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Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils

The Mio-Plio-Pleistocene faunal succession of Sardinia is discussed in the context of paleogeography and stratigraphy. Some material of a particular stratigraphic or taxonomic interest is described. The name *Sus sondaari* is introduced to replace the preoccupied name *Sus nanus*. Sardinia may have become an island during the Late Oligocene. Some of the Early Miocene taxa on Sardinia may have survived there from the time when Sardinia was still connected with the main land, others arrived later to the island. Part of these taxa survived till the Late Miocene, when Sardinia (and Corsica) became connected to the island of Tuscany. At this moment faunal exchange occurred between these areas. Some of the taxa known from the Baccinello area may have come from Sardinia. During the Messinian, Sardinia became connected to the mainland again, the endemic fauna went largely or completely extinct and a balanced fauna entered. During the earliest Pliocene Sardinia (and Corsica) became isolated again and an endemic fauna was formed. Possibly only once, at the beginning of the Middle Pleistocene, new elements were introduced. Twice Sardinia changed from mainland to insular conditions. Both times an endemic fauna with reduced diversity evolved from a mainland fauna. This occurred also in other islands. A possible explanation for such a process is that the carrying capacity of an island is insufficient for viable populations of large carnivores. The larger the island, the larger the carnivore that can survive on it. The dog *Cynotherium* could survive on Sardinia. The absence of large carnivores may lead to increased competition between herbivores, resulting in reduction in species abundance. Only when large carnivores are lacking, certain typical island adaptations, such as low gear locomotion, evolve.

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INTRODUCTION

Already during the earlier part of the past century, fossil mammals were collected from Sardinia. Collecting continued and, particularly in the last thirty years, a better view of the Miocene and Pliocene was obtained. A locality of particular interest is Capo Figari. At the end of the 19th century and/or the beginning of the 20th, Forsyth Major collected fossils from Capo Figari. This collection is stored in the Naturhistorisches Museum Basel (NMB) and the Istituto di Geologia Firenze (IGF). It is not known whether they come from a single fissure or from several, nor whether this, or these fissures are the ones we know now. In the first half of the 20th century, collections were made at Capo

Figari by D. Bate (stored in the Natural History Museum, London - NHML) and E.G. Dehaut (stored in Turin) and in 1970 a team from the University of Rome collected from probably the same fissure as Dehaut (Gliozzi & Malatesta 1980). Up to then, all material from Capo Figari seems to have been considered as of the same age, though estimates of this age ranged from Pliocene to Middle Pleistocene.

A team of the University of Utrecht, lead by Paul Sondaar, collected in 1977 from several different localities at Capo Figari. Two of the localities are fissure fillings at the top of the hill near the signal station. They are named Capo Figari I and Capo Figari II. There are some more localities near the sea. The collection from Capo Figari I includes remains of the insectivores *Nesiotites corsicanus* and Talpidae indet., the bat Chiroptera indet., the lagomorph *Prolagus figaro*?, the rodents *Rhagamys minor* and *Tyrrhenoglis figariensis,* and the bovid *Nesogoral melonii,* whereas Capo Figari II yielded Talpidae indet., Chiroptera indet., *Prolagus sardus, Rhagamys* cf. *orthodon, Tyrrhenoglis figariensis, Tyrrhenicola* sp. (primitive), the latter genus being an arvicolid rodent. Possibly the first publication of different faunal lists for the different localities are the lists of the glirids by Zammit Maempel & De Bruijn (1982). This and the excavations at Corbeddu gave rise to the recognition of two faunal units: the Middle and Late Pleistocene (and even Holocene) '*Tyrrhenicola* fauna' and the earlier '*Nesogoral* fauna' (Sondaar 1986; Sondaar *et al.* 1984, 1986, 1988).

Late Pliocene remains from Nuraghe Su Casteddu were first described by Esu & Kotsakis (1979). Early Pliocene remains were described by Pecorini *et al.* (1973) from the locality of Mandriola at Capo Mannu. A team from the University of Utrecht collected also from Capo Mannu. Though the first few fossils from the lower Miocene of Oschiri were collected at the beginning of the 20th century

(NHML), a team from Utrecht (IVAU) (De Bruijn & Rümke 1973) made a more extensive collection. Both collections are possibly not from the same locality, but the fossilisation suggests that they are from the same beds. Upper Miocene remains were only recently described (Cordy & Ginesu 1994).

Although I never excavated with Paul at Corbeddu, I have followed the research on Sardinia from near. Since I studied the little pig from Capo Figari (Van der Made 1988), I have a particular interest in the older part of the history of Sardinia. I planned to write a paper on the subject, but this remained a plan for many years. Kotsakis discussed the taxonomy, stratigraphy and biogeography of Sardinian mammals in many papers (Esu & Kotsakis 1983; Kotsakis 1980, 1984a and b; Kotsakis & Palombo 1979). The description and discussion of some inedited material from Capo Figari, Capo Mannu and Oschiri, and some original ideas on the 'Baccinello faunas', also found at Sardinia, results in a new interpretation of the Sardinian stratigraphy and biogeography. There are many citations of aberrant species from the localities. These include recent or Holocene remains that later workers supposed to have been mixed with the Pleistocene fossils, or remains of fossil mainland species of micro mammals, that are supposed to have been brought to the island in the stomachs of birds of prey. Such citations are not discussed here.

Measurements and their abbreviations
Measurements after Van der Made (1989, 1996):

DAP = Antero posterior diameter;
DAPd = DAP of the distal part of a bone;
DAPp = DAP of the proximal part of a bone;
DTa = Transverse diameter of the anterior lobe of a tooth;
DTd = Transverse diameter of the distal part of a bone;
DTp = Transverse diameter of the posterior lobe of a tooth or proximal part of a bone;
DTpf = Transverse diameter of the proximal facet of a bone;

Hla = Height of the crown of a tooth measured at the labial side;

Hli = Height of the crown of a tooth measured at the lingual side;

Lint = Internal or medial length of the astragalus;

Lext = External or lateral length of the astragalus;

Lm = Minimal or median length of the astragalus.

THE TAXA

The distribution of the taxa is indicated in Figure 1. Tooth nomenclature used in this section is after Van der Made (1996).

Insectivora

Erinaceidae indet.

Pecorini *et al.* (1973) mentioned an indeterminate genus of erinaceid from the locality of Mandriola at Capo Mannu that did not seem to be known from Europe. The material was not described.

Crocidosorex antiquus (POMEL, 1853)
De Bruijn & Rümke (1973) described material assigned to this species from Oschiri. This soricid is known from the mainland of Europe from the localities Saulcet, Chavroches and Montaigu-le-Blin.

Asoriculus* (=*Episoriculus*) aff. *gibberodon
(PETÉNYI, 1864)
Asoriculus corsicanus (BATE, 1945)
Asoriculus similis (HENSEL, 1855)
Hensel based the species *Sorex similis* on material from Monreale de Bonaria near Cagliari. Bate (1945b) named the genus *Nesiotites* for shrews from the Baleares, Corsica and Sardinia, indicated *N. hidalgo* from Majorca as type species and described *Nesiotites corsicanus* from the Teppa di Lupino cave in Corsica. *Episoriculus* is considered to be the ancestor of *Nesiotites* (Reumer 1980 a, b). Esu & Kotsakis (1979) described *Episoriculus* aff. *gibberodon* from the late Pliocene locality of Nuraghe Su Casteddu (the species name *gibberodon* is currently placed in the genus *Asoriculus* KRETZOI, 1959; see Hutterer 1994). Kotsakis

(1980) believed that the ancestor of *Nesiotites* entered Crosica and Sardinia in the latest Miocene and suggested that the shrews from the Baleares and those from Corsica and Sardinia might belong to different lineages. *N. corsicanus* is cited from Capo Figari I (Zammit Maempel & De Bruijn 1982). The latter species is cited from a number of younger localities: Cava Albastro, Cava Grande and Santa Lucia in the Is Oreris area (Gliozzi *et al.* 1984), Monte San Giovanni (Bate 1945b), Dragonara (Malatesta 1970) and Corbeddu (Sondaar *et al.* 1988).

The available data make it likely that the shrews arrived during the Messinian to Corsica, Sardinia and the Baleares. From the Pliocene onwards, the Corso-Sardinian and Balearic populations became isolated from the mainland population and from each other. Both insular populations independently became larger. The evolution in both lineages was parallel. The genus *Nesiotites* as applied at present is polyphyletic. I am not in favour of the use of more names than necessary (Van der Made 1988); if the ancestor of an island species or lineage is known, the classification in a different genus obscures relationships. I propose to place the Corso-Sardinian species in the genus *Asoriculus*.

