalanx, the distal articulation looks disproportionately large.

The **third phalanx** (Pl. 3, Fig. 4) is wide and short and has a wide plantar surface.

DISCUSSION

The material from Sta. Lucia and Capo Figari (FM collection) belongs to a species of deer that shares a number of morphological characters with the material that is normally assigned to *M. cazioti*. Without being exhaustive, these include: P_2 with well developed parastylids, P_4 with a metaconid that is rounded anteriorly and which leaves the anterior valley wide open, a mandible that is not pachyostotic, and roughly the degree of robusticity of the

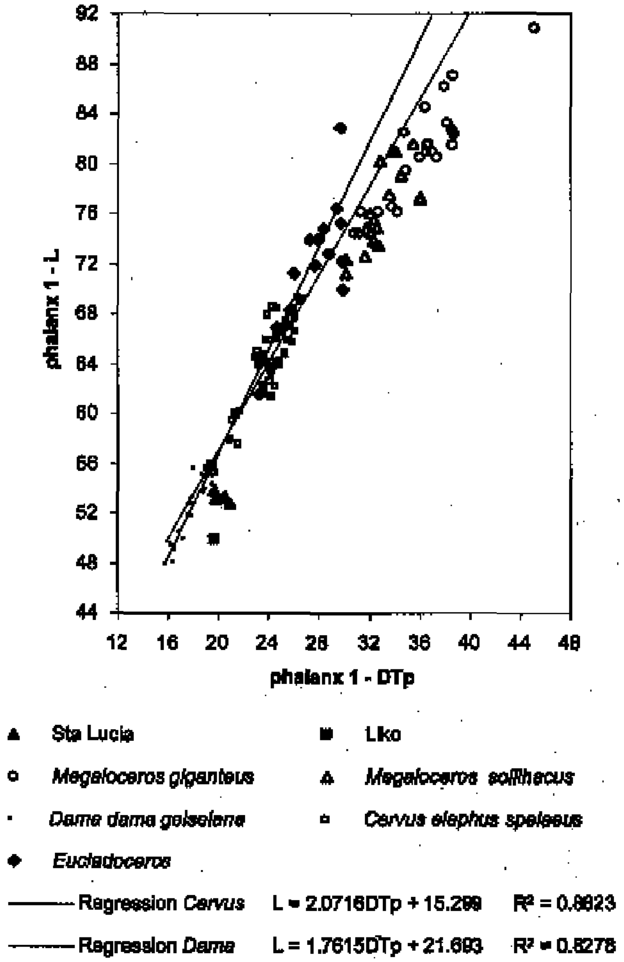

Fig. 7. Bivariate diagram of the first phalanx (L = length, DTp = proximal width; values in mm). *Megaloceros sardus* n.sp. from Sta. Lucia (IVAU), "*Candiacervus*" sp. from Liko (IVAU), *Cervus elaphus spelaeus* from Neumark Nord (LVH), *Dama dama geiselana* from Neumark Nord (LVH), *Megaloceros giganteus* from "Ireland" (NHM), the *Megaloceros solilhacus* and other large deer from Ubeidiya (HUJ), Voigtstedt (IQW), Süssenborn (IQW), Soleilhac (MCP) and West Runton (NHM), *Eucladoceros tegulensis* from Tegelen (NMMa, NNML), *Eucladoceros dicranios* from Il Tasso (IGF), and *Eucladoceros giulii* and large deer from Untermassfeld (IQW), Atapuerca Gran Dolina (MB), Apollonia 1 (AUT).

