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

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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.

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; PA-LOMBO, 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 Balearics. 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 “*Tyrrenicolae* 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 *Tyrrenicolae* cervid and the dog *Cynootherium* 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. meloni*, was reported from the locality Capo Figari II, which also yielded a primitive *Tyrrenicolae* (VAN DER MADE, 1999). A caprine, clearly different from *Nesogoral* in association with a primitive *Tyrrenicolae* 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 “*Præmegaceros-Tyrrenicolae* complex” in two, the older third “faunal 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 Sar-
dinia: the Pliocene/Early Pleistocene “Nesogoral faunal
complex” (including Mandriola and Capo Figari/Orosei 1
subcomplexes) and the earliest? Middle Pleistocene/Ho-
locene “Microtus (Tyrhenicola) 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 DEPERET, 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 Tutavista 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, Tyrhenicola, Rhaganyss 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, O-
saka 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:

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dbu</td>
<td>Depth of the mandible, measured below each cheek tooth from P3 to M3. Normally the depth is measured at the linguo-side (D; VAN DER MADE, 1989), but this is not possible here.</td>
</tr>
<tr>
<td>DAP</td>
<td>Antero posterior diametre (or length in a tooth).</td>
</tr>
<tr>
<td>DAPb</td>
<td>DAP measured at the base of a tooth.</td>
</tr>
<tr>
<td>DAPd</td>
<td>DAP of the distal end of a bone.</td>
</tr>
<tr>
<td>DAPdf</td>
<td>DAP of the distal facet of a bone.</td>
</tr>
<tr>
<td>DAPn</td>
<td>DAP of the “neck” of a bone; the minimal DAP.</td>
</tr>
<tr>
<td>DAPp</td>
<td>DAP of the proximal end of a bone.</td>
</tr>
<tr>
<td>DAPpf</td>
<td>DAP of the proximal facet of a bone.</td>
</tr>
<tr>
<td>DAP3 (DAP4)</td>
<td>DAP of the distal articulation of the third (fourth) metapodial.</td>
</tr>
<tr>
<td>DT</td>
<td>Transverse diametre or width.</td>
</tr>
<tr>
<td>DTa</td>
<td>DT of the anterior lobe of a tooth.</td>
</tr>
<tr>
<td>DTd</td>
<td>DT of the distal end of a bone.</td>
</tr>
<tr>
<td>DTdf</td>
<td>DT of the distal facet of a bone.</td>
</tr>
<tr>
<td>DTm</td>
<td>DT of the middle lobe of the D3, or minimal DT of a bone, generally near the middle.</td>
</tr>
<tr>
<td>DTn</td>
<td>DT of the “neck” of a bone; the minimal DT.</td>
</tr>
<tr>
<td>DTP</td>
<td>DT of the anterior lobe of a tooth.</td>
</tr>
<tr>
<td>DTPf</td>
<td>DT of the proximal facet of a bone.</td>
</tr>
<tr>
<td>DTpp</td>
<td>DT of the third lobe in a M3.</td>
</tr>
</tbody>
</table>
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 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 sollihacuis 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 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 et ALAMOBO, 1996), was frequently employed, whereas other names, such as “Ortogonoceros” or “Psekupsceroces”, 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 these are some vertebrae from Sta. Lucia, which are not included here.

The $P_2$ (Pl. 1, Figs. 1 & 4) has a rounded lingual side with only a faint groove 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 $P_4$ of LISTER, 1996).

The $P_3$ (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 groove 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 $P_2$).

The $P_4$ (Pl. 1, Fig. 1) has a remarkably flat buccal wall. Like the $P_2$, it has a very simple shape; its lingual wall is more inclined (Pl. 1, fig. 1d).

The $M_1$ and $M_2$ (Pl. 1, Fig. 1) have similar morphologies. A lingual interlobular column is not present at all. 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 $M_3$ (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
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 P2 (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 P2 in M. cazioti (Pereira, 2000).