Geotrypus oschiriensis RÜMKE, 1973
The species was described on the basis of material from Oschiri. Other species of the same genus are known from a number of Eocene, Oligocene and Early Miocene European localities.

Nuragha schreuderae RÜMKE, 1973
Rümke (1973) named this species and genus of talpid on the basis of material from Oschiri. The species could not be related to any of the known forms.

***Talpidae indet. / Talpa* sp.**
Talpa tyrrhenica BATE, 1945
Bate (1945a) based the species *Talpa tyrrhenica* on material from Monte San Giovanni.
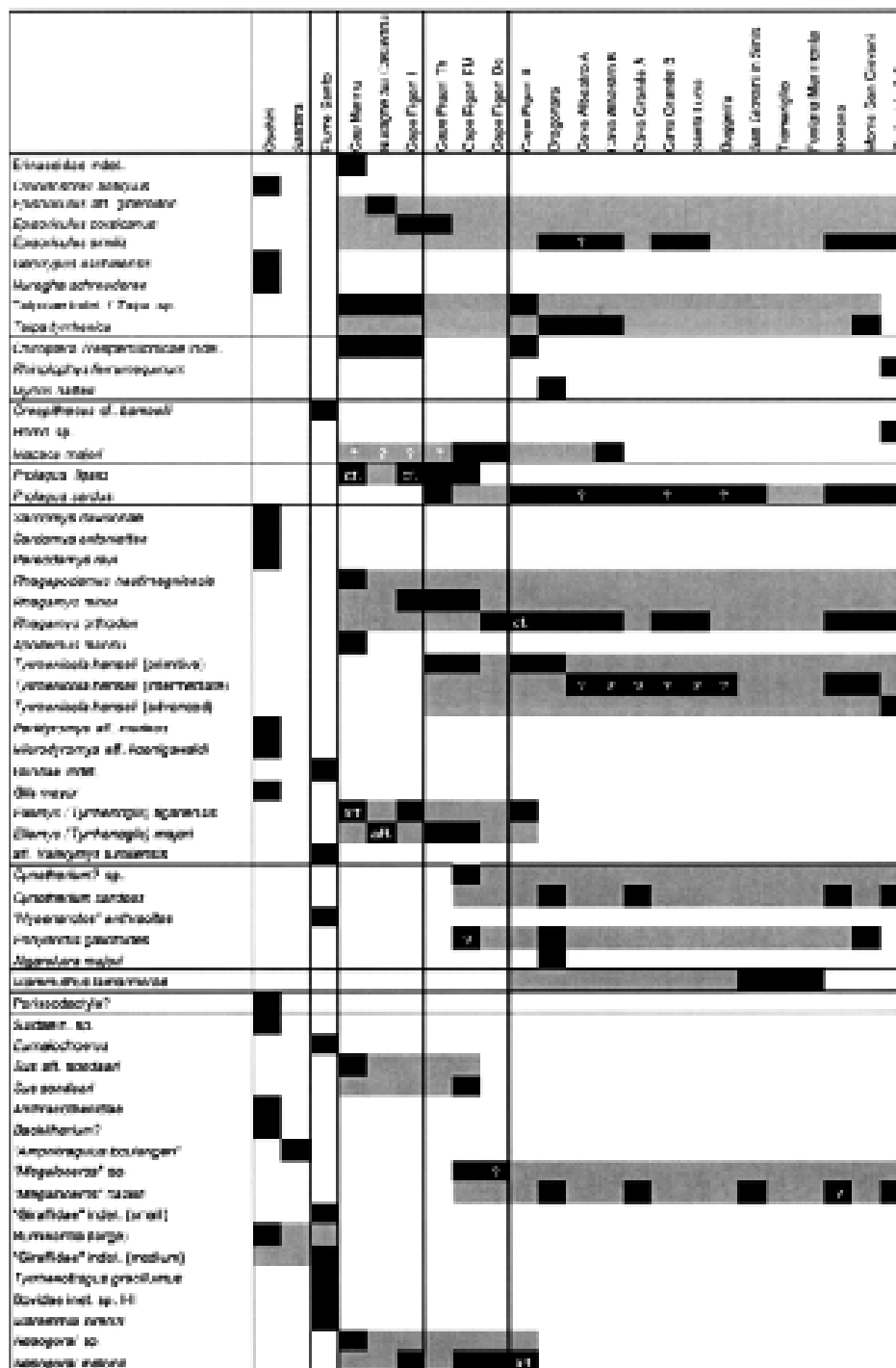
Figure 1   Range chart for the Neogene and Pleistocene endemic mammals from Sardinia. The localities are indicated from old (left) to young (right). Vertical lines indicate faunal exchange with mainland or Tuscany. The position relative to the early Middle Pleistocene event is unknown for the possibly mixed collections of Major (FM), Dehaut (De) and Thaler (Th). Question marks, 'cf.' and 'aff.' indicate that the genus is present in that locality, but that the specific assignation is insecure. Lineages are indicated as a grey rectangle, the actual presence is indicated in the common way in black. For *Macaca majori*, a hypothetical early entry is indicated (grey and question marks).

The species is also known from Cava Alba (Gliozzi *et al.* 1984) and Dragonara (Malatesta 1970). Material from Capo Mannu was assigned to Talpidae indet. (non Desmaninae) (Pecorini *et al.* 1973), from Capo Figari I & II to Talpidae indet. (pers. comm. of P.Y. Sondaar to Van der Made, 1988) and from Nuraghe Su Casteddu to *Talpa* sp. (Esu & Kotsakis 1979). It is possible that these indeterminate remains belong to the *T. tyrrhenica* lineage, which thus entered in Corso-Sardinia during the Messinian.

Chiroptera

Chiroptera indet. / Vespertilionidae indet.
Rhinolophus ferrumequinum (SCHREBER, 1774)
Rhinolophus hipposideros (BECHSTEIN, 1800)
Myotis myotis (BORKHAUSEN, 1979)
Myotis capaccinii (BONAPARTE, 1837)
Nyctalus cf. lasiopterus (SCHREBER, 1780)
Miniopterus schreibersi (KUHL, 1819)
Material from Capo Mannu was assigned to Vespertilionidae (*de type myotodonte*) (Pecorini *et al.* 1973), from Capo Figari I & II to Chiroptera indet. (pers. comm. of P.Y. Sondaar to Van der Made, 1988) and from Nuraghe Su Casteddu to Chiroptera indet. (Esu & Kotsakis 1979). *Myotis nattereri* was cited from Dragonara (Malatesta 1970), but Kotsakis (1987) described *M. myotis*; it is not clear to me whether this is based on the same material, though this seems likely. *Rhinolophus ferrumequinum* and Vespertilionidae indet. were cited from Corbeddu (Sondaar *et al.* 1988, Kotsakis 1987). *Rhinolophus ferrumequinum, Rhinolophus hipposideros, Myotis capaccinii, Nyctalus* cf. *lasiopterus* and *Miniopterus schreibersi* were described from a cave between Punta Padrebellu and Omo Morto (Kotsakis 1987). These species are living mainland species that apparently were not hindered by narrow sea straits.

Primates
Oreopithecus **cf.** *bambollii*
Cordy & Ginesu (1994) and Kotsakis *et al.* (1997) reported the primate *Oreopithecus* cf. *bambollii* from Fiume Santo. *O. bambollii* was known from the endemic island faunas from Tuscany and has been placed in the Cercopithecoidea and in the Hominoidea. Currently, the latter position is the more accepted and the genus is supposed to be a descendant of *Dryopithecus* (Moyà-Solà & Köhler 1997). *Oreopithecus* is known from the Baccinello V1 and V2 faunas (Rook 1993). These faunas are correlated to MN 11 and MN 12or MN 13 respectively (Engesser 1989), though evidence of the suid in the V2 fauna suggests that this level might be as old as late MN 11 or 8.0-8.5 My (see discussion on *H. etruscus* below); the V1 fauna being still older. The last record of *Dryopithecus* is from the lower part of MN 10 (Andrews *et al.* 1996). It seems likely that *Oreopithecus* arrived at the islands, during a sea level low stand. There are two sea level low stands, that are of interest here, one at 11.5 My and another 8.2 My ago (Haq *et al.* 1987, Miller *et al.* 1996). The one 8.2 My ago is later than the extinction of *Dryopithecus*. This would mean a very early presence of *Oreopithecus* either in the islands of Tuscany or Corso-Sardinia, or in both.