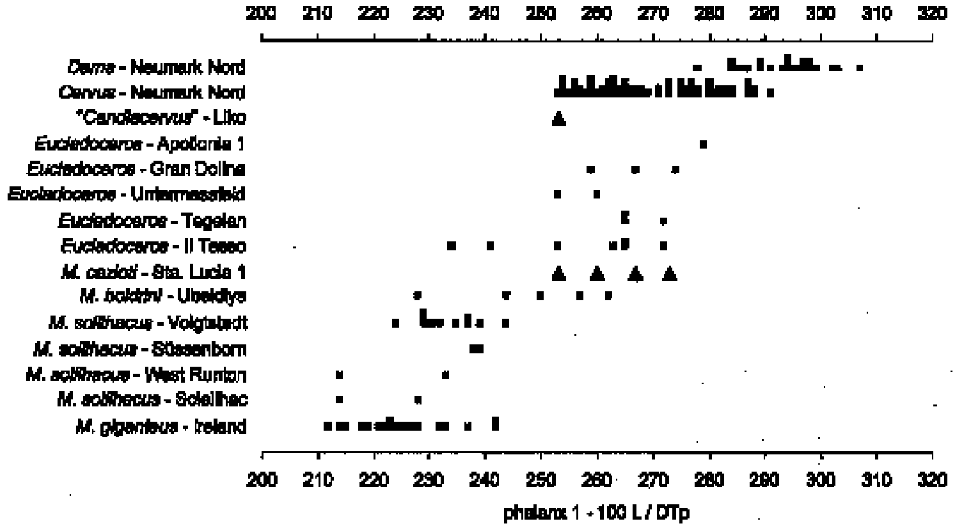

Fig. 8 Robusticity index (= 100 L / DTp) of the first phalanx. Provenance of data as in Fig. 4.

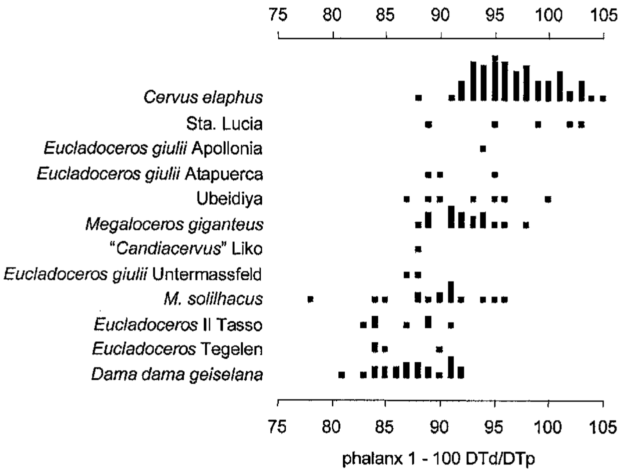

Fig. 9 The relative width of the distal articulation of the first phalanx. Provenance of data as in Fig. 4.

metacarpal. These and other similarities suggests a close relationship.

However, the material from Sta. Lucia is clearly larger than that from Dragonara and Corbeddu (Sardinia) and Coscia, Corte and Maccinagio (Corsica), which are considered to be typical *M. cazioti*. It is close to material from Monte Tuttavista ("XI canide" and "XI mar2002" fissures), but it is still much smaller than the material from Sadali described by PALOMBO *et al.* (2003) and PALOMBO & MELIS (in press). The size differences between Sta Lucia and the more typical *M. cazioti*, being in the order of 25 to 40%, are considerable. Such differences are usually not found in a single species. Therefore it is assumed that this material represents a different species, for which the name *M. sardus* is proposed.

A progressive decrease in the Sardinian deer lineage was hypothesised already by different authors (e.g. COMASCHI CARIA, 1955; AZZAROLI, 1961; CALOI *et al.*, 1981, 1988), even if no incontestable evidence of this trend was available at that time. This hypothesis is reinforced here by the description of large deer from Sta. Lucia and Capo Figari. The dates for Sta. Lucia and Capo Figari II, around 450 and 367 ka respectively, suggest that the large *M. sardus* is older than the smaller *M. cazioti*, which occurs in localities that are known to be Late Pleistocene or early Holocene (e.g. KLEIN HOFMEIJER, 1996). As mentioned above, deer of similar size have been found at Monte Tuttavista in the fissure fillings "XI canide" and "XI mar2002" associated to a quite advanced faunal assemblage, with *Tyrrhenicola henseli* and *Rhagamys ortodon* (ABAZZI *et al.*, 2004).