The P3 (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 P4 (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-
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 (= *Præmegaceros verticornis* of Vekua, 1996) and Apollonia (= *Megaloceros* sp. of Kostopoulos, 1997) the metaconids tend to be placed more forward 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 column 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*₁₂, 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 *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 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
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 not fused and no particularities in their morphology were observed. Their size is slightly 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); “Candiacervus” various species of Pleistocene Cervidae from Crete (IVAU, SMNK); Megaloceros giganteus (Lister, 1994); Megaloceros solilhacus and related forms from Ubeidiya (HUJ), Voigtstedt (IQW), Süssemborn (IQW), Solothurn (MCP), Trimingham (NMM), Siedenstand (NMM), Mundesley (NMM), and Petralona (AUT); M. cazioti from Corbeddu (Klein Hofmeijer, 1996); M. sardus n.sp. from Santa Lucia I (IVAU); Encheladoceros dizianus lineages from Valdarno (IGF); Dama carburangelensis from Capo Tindari (Glozzoli & Malatesta, 1982); Encheladoceros giglii and similar forms from Untermassfeld (IQW), Venta Micena (Menesnède, 1987), Atapuerca TD4 (MB), Apollonina 1 (AUT) and Akhkalkalaki (GSMT); Cervus elaphus from Voigtstedt (IQW), Petralona (AUT) and Neumark Nord (LVH); recent Cervus elaphus from Corsica (IPH); Cervus elaphus siciliae from Puntali (Glozzoli, Malatesta & Scalone, 1983); recent Dama megapotamica (HUJ); Damalike 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), Moshbach (NMM), Grotte des Cerises (MRA), Ehrendorf (IQW), Lehringen (HMV) and recent from Spain (MNCN) and the Netherlands (NNML).

Table 2

<table>
<thead>
<tr>
<th>Measure</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAP</td>
<td>25.6</td>
<td>25.4</td>
</tr>
<tr>
<td>DAP</td>
<td>25.4</td>
<td>25.3</td>
</tr>
<tr>
<td>HP</td>
<td>7.2</td>
<td>7.4</td>
</tr>
<tr>
<td>DP</td>
<td>7.4</td>
<td>7.6</td>
</tr>
<tr>
<td>TP</td>
<td>15.9</td>
<td>15.9</td>
</tr>
<tr>
<td>F</td>
<td>0.9</td>
<td>0.8</td>
</tr>
<tr>
<td>S</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>T</td>
<td>0.8</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Fig. 3. The metacarpal index 100 L / DTw in selected Cervidae. Sta. Lucia is indicated with a triangle. Cervus cerigenis from Kandilia Cave at Karpathos (Kuss, 1975) and Cervus aff. cerigenis from Karpathos I and II (IVAU); “Candiacervus” various species of Pleistocene Cervidae from Crete (IVAU); Megaloceros giganteus (Lister, 1994); Megaloceros solilhacus and related forms from Ubeidiya (HUJ), Voigtstedt (IQW), Süssemborn (IQW), Solothurn (MCP), Trimingham (NMM), Siedenstand (NMM), Mundesley (NMM), and Petralona (AUT); M. cazioti from Corbeddu (Klein Hofmeijer, 1996); M. sardus n.sp. from Santa Lucia I (IVAU); Encheladoceros dizianus lineages from Valdarno (IGF); Dama carburangelensis from Capo Tindari (Glozzoli & Malatesta, 1982); Encheladoceros giglii and similar forms from Untermassfeld (IQW), Venta Micena (Menesnède, 1987), Atapuerca TD4 (MB), Apollonina 1 (AUT) and Akhkalkalaki (GSMT); Cervus elaphus from Voigtstedt (IQW), Petralona (AUT) and Neumark Nord (LVH); recent Cervus elaphus from Corsica (IPH); Cervus elaphus siciliae from Puntali (Glozzoli, Malatesta & Scalone, 1983); recent Dama megapotamica (HUJ); Damalike 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), Moshbach (NMM), Grotte des Cerises (MRA), Ehrendorf (IQW), Lehringen (HMV) and recent from Spain (MNCN) and the Netherlands (NNML).
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

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

<table>
<thead>
<tr>
<th>Bone</th>
<th>S.A.</th>
<th>B.M.</th>
<th>R.M.</th>
<th>H.B.</th>
<th>S.A.</th>
<th>B.M.</th>
<th>R.M.</th>
<th>H.B.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radius</td>
<td>31.3</td>
<td>31.1</td>
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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. 4. Bivariate diagram of the ratio proximal width/greatest length against greatest length of the metacarpus. Provenance of data as in Figure 1.

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 5
Measurements (in mm) of the carpals, cuneiform and sesamoid of *Megaloceros sardus* n.sp. from Sta Lucia I (IVAU).

<table>
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<tr>
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<th>DP</th>
<th>DAP</th>
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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).

**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: P2 with well developed parastylids, P4 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 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.
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), Voigststedt (IQW), Süssenborn (IQW), Soleilhac (MCP) and West Runton (NHM), *Eucladoceros tegulensis* from Tegelen (NMMa, NNML), *Eucladoceros dierantios* 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.
Sadali described by PALOMBO (fissures), but it is still much smaller than the material from Monte Tuttavista ("XI canide" and "XI mar2002" associated to a quite advanced faunal assemblage, Tuttavista in the fissure fillings "XI canide" and "XI mar2002") 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 P4 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.

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