Oreopithecus was recently interpreted to be terrestrial, bipedal and shuffling with short stride length and low speed (Köhler & Moyà-Solà 1997). It was supposed to have evolved this behaviour because of the absence of carnivores in the insular environment where it lived. The large carnivore *Hyaenarctos? anthracites* first described from Monte Bamboli has now been cited from Fiume Santo. Its presence at the first locality has been explained away by doubting the stratigraphical context (pers. comm. S. Moyà-Solà). This is not possible anymore, after the find at Fiume Santo; *Oreopithecus* and the large carnivore were sympatric. The interpretation of *Oreopithecus* as slow and terrestrial due to the absence of carnivores is not satisfactory.

Homo sp.

Sondaar *et al.* (1986) assigned human remains from Corbeddu to *Homo* sp. and hypothesised that man reached Sardinia during the early Middle Pleistocene. Spoor & Sondaar (1986) describe some of the specimens in more detail and differences with *Homo sapiens* were pointed out. Sondaar *et al.* (1991) interpreted the lithic industry of Sardinia to be different from that of the mainland.

Macaca majori AZZAROLI, 1946

Gliozzi & Malatesta (1980) stated that Dehaut based *Ophthalmomegas lamarmorae* on primate molars and, what appeared later to be, a skull cap of an eagle, from Capo Figari, reason for Azzaroli (1946) to name the species *Macacus majori*, based on material collected by Major and stored in the IGF (Gliozzi & Malatesta 1980). There is also material of the macaque in the Major collection in the NMB. The reason that Dehaut included material that in reality belongs to two species in the description of a new species does not invalidate that taxon. I do not know the early literature on this macaque, but the possibility exists that Dehaut's taxa are available and, depending on the type, that the species name is a senior synonym of *Macaca majori*.

The species was also found at Cava Albastro, where also *Nesiotites similis*, *Prolagus sardus*, *Rhagamys orthodon* and *Tyrrhenicola* were found (Gliozzi *et al.* 1984). I interpreted this as an indication that *M. majori* belongs to the '*Tyrrhenicola* fauna' (Van der Made 1988), implying a Middle to Late Pleistocene age. Kotsakis (1980) considered *M. florentina* from the Villafranchian as the probable ancestor of *M. majori*. Sondaar (1987) considered *Macaca majori* to be part of the '*Nesogoral* fauna'. *Macaca* first appeared in Europe in MN 13 (Andrews *et al.* 1996), that is during the Messinian Crisis. *Macaca* may have reached Sardinia then. In view of the fact that *Nesogoral* is now also known from Capo

Figari II and thus survived into the Middle Pleistocene, presence of *Macaca* in the Middle Pleistocene of Sardinia does not exclude that the lineage entered during the Messinian. A detailed comparison of *M. majori* with the mainland forms may shed light on the question.

Lagomorpha

Prolagus figaro LÓPEZ, 1975
Prolagus sardus WAGNER, 1825

Prolagus figaro was first described from Capo Figari (though the name seems to refer to the Barber of Seville) on the basis of material collected by Thaler (López Martínez & Thaler 1975). It is a large species, much larger than *P. sardus*. Wagner seems to have based *P. sardus* on material from Bonaria near Cagliari (Tobien 1935). Material from Capo Mannu (López Martínez & Thaler 1975) and from Capo Figari I (Zammit Maempel & De Bruijn 1982) was assigned to *P.* cf. *figaro*. *P. sardus* is also present in the Thaler collection from Capo Figari (suggesting that material from different levels was mixed) and it was mentioned by Major from Capo Figari, though material in the NMB collection is large and more likely represents *P. figaro*. *P. sardus* is cited from Capo Figari II (Zammit Maempel & De Bruijn 1982), Bonaria and Monte San Giovanni (Bate 1945a), San Giovanni in Sinis (Kotsakis 1980), Dragonara (Malatesta 1970), Corbeddu (Sondaar *et al.* 1986, 1988), Cava Albastro, Cava Grande, Santa Lucia and from a cave between Punta Padrebellu and Omo Morto (Kotsakis 1987) and a *Prolagus* sp. from Buggerru, all in the Is Oreris area (Gliozzi *et al.* 1984). The subspecies *P. figaro deapereti* is present in the locality of Perpignan (MN 14). *P. figaro figaro* seems to have entered Sardinia during the Messinian. *P. sardus* is no descendant of *P. figaro*, but seems to have entered Sardinia during the Pleistocene (López Martínez & Thaler 1975).

Rodentia

Sardomys dawsonae DE BRUIJN, 1973
Sardomys antoniettae DE BRUIJN, 1973
Pereddamys rayi DE BRUIJN, 1973
These ctenodactylid genera and species were described on the basis of material from Oschiri. They were supposed to have come from Asia through Africa.

aff. *Huerzlerimys turoliensis* (MICHAUX, 1969)
Kotsakis *et al.* (1979) cited 'aff. *Valerymys turoliensis*' from Fiume Santo. This is a mainland species, currently placed in *Huerzelerimys*, that evolved during the second half of MN 11 from *H. vireti*, which in turn evolved from the MN 10 *H. minor* (Van Dam 1997). One of the characteristic changes in this lineage is size increase. Engesser (1989) used these murids for the stratigraphy of the V0-2 faunas from which he described respectively: *Valerymys vireti, V. oreopitheci* and *Anthracomys majori*. The whole of this evolution of three successive forms may well have occurred within MN 11. In that case the radiometric date from the V2 level and the stage of evolution of *Hippopotamodon etruscus* would fit very well (see also discussion on the suid). It is diffi-cult to interpret the Fiume Santo murid.

Apodemus mannu THALER, 1973
Thaler (Pecorini *et al.* 1973) described the giant form *Apodemus mannu* from the locali-ty of Mandriola at Capo Mannu. *Apodemus* first appeared in Europe in MN 13, which is during the Messinian Crisis. Mandriola is believed to be just posterior to this event (MN 14).

Rhagapodemus hautimagniensis MEIN & MICHAUX, 1970
Rhagamys minor BRANDY, 1978
Rhagamys orthodon (HENSEL, 1856)

The murid *Rhagapodemus hautimagniensis* is known from the mainland of Europe and from Capo Mannu (Pecorini *et al.* 1973).

Brandy assumed that this species gave rise on Corsica and Sardinia to the *R. minor-ortho-don* lineage, which is characterised by size increase. The type of *R. minor* is from the collections of Thaler at Capo Figari. The list of this material (Brandy 1978) includes main-ly primitive forms, but also *Prolagus sardus*. Some mixture seems to have occurred. I could not consult Hensel's publication and do not know the type locality of *R. orthodon*. The type species of the genus *Rhagamys* MAJOR, 1905 is *R. orthodon*. The genus is endemic to Corsica and Sardinia. Material from Capo Figari I and in the Forstyh Major collection of Capo Figari was reported to be small by Zammit Maempel & De Bruijn (1982), who where unaware of Brandy's paper. The material probably represents *R. minor*. Material from Capo Figari II was assigned to *R.* cf. *orthodon* and from Capo Figari III to *R. orthodon*. *R. orthodon* is cited from Bonaria (Bate 1945b), Monte San Giovanni (Bate 1945a), Dragonara (Malatesta 1970), Corbeddu (Sondaar *et al.* 1988), cave between Punta Padrebellu and Omo Morto (Kotsakis 1987) and from Cava Albastro, Cava Grande, Santa Lucia and Buggeru in the Is Oriris area (Gliozzi *et al.* 1984).

Tyrrhenicola henseli MAJOR, 1905
A primitive *Tyrrhenicola* is cited from Capo Figari (collection Thaler; Brandy 1978) and Capo Figari II (pers. comm. P.Y. Sondaar to Van der Made 1988). *Tyrrhenicola henseli* is cited from the Major collection from Capo Figari (Gliozzi & Malatesta 1980), Siniscola levels C and E (Mezzabotta *et al.* 1996), Bonaria (Bate 1945b), Monte San Giovanni (Bate 1945a), Dragonara (Malatesta 1970), Corbeddu (Sondaar *et al.* 1988), cave between Punta Padrebellu and Omo Morto (Kotsakis 1987), Cava Albastro, Cava Grande, Santa Lucia and Buggerru in the Is Oriris area (Gliozzi *et al.* 1984).

Mezzabotta *et al.* (1996) considered *Tyrrhenicola* a subgenus of *Microtus* and stu-died *M. (T.) henseli* from a number of

localities and concluded that those from Capo Figari and Dragonara are the most primitive, those from Monte San Giovanni and Bonaria are intermediate and those from Corbeddu are more derived.

Peridyromys* aff. *murinus (POMEL, 1853)
Microdyromys* aff. *koenigswaldi DE BRUIJN, 1965
Glis major DE BRUIJN, 1973
These glirids are present in Oschiri, which is the type locality of *G. major*. They have European affinities. De Bruijn & Rümke (1973) described all material, but Daams (1981) placed the material that originally was assigned to *Myomimus* sp. in *Peridyromys* aff. *murinus.*

Gliridae indet.
Kotsakis *et al.* (1997) cited an indeterminate glirid of large size from Fiume Santo.