PALOMBO & MELIS (in press) suggest a size decrease in the Sardinian *Megaloceros* and assume that the, not yet named, new and very large species from the Su Fossu de Cannas Cave (Sadali) is the most primitive representative of the genus in Sardinia and is ancestral to *M. cazioti*. However, the deer from Sadali differs from *M. sardus* and *M. cazioti* in its larger size and morphological features, such as the depth and the curved horizontal ramus of the mandible, the proportionally smaller teeth and the more elongate, slender metacarpal.

The morphological characters shared by the three Sardinian species suggest an ancestor-descendant relationship. Such a relationship seems logical, since otherwise additional dispersals of deer into the islands of Sardinia and Corsica have to be assumed. The size cline might be of stratigraphic interest, but additional work should confirm its validity for such aims. It suggests the approximate sequence: Sadali with *Megaloceros* n. sp., next Sta. Lucia, Capo Figari and fissures "XI canide" and "XI mar2002" at Monte Tuttavista, with *M. sardus*, next Dragonara, Monte Tuttavista (fissure VII 2) and Coscia with large *M. cazioti*, and Corbeddu and Corte with small *M. cazioti*. The transition of *M. sardus* to *M. cazioti* and the transition of the Orosei 2 to the Dragonara "faunal sub complex" are likely to have occurred after some 367 Ma ago.

The origin of the endemic deer from Sardinia and Corsica are still under debate, though most authors believe *M. cazioti* to be related to one of the large deer of the early and Middle Pleistocene, it has also been suggested that it might be related to *Dama* (KLEIN HOFMEIJER, 1996, foot note p. 8). This seems unlikely for various reasons:

1) The cranial morphology of *M. cazioti* is similar to that in the giant deer (cf. CALOI & MALATESTA, 1974).
2) The P_4 morphology in *M. cazioti* and its ancestor *M. sardus* is consistently unlike in *Dama*, whereas similar morphologies do occur in some of the large deer of the Pleistocene of Europe.
3) The morphology of some bones (e.g. scapula, metacarpal) differs from that in *Dama*.
4) The large *M. sardus* is much larger than any *Dama* and if *Dama* would be its ancestor, this would imply a considerable size increase in insular environment. Large mammals tend to decrease in size in insular environment.

ACKNOWLEDGEMENTS

We thank the following persons for access to material: M. ARCA (SBASN), AMPRIMOZ (MCP), J. BAREIRO (MNCN), R. CARLINI (MCZR), B. CASTILLO (MB), E. CIOPPI (IGF), E. CRÉGUT-BONNOURE (MRA), A. CURRANT (NHM), B. ENGESSER (NMB), E. FREY (SMNK), J.H. GRÜNBERG (LVH), J. JAGT (NMMa), R.D. KAHLKE (IQW), H. LUTZ (NMM), D. MANIA (Jena), R. MANNI (MPUSR), R. MATTEUCCI (MPUSR), H. MELLER (LVH), A.J. VAN DER MEULEN (IVAU), W. MUNK (SMNK),M.PATOU-MATHIS (IPH), C. SMEENK (NNML), C. SPANU (MPC), late E. TCHERNOV (HUJ), E. TSOUKALA (AUT), C. TUVERI (SBASN), A. VEKUA (GSMT), J. DE VOS (NNML). During this study JvdM recieved support from project BOS2003-08938 -C03-02.

REFERENCES

ABAZZI, 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.F.M., & B. WILKENS (2004). Plio-Pleistocene fossil vertebrata of Monte Tuttavista (Orosei, Eastern Sardinia, Italy), an overview. *Rivista Italiana di paleontologia e Stratigrafia*, 110 (3), 603-628.

ANTONIOLI, F., GIROTTI, O., ORPU, P., & M. VOLTAGGIO (1998). Il deposito fossile a cervi nani nella Grotta Sommersa di Punta Giglio (Alghero): considerazioni paleoambientali dallo stadio 5 al presente, 78- 81.

ARAMBOURG, C. (1932). Note préliminaire sur une nouvelle grotte à ossements des environs d'Alger. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 23, 154-162.