Eliomys (Tyrrhenoglis) figariensis ZAMMIT MAEMPEL & DE BRUIJN, 1982
Eliomys (Tyrrhenoglis) majori ENGESSER, 1976
Engesser (1976) named the glirid species and genus *Tyrrhenoglis majori*; the type material is from the collections from Capo Figari by Major. Zammit Maempel & De Bruijn (1982) included *Tyrrhenoglis* as a subgenus in *Eliomys*, described *E. (T.) figariensis* from type locality Capo Figari I as well as from Capo Figari II and assigned the material described by Pecorini *et al.* (1974) from Capo
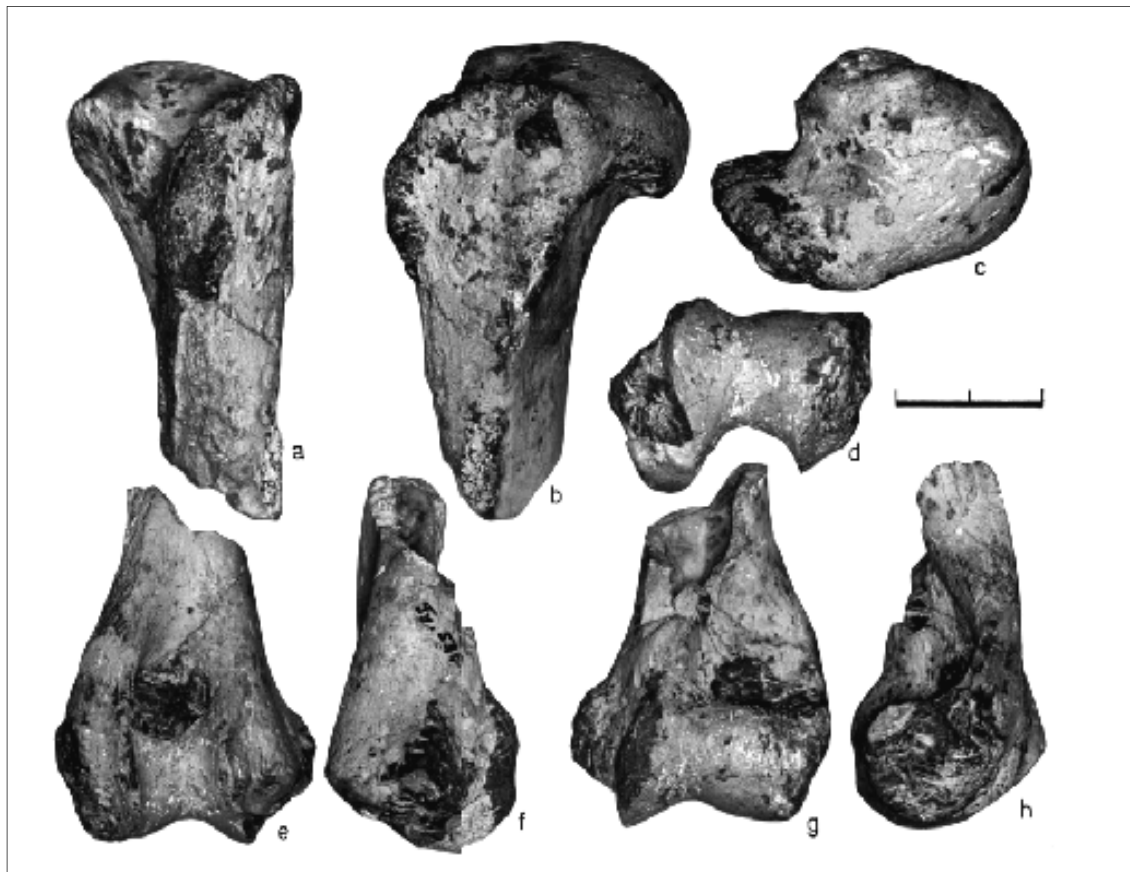

Figure 2 *Cynotherium*? sp. from Capo Figari (FM). Ty 5363 proximal fragment of **a** left humerus: a anterior, **b** lateral and, **c** proximal views. Ty 5362 distal fragment of a left humerus: **d** distal, **e** posterior, **f** medial, **g** anterior, and **h** lateral views. The bar represents 2 cm.
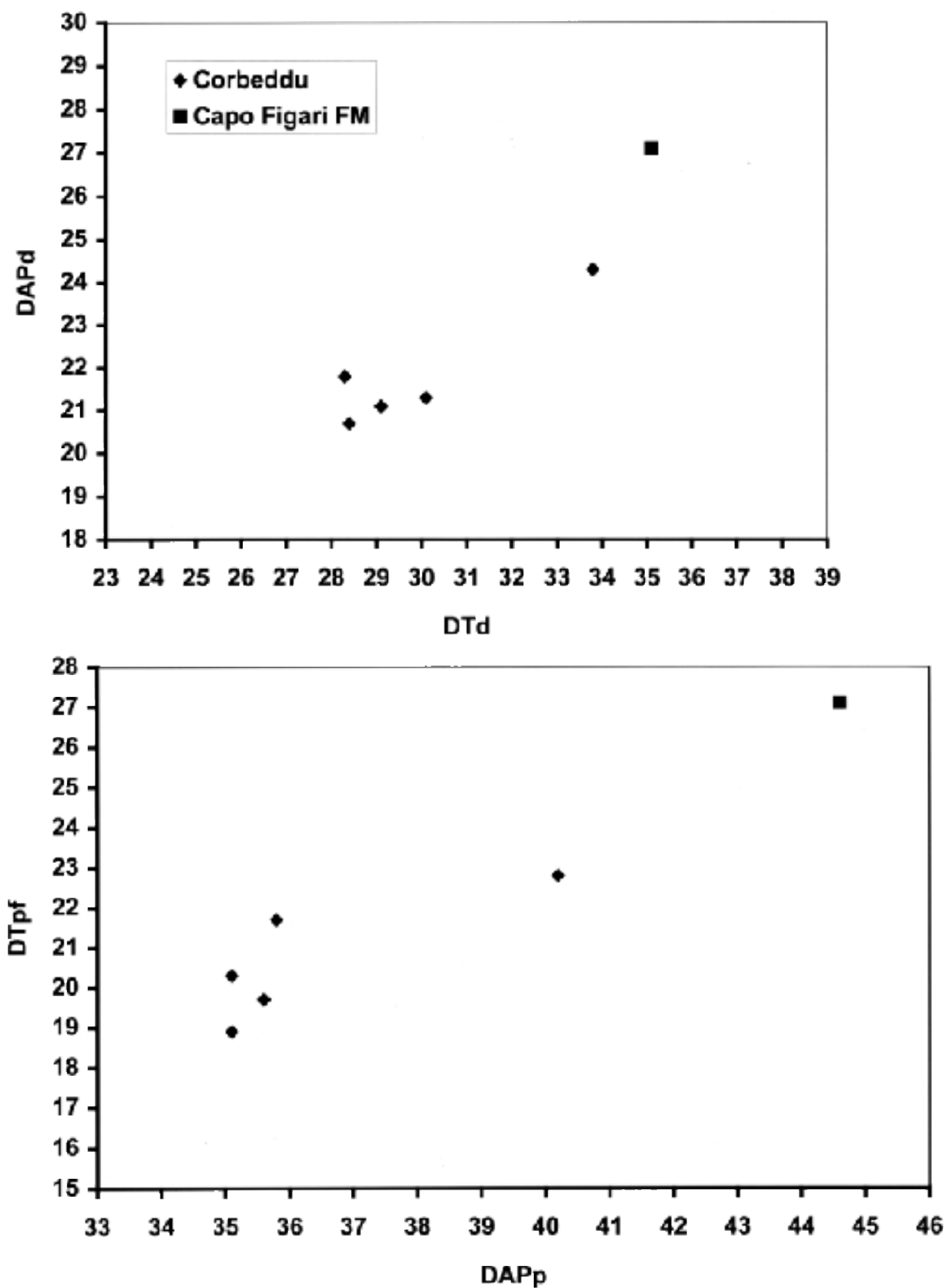
Figure 3 Bivariate plots of the distal (above) and proximal (below) humerus of *Cynotherium?* sp. from Capo Figari (squares) and *C. sardous* from Corbeddu (diamonds).

Mannu to *E. (T.)* aff. *figariensis*. The same authors assigned material from Nuraghe Su Casteddu, described by Esu & Kotsakis (1979), as *Hypnomys* to *E. (T.)* aff. *majori*. The stratigraphic distribution suggests that there were already two parallel lineages in the Pliocene. The separation into two lineages might be the result of the separation of the populations on Corsica and Sardinia during high sea level stands. Engesser (1976) supposed that *T. majori* evolved from *Anthracoglis* of the Baccinello V1 or V2 fauna. If this is the case, the lineage must have survived the Messinian crisis on Sardinia and/or Corsica. Alternatively, there may have been parallel evolution; it is not common for island endimics to survive in fully continental conditions.

Carnivora

'Hyaenarctos' antracites WEITHOFER, 1889
Kotsakis *et al.* (1997) cited *'Hyaenarctos' antracites* from Fiume Santo. The species is based on material from Monte Bamboli. Kotsakis (1984) discussed the material from Monte Bamboli, which has been attributed also to *Amphicyon*, and concludes that it is difficult to decide whether the material belongs to *Indarctos, Hyaenarctos* or *Agriotherium*. Two localities that can be correlated to the V2 level have this large carnivore, which thus seems to be typical for this level.

Cynotherium?
Cynotherium sardous STUDIATI, 1857
The species *Cynotherium sardous* was based on material from Bonaria. *C. sardous* is also the type species of the genus. The species is also described from Dragonara (Malatesta, 1970) and is cited from Cava Grande (Gliozzi *et al.* 1984) and Corbeddu (Sondaar *et al.* 1988, Eisenmann 1990, Eisenmann & Van der Geer 1999). Kotsakis (1980) reviewed literature on the dog and concluded that its ancestor is likely to be either *Canis etruscus* or *Cuon majori*, which might be a synonym

of the former species. There are two fragments of a humerus (Fig. 2) in the Major collection from Capo Figari (NMB), Ty 5363 and Ty 5362. There is no *foramen entepicondyloideum*, which occurs in Felidae and Hyaenidae. The specimens are considerably larger than seven specimens from Corbeddu (Fig. 3). The specimens from Capo Figari may belong to a canid, even to *Cynotherium*, but the size difference is such, that it seems unlikely they present *Cynotherium sardous*. They might represent an ancestral form. An alternative to the idea that the corso-sardinian dogs evolved from *Canis estruscus* or a similar form, is that a form close to *Canis cipio* or *'Canis' monticinensis* entered Corsica and Sardinia during the Messinian. These dogs were present in Turolian localities like Concud, Venta del Moro and Brisighella (Rook 1992). Still another alternative is that it is related to *Nyctereuts* or *Xenocyon*. The first showed similarities in skull proportions and of the second no skulls are known and Eisenmann (1990) did not further discuss the two as possible ancestors; see also Eisenmann & Van der Geer 1999.

Enhydrictis galictoides MAJOR, 1902
Algarolutra majori (MALATESTA, 1978)
Sardolutra ichnusae (MALATESTA, 1977)
Megalenhydris barbaricina WILLEMSEN & MALATESTA, 1987
Four mustelids are known from Sardinia; one musteline and three lutrines. The endemic musteline *Enhydrictis galictoides* is supposed to have descended from *Enhydrictis ardea*. This mainland species is known from the Villafranchian localities of St. Vallier and Olivola (Kotsakis, 1980). Malatesta and Willemsen (1986) named the genus *Algarolutra* with the species *Cyrnaonyx majori* as type species. This species is based on material from Dragonara. Willemsen (1992) named the genus *Sardolutra*. The type species is *'Nesolutra' ichnusae* and the type of this species is an isolated skeleton found in the Grotta di Nettuno in beds that are probably of Weichselian age. The lutrine

Megalenhydris barbaricina is based on material from the Ispiginoli cave near Dorgali, an isolated find of unknown stratigraphic position. The genus is monospecific.

Proboscidea

Mammuthus lamarmorae (MAJOR, 1883)
The types of this species are from Fontana Marimenta near Gonessa. Malatesta (1954) described a molar from Tramariglio. These remains indicate a dwarf form close to *Mammuthus meridionalis*. *M. lamarmorae* is also cited from San Giovanni in Sinis (Kotsakis 1980).

Perissodactyla?

Some scraps of enamel from Oschiri (IVAU) might represent a perissodactyl. If this would be the case, this is probably the only perissodactyl known from an endemic island fauna. Perissodactyls are no good swimmers and therefore they do not form part of the typical island faunas. It is possible that this animal was on Sardinia when it separated from southern France during the Oligocene and then survived some time on the island.

Artiodactyla

Suidae sp.
Some remains from Oschiri (IVAU) represent a suid and indicate shortening of the legs, an adaptation common in endemic island environment. The remains clearly belong to a suid and not to a palaeochoerid. The only suid known of this age are *Hyotherium* (MN1-6) and *Xenochoerus* (MN 2b-3).

Hippopotamodon etruscus (MICHELOTTI, 1861)?
A suid is cited from Fiume Santo (Kotsakis *et al.* 1997). This is probably '*Eumaiochoenus*'. Hürzeler (1982) introduced the name *Eumaiochoenus* for the species '*Microstonyx*' *etruscus* from Monte Bamboli and Bacinello

level V2 (also known under the mistaken name of '*Microstonyx choeroides*'). The affinities of this form with the large Turolian mainland suids of the genus *Microstonyx* have been clear since a long time (Pilgrim 1926, Hünermann 1969, Van der Made & Moyà-Solà 1989, Van der Made 1997a). Pilgrim (1926) introduced the names *Dicoryphochoenus* and *Microstonyx*. Pickford (1988) showed that *Hippopotamodon* has priority over *Dicoryphochoerus*. It is becoming increasingly clear that *Hippopotamodon* and *Microstonyx* form a closely related group of suids, that all could conveniently be placed in *Hippopotamodon* (see classification by Van der Made 1997b) and in reality there is little reason for recognising a monospecific genus *Eumaiochoenus*.

H. etruscus is known from Monte Bamboli and from the Baccinello V2 level, but not from the V1 level. It seems to have evolved from an early stage of evolution of the *H. erymanthius brevidens* (MN 11) - *H. e. erymanthius* (MN 12) lineage, suggesting that it entered in MN 11 or early in MN 12 in Tuscany (Van der Made 1997a). Considering the ages for MN 11 (Van Dam 1997), this is in line with the radiometric date of 8.0-8.5 My for the V2 level (Hürzeler 1982), but older than the MN 12/13 age suggested by Engesser (1989). Haq *et al.* (1987) reported a sea level low stand 8.2 My ago. Even though islands remain isolated to some extend, such moments tend to be the moments when new elements are introduced in the endemic environment. If *H. etruscus* was really present on Sardinia, it is likely to have entered 8.2 My ago simultaneously in Corso-Sardinia and in Tuscany, which then formed one large island.

Sus sondaari new name
Sus aff. *sondaari* new name
Sus nanus was the name I gave to a small pig in the Major collection from Capo Figari (Van der Made 1988). The name is however, preoccupied by *Sus scrofa nanus* NEHRING, 1864, which is a domestic pig. A replacement

name should be given, and what other name could be given on this occasion than *Sus son-daari* in honour of Paul Sondaar? Holotype, diagnosis etc. remain the same as published by Van der Made (1988). The material from Capo Mannu figured by me as *Sus* a ff. *nanus* becomes of course *Sus* a ff. *sondaari*.

The little pig is a descendant of *Sus arvernen-sis* and arrived at Sardinia during the Messinian (Van der Made 1988). Evolutive tendencies in this endemic lineage are: size decrease, increase in crown height of the first incisors, P4 and molars, increase in enamel thickness, simplifi-cation of molar structure (loss of crests or lobes of the cusps), reduction in size of the anterior premolars, loss of the p1, and shorten-ing of the anterior part of the mandible. A peculiarity for an endemic island pig is that its third metacarpal (the only postcranial element known) is not short compared to the tooth row and is even long compared to its own DAP and DT values; it is slender. Moreover, the crest on the distal articulation surface is pronounced and the proximal articulation surface flat as in artiodactyls that are more cursorial than the majority of pigs. The dental adaptations are to be expected in an island form, but possible cursorial adaptations instead of a change to low-gear locomotion is unexpected.

Anthracotheriidae

Some bones from Oschiri (IVAU) are inter-preted as an anthracothere. It has been sugge-sted that *Anthracotherium* was present on Corsica and Sardinia, when these separated from the mainland; when the Corso-Sardinian island became connected to the Tuscan island, this form may have given rise to the *Anthracotherium* known from Tuscany (Van der Made 1999).

Bachitherium?
Some bones from Oschiri (IVAU) might represent a *Bachitherium.* This form may have been present on Sardinia, when the island became separated from the mainland.