ARAMBOURG, C. (1938). Mammifères fossiles du Maroc. *Mémoire de la Société de l'Histoire Naturelle de Maroc*, 46, 1-72.

AZZAROLI, A. (1952). La sistematica dei Cervi Giganti e i Cervi Nani delle isole. *Atti Soc. Tosc. Sci. Nat., Mem.(A)*, 59 , 119-127.

AZZAROLI, A. (1961). Il nanismo nei cervi insulari. *Palaeont. Ital.*, 56, 1-31.

AZZAROLI, A. (1979). Critical remarks on some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Palaeont. It.*, n.s. 41, 71, 5-16.

AZZAROLI, A. & P. MAZZA (1992). The cervid genus *Eucladoceros* in the Early Pleistocene of Tuscany. *Palaeont. Ital.*, 79, 43-100.

CALOI, L. & A. MALATESTA (1974). Il cervo pleistocenico di Sardegna. *Mem. Ist. It. Paleont. Umana*, n.s., 2, 163-246.

CALOI, L., KOTSAKIS, T. & M.R. PALOMBO (1988). La Fauna a vertebrati terrestri del Pleistocene delle isole del Mediterraneo. *Geologica Romana*, 25 (1986), 235-256.

CALOI, L., KOTSAKIS, T., PALOMBO, M.R. & C. PETRONIO (1981). Il giacimento a vertebrati del Pleistocene superiore di San Giovanni in Sinis (Sardegna occidentale). *Rend. Acc. Naz. Lincei*, s. 8, 69(1980), 185-197, Roma.

CALOI, L. & M.R. PALOMBO (1996). Il megacerino di Dragonara, interpretazione funzionale di alcuni caratteri cranici. *Geologica Romana*, 31 (1995), 29-40.

COMASCHI CARIA, I. (1955). Resti di cervidi nel Quaternario di Porto Vesme. *Rivista Italiana di Paleontologia e Stratigrafia*, 61(1), 17-27.

COMASCHI CARIA, I. (1956). Specie nuova nel Quaternario di Alghero (Sardegna): *Rendiconti Seminario della Facoltà di Scienze, Univ. Cagliari*, 25(3-4), 1-6.

CORDY, J.M. & A. OZER (1972). Découverte d'un crâne de cervidé mégacérin (*Nesoleipoceros cazioti*) dans le Quatenaire de la Sardaigne septentrionale. *Annales de la Société géologique de Belgique*, 95, 425-449.

DEHAUT, E.G. (1911). *Materiaux pour servir a l'Histoire zoologizue et paléontologique des iles de Corse et de Sardaigne. Fascicule 1*. Paris, G. Steinheil Éditeur.

DI STEFANO, G. (1994). Il daino pleistocenico dell'Eurasia. *PhD umpublished thesis, VII cycle, University of Modena, Bologna, Firenze, Roma.*

DI STEFANO, G. (1995). Identification of fallow deer remains on the basis of its skeletal features: taxonomical considerations. *Bolletino della Società Paleontologica Italiana*, 34(3), 323-331.

GINESU, S., SIAS, S., CORDY, J-M., TRENINI, L., MELE, A., SERRA, A., VIRGILIO, P. & A. ZARA (1998). Grotta di Nuraghe (Sassari), esplorando il passato. *Speleologia,* 38, 52-60.

GLIOZZI, E. & A. MALATESTA (1982). A megacerine in the Pleistocene of Sicily. *Geologica Romana*, 21, 311-389.

GLIOZZI, E., MALATESTA, A. & M.R. PALOMBO (1984). Upper Pleistocene small mammal associations in the Is Oriris area (Iglesiente, SE Sardina). *Geologica Romana*, 23, 121-129.

GLIOZZI, E., MALATESTA, A. & E. SCALONE (1983). Revision of *Cervus elaphus sicilae* Pohlig, 1893, Late Pleistocene endemic deer of the Siculo-Maltese district. *Geologica Romana*, 29, 307-353.

HADJOUIS, D. (1990). *Megaceroides algericus* (LYDEKKER, 1890), du gisement des Phachochères (Alger, Algérie). Étude critique de la position systématique des *Megaceroides*. *Quaternaire*, 1(3-4), 247-258.