'Amphitragulus boulangeri'
Comaschi Caria (1953) described a mandible from Sardara as *Amphitragulus boulangeri*. The specimen is an isolated find, but was assumed to be of Early Miocene age. The description was short and taxonomically important information was omitted. Sardinia being an island then, it seems unlikely that the mainland *A. boulangeri* was present. The age of the ruminant from Sardara is under discussion (Esu & Kotsakis 1983): whereas it has been originally attributed to the Burdigalian, it might even be of Oligocene age. As long as its taxonomy and age are not clear the find is of very limited value in bio-geography.

Megaloceros sp.
Megaloceros? cazioti (DEPÉRET, 1897)
Cervus cazioti DEPÉRET, 1897 is based on material from Corsica, but also occurs on Sardinia and *Cervus algarensis* Comaschi Caria, 1955 is based on remains from Il Cantaro of Weichselian age. In addition, *Megaceros cretensis* and *Orthogonoceros ver-ticornis* have been cited from Sardinia (Caloi & Malatesta 1974, Kotsakis 1980). Some of these species have also been placed in *Nesoleipoceros*, but this genus is not common-ly accepted. *Megaceros*, *Praemegaceros* and *Megaceroides* are considered to be synonyms of *Megaloceros* (Lister 1993). Most authors coincide in that the remains from Sardinia and Corsica belong to a megacerine; if this is really the case, the name *Megaloceros* should be applied. Kotsakis (1980) already noted that there are size differences in the material. Fossils in the collection of Major from Capo Figari are larger than those from Corbeddu assigned to *M. cazioti*. It seems like-ly that there was more than one deer species on Sardinia, though the presence of *M. creten-sis*, an endemic of Crete, and *M. verticornis*, of the mainland, seems unlikely. The different Sardinian species might, or might not form a lineage. A revision of all material seems neces-sary, as already stressed by Kotsakis (1980). A *Cervus* sp. is cited from Bonaria (Bate

1945b), *Nesoleipoceros cazioti* from Dragonara (Malatesta 1970) and *Megaloceros cazioti* is described and figured from Corbeddu (Klein Hofmeijer 1996). Kotsakis (1980) mentioned deer from Grotta dell'Inferno, Portovesme and Carmas and Maritza. The robusticity index (L/DTd) of the metacarpal of *M. cazioti* from Corbeddu is 5.6 (average measurements from Klein Hofmeijer 1996). *M. soleilhacus* ('*M. verti - cornis*') has been mentioned as a possible ancestral form to *M. cazioti* (Kotsakis 1980). This form tends to have a robusticity index of less than 5 (Van der Made in press). *Eucladoceros*, *Arvernoceros* and *Cervus* tend to have indices between 6.5 and 5, *Dama*-like deer have even more slender metapodials. Either *M.? cazioti* descended from *M. soleilhacus* and became more cursorial (contrary to island evolution tendencies), or we should consider the possibility that it evolved from one of the other genera. The lack of a bez-tine seems to eliminate *Cervus elaphus* as a candidate. *Eucladoceros dicranios* and *E. tegulensis* seem to have too complex antlers. *Eucladoceros giulii* has a brow tine that originates high above the burr and, though not well known, the antlers do not seem to be very complex. The possibility of a descendance from *Dama*-like deer, a form close to *Eucladoceros tetraceros*, or from *E. giulii*, or from *Arvernoceros* merits further investigation.

Ruminantia sp.
'Giraffidae indet. I & II'
A ruminant approximately the size of a fallow deer was found at Oschiri. The animal is, however, no deer and resembles in its molar structure an animal from Casteani that has been classified either as a bovid or a giraffid, and was named *Umbriotherium azzarolii* by Hürzeler & Engesser (1976). This name however remained a nomen nudum (Kotsakis 1984a, b). It is well possible that the animal from Oschiri is no cervid, bovid or giraffid, but a primitive ruminant, present in Corsica and Sardinia when they separated from the mainland. It is also possible that this ruminant gave rise to '*Umbriotherium*' when Sardinia came into contact with Tuscany. Kotsakis *et al.* (1997) cited '*Giraffidae* indet. I (medium size), *Giraffidae* indet. II (small size)' from Fiume Santo. The larger 'giraffid' may well be identical with '*Umbriotherium*'.

Maremmia lorenzi HÜRZELER, 1983
Cordy & Ginesu (1994) and Kotsakis *et al.* (1997) cited *Maremmia lorenzi* from Fiume Santo. Hürzeler & Engesser (1976) introduced these specific and generic names for the endemic bovid *M. haupti* from the V1 level in the Baccinello basin, but the names are available since the publication of the diagnosis by Hürzeler (1983), who also introduced the name *Maremmia lorenzi* for bovids from the younger V2 level. The presence of *Maremmia lorenzi* in Fiume Santo suggests that the locality is of about the same age as the V2 level, that is, MN 11 or about 8.0-8.5 My (see discussion on *M. etruscus*).

Tyrrhenotragus gracillimus (WEITHOFER, 1888)
'Bovidae indet. I (small size)'
'Bovidae indet. II (very small size)'
Kotsakis *et al.* (1997) cited the three bovids from Fiume Santo. The type locality of *T. gracillimus* is Monte Bamboli. Hürzeler & Engesser (1976) introduced the name *Tyrrhenotragus*, which remained a nomen nudum. Kostakis (1984) considers the name valid because of the publication by Thomas (1984). A *T.* aff. *gracillimus* is cited from the V1 level (Hürzeler & Engesser 1976). Thomas (1984) interpreted *Tyrrhenotragus* to be a neotragine, though he noted that the position of the horn core was posterior, approaching the position in the Cephalophini. This is already a derived character, though not yet fully developed as in the recent cephalophines. The orientation of the horn core also approaches the state in the Cephalophini. Work in progress suggests that the Cephalophini have an origin outside Africa, not later than the Late Miocene.

Tyrrhenotragus may well be one of the first cephalophines.

Nesogoral sp.
Nesogoral melonii (DEHAUT, 1911)

Gliozzii & Malatesta (1980) introduced the name *Nesogoral* for the bovid '*Antilope*' *melonii*, a species that is based on material from Capo Figari (Dehaut collection). They concluded that *Nesogoral* and an endemic bovid from the Baleares, *Myotragus*, are closely related and that the ancestor of both reached the islands during the Messinian crisis, when the Mediterranean sea level dropped several kilometres. A striking difference between the two endemic genera is that *Myotragus* has extremely shortened metapodials, whereas those of *Nesogoral* are not shortened. Shortened metapodials form part of a set of adaptations that has been named

'low gear locomotion' and that is typical for dwarfed island species (Leinders & Sondaar 1974). Pecorini *et al.* (1973) mentioned 'Caprinae?' from the locality Mandriola at Capo Mannu in the Capo Mannu Formation. There are some specimens of a caprine in the IVAU collection that are assigned here to *Nesogoral* sp.

A **left p2** (Fig. 4a-c; DAP 6.8, DTa 4.1, DTp 5.4, Hli >7.3, Hla >7.1) has a pointed protoconid and a protoprecristid that rapidly becomes lower away from the tip of the protocone at its end it curves lingually without forming a cusp that could be called paraconid. The protoendocristid is directed posterolingually. There is a large triangular facet covering most of the posterior part of the tooth. The size is roughly comparable to that of the homologous tooth in *N. melonii* as
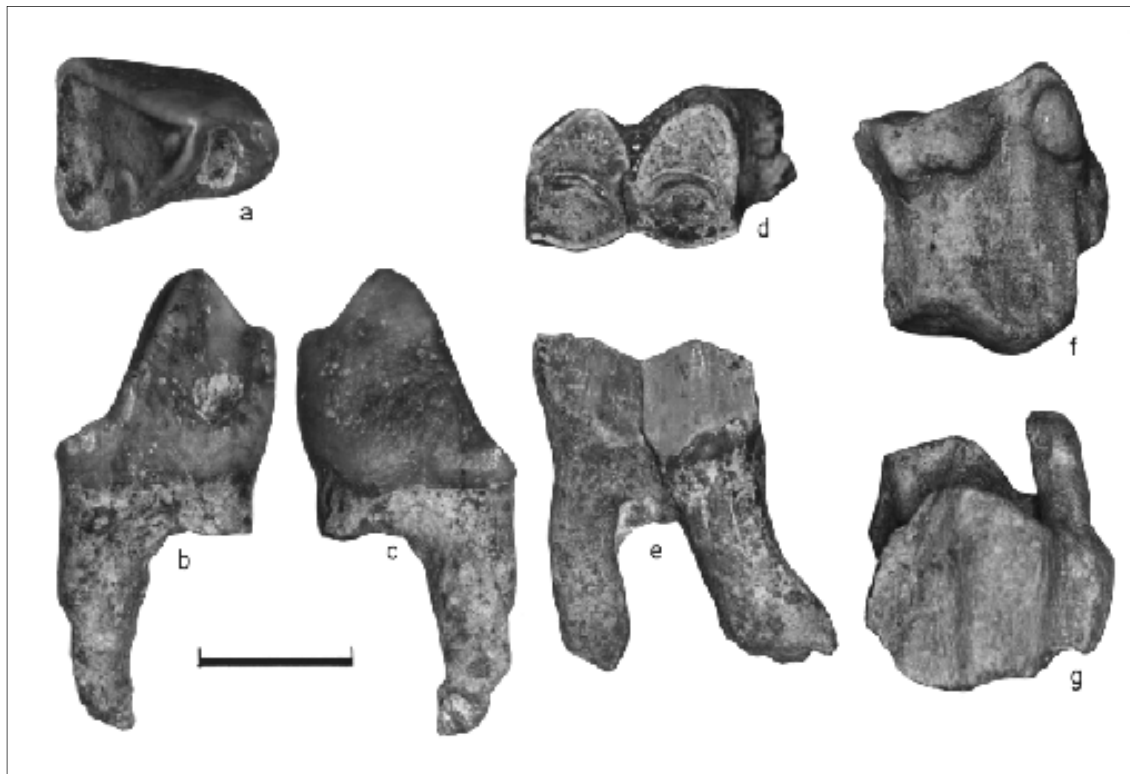

Figure 4 *Nesogoral* sp. from Capo Mannu. Left p2: **a** occlusal, **b** lingual and **c** buccal views. Right m1-2: **d** occlusal and **e** lingual views. Distal fragment of right tibia: **f** distal and **g** posterior views. The bar represents 0.5 cm for figures a-c, and 1 cm for figures d-g.

indicated by Gliozzi & Malatesta (1980). Several early caprines have recently been described. *Aragoral mudejar* from La Roma 2 (Spain; MN 10; Alcalá & Morales 1997, Alcalá 1994) and *Norbertia hellenica* from Maramena (Greece; MN13/14; Köhler *et al.* 1995) have much lower p2.

A worn selendont **right m1-2** (Figure 4d-e; DAP 14.3, DTa 8.6, DTp 9.1) has a fairly flat lingual wall like in bovids and unlike in cervids. Like the Caprinae, it lacks a buccal stylid. The tooth is too much worn to show a possible goat fold. The size is in the range for the m2 of *N. melonii* as given by Gliozzi & Malatesta (1980).

The anterior part of a **left lower molar** (DTa 6.7) is much worn, but of similar morphology as the previous tooth. Though the second lobe may have been wider, the size of this tooth

may have been comparable to those of the m1 of *N. melonii* as given by Gliozzi & Malatesta (1980).

The central part of an **upper molar** has the crests arranged in a bovid manner. It seems to have been rather hypsodont; besides it does not show any important characters and it cannot be measured.

A distal part of a **right tibia** (Fig. 4f-g; DAPd 18.0) has the morphology that is typical for ruminants (deep groves for the proximal pulley of the astragalus, oriented in anteroposterior direction). In size it goes well with the dental remains.

Nesogoral is a much more hypsodont animal than *Aragoral* and *Norbertia*. Unless hypsodonty was acquired in insular environment, the latter genera cannot be ancestral to
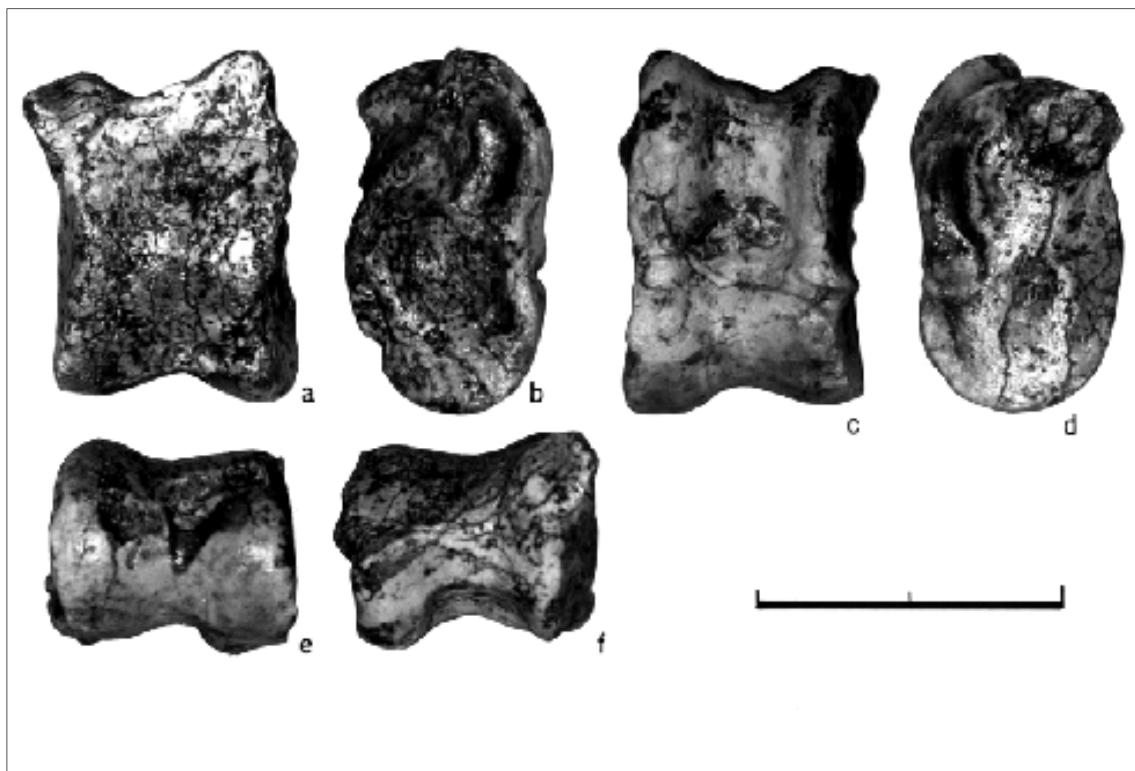

Figure 5 *Nesogoral* aff. *melonii* from Capo Figari II. Right astragalus: **a** posterior, **b** lateral, **c** anterior, **d** medial, **e** distal and **f** proximal views. The bar represents 2 cm.
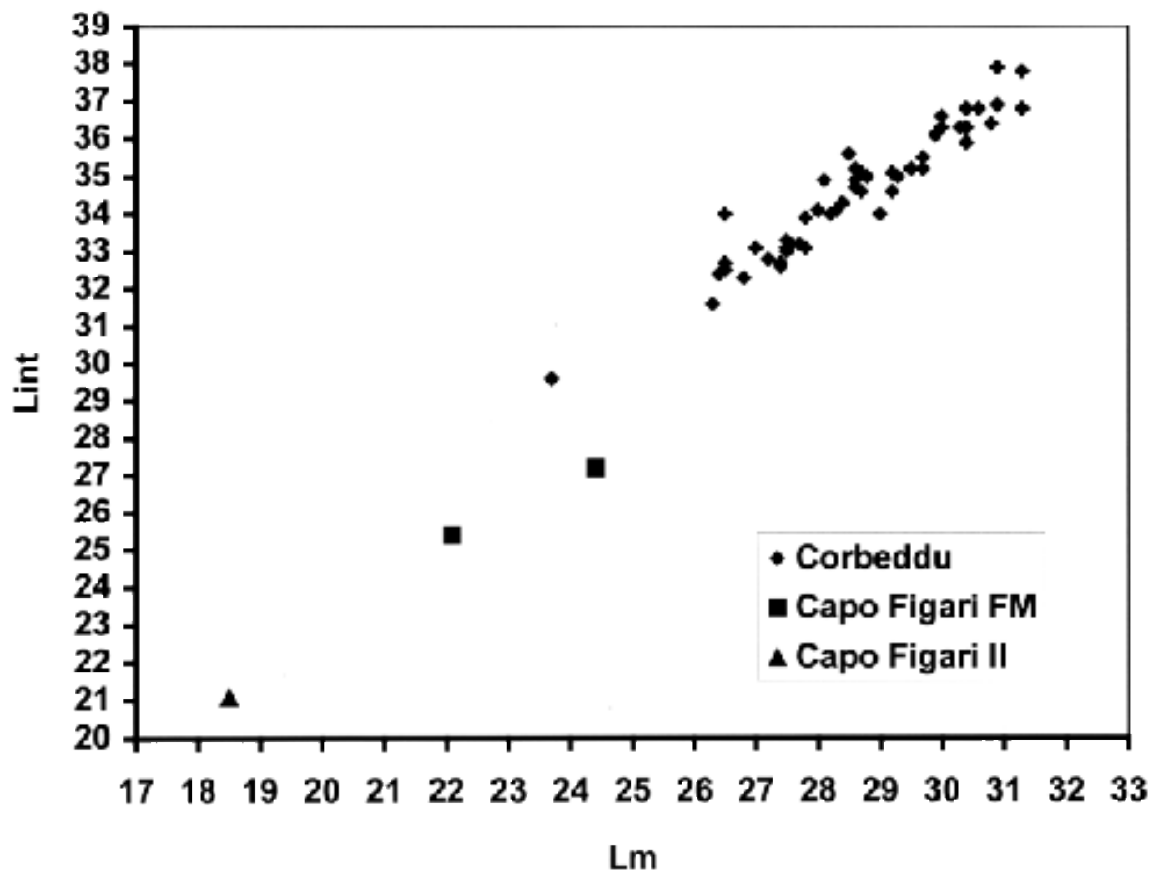
Figure 6 Bivariate plot of the astragalus. Squares = *Nesogoral melonii* from Capo Figari oc; triangle pointing upwards = *Nesogoral* from Capo Figari II; Diamonds = '*Megaloceros*' *cazioti* from Corbeddu.