HSÜ, K.J., MONTADERT, M., BERNOUILLI, D., CITA, M.B., ERKISON, A., GARRISSON, A.E., KIDD, R.B., MILIERÉS, F., MÜLLER C. & R. WRIGHT (1977). History of the Mediterranean Salinity Crisis. *Nature*, 267, 399-403.

JOLEAUD, L. (1914). *Cervus (Megaceroides) algericus* Lydekker. *Comptes Rendues de la Société Biologique de Marseille*, 76, 737.

KAHLKE, H.D. (1956-59). *Die Cervidenreste aus den Altpleistozänen Ilmkiesen von Süssenborn bei Weimar*. Akad.Verlag, I-III, 1-62; 1-44; 1-45.

KAHLKE, H.D. (1958). *Die Cervidenreste aus den Altpleistozänen Tonen von Voigstedt bei Sangershausen*. Akad. Verlag, I-III.

KAHLKE, H.D. (1969). Die Cerviden-Reste aus den Kiesen von Süssenborn bei Weimar: Paläont. Abh. A, III(3/4), 547-609.

KAHLKE, H.D. (1997). Die Cerviden-Reste aus dem Untepleistozän von Untermassfeld. *In:* R.D. KAHLKE (*Ed.*) *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*. Bonn, Dr. RUDOLF HABELT GMBH, 181-275, plates 34-44.

KLEIN HOFMEIJER, G. (1996). *Late Pleistocene deer fossils from Corbeddu cave - implications for human colonization of the island of Sardinia*. Thesis University of Utrecht, 1-437.

KOSTOPOULOS, D. (1997). The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia 1. The fossiliferous site "Apollonia-1", Mygdonia basin of Greece. *Geodiversitas*, 19(4), 845-875.

KOTSAKIS, T. (1980). Osservazioni sui vertebrati Quatenari della Sardegna. *Bolletino della Società geoligica Italiana*, 99, 151-165.

KOTSAKIS, T. (1986). Paléobiogéograpie des mammifères continentaux de a Méditerranée occidentale au Néogène. *Giornale di Geologia*, third series, 48(1-2), 145-152.

KOTSAKIS, T. & M.R. PALOMBO (1979). Vertebrati continentali e paleogeografia della Sardegna durante il Neogene. *Annales Géologiques des Pays Hélléniques*, tome hors serie, 2, 621-630.

KUSS, S.E. (1975). Die pleistozäne Hirsche des ostmediterranen Insel Kreta, Kasos, Karpahtos und Rhodos (Griechenland). *Ber. Naturf. Gesellschaft Freiburg in Br.*, 65, 25-79.

LEONARDI, G. & C. PETRONIO (1974). I cervi pleistocenici del bacino diatomitico di Riano (Roma). *Mem. Acc. Naz. Lincei*, S. 8, 12 (3), 103-208.

LEONARDI, G. & C. PETRONIO (1976). The fallow deer of European Pleistocene. *Geologica Romana*, 15, 1-67.

LEINDERS, J.M. & P.Y. SONDAAR (1979). On fuctinional fusions in the footbones of ungulates. *Zeitschrift für Säugetierkunde*, 39, 109-115.

LISTER, A.M. (1993). The stratigraphical significance of deer species in the Cromer Forest-bed Formation. *Journal of Quaternary Science*, 8(2), 95-108.

LISTER, A.M. (1994). The evolution of the giant deer, *Megaloceros giganteus* (Blumenbach). *Zoological Journal of the Linnean Societey*, 112, 65-100.

LISTER, A.M. (1996). The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). *International Journal of Osteoarchaeology*, 6, 119-143.

MADE, J. VAN DER (1988). *Sus nanus* nov. sp. a Pliocene dwarf pig from Capo Figari (Sardinia). *Bolletino della Società Paleontologica Italiana*, 27 (3), 367-378, 3 pls.

MADE, J. VAN DER (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.

MADE, J. VAN DER (1996). Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contributions to Tertiary and Quaternary Geology*, 33(1-4), 3-254, microfiche 1-54.

MADE, J. VAN DER (1999). Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. *Deinsea*, 7, 377-360.

MADE, J. VAN DER (2001). Les ongulés d'Atapuerca. Stratigraphie et biogéographie. *L'Anthropologie*, 105 (1), 95-113.

MADE, J. VAN DER (2004). The status of *Conohyus giganteus* (Nyanzachoerini, Tetraconodontinae, Suidae) - Reply to Pickford (2001). *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 94, 157-167.

MADE, J. VAN DER & J. RODRξGUEZ (2003). Increased molar enamel thickness as an adaptation to insular environment. Insular vertebrate evolution, the paleontological approach. Palma de Mallorca, 16-19/9/2003. Abstract, 74-75.

MELIS, R.T., PALOMBO, M.R. & M. MUSSI (2003). The Gonnesa (Western Sardinia, Italy) Late Pleistocene sequence. *In:* WRANDER, J. *(Ed.) Island biogeography*. BAR.

MENÉNDEZ, E. (1987). Cérvidos del yacimiento del Pleistoceno inferior de Venta Micena-2, Orce (Granadoa, Espa•a). *Paleontologia i Evoluci½*, mem. esp. 1, 181-236.

PALOMBO, M.R. (in press). Biochronology of the Plio-Pleistocene terrestrial mammals of Sardinia: the state of art

PALOMBO, M.R. & R. MELIS (in press). Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia, Italy): the oldest deposit holding megalocerine remains in the Pleistocene of Sardinia. *Monographs Nat. Hist. Soc. Balearic Islands*.

PALOMBO, M.R., MELIS, R., MELONI, S. & C. TUVERI (2003). A new cervid in the Pleisocene of Sardinia: preliminary report. *Bolletino della Società Paleontologica Italiana*, 42(1-2), 157-162.

PEREIRA, E. (2000). Présence du Cervidé *Megaloceros (Nesoleipoceros) cazioti* (DÉPERET, 1897) dans le gisement pléistocène de Corte (Corse). *Geodiversitas*, 22(3), 433-455.

PEREIRA, E. & M.F. BONIFAY (1998). Étude préliminaire des restes de cervidés de la Grotte de la Coscia (Rogliano - Haue Corse). *Paleo*, 10, 43-60.

PEREIRA, E., MICHAUX, J. & S. MONTUIRE (2003). New data on the extinct rodents of Corsica *Rhagamys* and *Microtus (Tyrrhenicola)* (Mammalia, Muridae). *Abstracts Int. Symp. Insular Vertebrate Evolution, the palaeontological approach, september 16-19 2003, Mallorca*, 55.

SIGOGNEAU, D. (1960). Étude d'un cervidé Pléistocène de Corse. *Annales de Paléontologie*, 46, 49-77, pls.6-8.

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. & D. ESU (1984). First report on a Palaeolithic culture in Sardinia. *In:* W.H. WALDREN, R. CHAPMAN, J. LEWTHWAITE & R.C. KENNARD *(Eds.)* The Deya Converence of Prehistory - Early settlement in the western Mediterranen islands and the peripheral areas. *BAR International Series*, 229, 29-47, Figs. 1-5, pls. 1-7.

SONDAAR, P.Y., SANGES, M., KOTSAKIS, T. & P.L. DE BOER (1986). The Pleistocene deer hunter of Sardinia. *Geobios*, 19(1), 17-25, pls. 1-3.

SPAAN, A. (1992). A revision of the deer from Tegelen (province of Limburg, The Netherlands). *Scripta Geologica*, 98, 1-85.

VEKUA, A. (1986). The Lower Pleistocene mammalian fauna of Akhalkalaki (southern Georgia, USSR). *Palaeontographica Italica*, 74, 63-96.

VOS, J. DE (1979). The endemic Pleisocene deer of Crete. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, Series B, 82(1), 59-90.

VOS, J. DE (1984). The endemic Pleistocene deer of Crete. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afd. Natuurkunde*, eerste reeks, 31, 1-110.