Nesogoral. The affinities of the Capo Mannu material seem to be much more with *Nesogoral* than with the other early caprines and are assigned here to *Nesogoral* sp. Apart from Capo Mannu, *Nesogoral* has only been cited from Capo Figari (Major Collection, Dehaut Collection) and in particular from Capo Figari I (Van der Made, 1988). In October 1988, I visited Capo Figari together with P. Weesie and R.D. Kahlke. I took a small sample from Capo Figari I and a larger one from Capo Figari II. This material is temporarily stored in the IVAU. The sample from Capo Figari II included *Tyrrhenicola, P. sardus*, possibly '*Asoriculus*' and a ruminant astragalus. The astragalus was in the same sediment as the vole remains.

The **right astragalus** (Fig. 5; measurements in Table 1) has the typical ruminant morphology with a distal pulley that is in line with the proximal pulley. The specimen is much smaller than the astragali from Corbeddu assigned to *Megaloceros cazioti* (Fig. 6) and it is even smaller than those of *Nesogoral melonii* from the old collections from Capo Figari by Major stored in the NMB. The size difference is such that the possibility exists that it belongs to a different species. The astragalus, which is much smaller than the astragali from Corbeddu assigned to *Megaloceros cazioti* (Fig. 6), is assigned here to *N.* aff. *melonii*.

Table 1 Measurements (in mm) of the astragalus of *Nesogoral melonii* from Capo Figari oc and *Nesogoral*? from Capo Figari II.

Loc.	no.	Lext	Lm	Lint	DTp	DTd
Capo Figari oc	Ty 5387	--	24.4	27.2	--	18.5
Capo Figari oc	Ty 5472	26.9	22.1	25.4	15.5	15.7
Capo Figari II	--	22.9	18.5	21.1	15.0	14.6

PALEOBIOGEOGRAPHY OF SARDINIAN LAND MAMMALS

Late Oligocene - Early Miocene

During the late Oligocene Corsica and Sardinia seem to have separated from Southern France (Esu & Kotsakis 1983). De Bruijn & Rümke (1973) interpreted the microfauna of Oschiri as being endemic and insular. *Geotrypus* last appears in localities that at present are placed in MN 1 and *Crocidosorex antiquus* is found in localities that at present are placed in MN 1 and 2 (De Bruijn & Rümke 1973; De Bruijn *et al.* 1992). The last citation of *Anthracotherium* is from MP 29 (Brunet & Vianey-Liaud 1987), the oldest European suid is from MN 1 (Van der Made 1990, 1994). The fauna includes ctenodactylids, which are known from Asia and Africa, but not from Europe, though they are known from the Oligocene of Mallorca and the Villafranchian of Sicily (Kotsakis 1984). The ctenodactylids are believed to have reached Sardinia during the Late Oligocene (De Bruijn & Rümke 1973). The large mammals may all be of European origin, though the affinities of the large ruminant are not clear. The simplest model for the population of Sardinia (a single Early Miocene event) becomes more complex with the incorporation of the large mammals from Oschiri. The *Anthracotherium* was either on Sardinia when it separated from the continent or got there when it was already an island (at the same moment as the ctenodactylids?), but not later than MP 29. *Geotrypus* might also have been on Sardinia when it became an island, or may have got there during MP29 or MN 1. *Crocidosorex antiquus* and the suid may have got onto the island during MN 1-2 (second event), and various possibilities exist for the rest of the fauna.

Eustatic sea level was high between 35 and 30 My ago and then dropped nearly instantly (geologically speaking) some 75 m and remained this low, or even lower between 30 and 25 My ago, after which it rose again for a couple of millions of years. There are several fluctuations in the 30-25 My interval, but sea level was always 120-40 m below the level of 33-24 My ago (Haq *et al.* 1987). The Corsican and Sardinian plate became disconnected from the main land during the Oligocene (Dercourt *et al.* 1986, Rögl & Steininger 1983, Rögl 1998). Whereas this was a slow and unidirectional tectonic process, the fluctuating sea level is likely to have had a more direct effect on the paleoge-ography. It is thus to be expected that during the early phase of separation, Corsica and Sardinia may have been intermittently con-nected to the mainland, whereas later, when they moved more southwards, the island(s) were intermittently closer and further away from the mainland. The period of 30-25 My ago corresponds to units MP 24-29 (Legendre & Lévêque 1997). Taking this into account, *Antracotherium* and *Geotrypus* may have been on Corsica and Sardinia when these areas became insular. The ctenodactylids entered Sardinia when it was insular, because they remained restricted to Sardinia. This is likely to have occurred during one of the sea

level lowstands during MP 28-29. Probably still later (MN1/2) *Crocidosorex antiquus* and the suid entered Sardinia.

Late Miocene

Nothing is known of the Middle Miocene land mammals of Corsica and Sardinia. The presence of *Oreopithecus* and *Maremmia* in the locality of Fiume Santo suggests that Sardinia, Corsica and Tuscany constituted one large island during part of the Late Miocene. The locality of Fiume Santo is correlated to the V2 level of the Baccinello basin. Rook (1993) correlated the localities of Casteani, Montemassi and Ribolla with the Baccinello V1 level. There is a bunodont anthracothere from Casteani (Kotsakis 1984). This form must have lived for a long time in isolation. The last bunodont anthracotheres in Europe went extinct during the latest Oligocene. In Africa no younger bunodont anthracothere is known than the lower Miocene (?) one from Malembe (*'Palaeochoerus' dartevellei* of Hooijer 1963). In the Indian Subcontinent the last large bunodont anthracothere is from the Lower Miocene; a small bunodont anthracothere possibly lived on till the Late Miocene, but is an unlikely ancestor for the anthracothere from Tuscany. *Anthracotherium* is known from the Oligocene of the North of Italy, but this was no isolated area and *Anthracotherium* could not survive here till the Late Miocene. It could have been present in Tuscany since the Oligocene, but in view of the known presence of an anthracothere in Sardinia, the most likely origin for the tuscan anthracothere is the one from Oschiri (Van der Made 1999). The *'Umbriotherium'* from Casteani might be a descendant of the large ruminant from Oschiri, as suggested above. If the two artiodactyls from Casteani evolved from the Oschiri forms, there must have been some connection between Tuscany and Sardinia in 'V1 time' (or earlier).

Connections between Sardinia, Corsica and Tuscany may have been permanent during

part of the Middle and/or Late Miocene or may have occurred only during sea level low stands. There was a sea level low stand about 11.5 My ago and another one about 8.2 My ago (Haq *et al.*, 1987; Miller *et al.*, 1996). These moments are also the moments when distance of the islands to the mainland is smallest and when dispersals from the mainland to the islands are more likely. Taking this into account, it seems likely that 11.5 My ago *Oreopithecus*, *Tyrrhenotragus* and *Maremmia* coming from the mainland reached Tuscany and probably Corsica and Sardinia. At the same time, *Anthracotherium* and *'Umbriotherium'*, coming from Sardinia and Corsica, may have reached Tuscany. *Hippopotamodon* reached Tuscany, Corsica and Sardinia 8.2 My ago, marking the onset of the V2 fauna.

Pliocene - Early Pleistocene

During the Messinian the Mediterranean became disconnected from the Atlantic Ocean and large parts of the Mediterranean became land; Corsica, Sardinia and Tuscany became connected to the mainland (Rögl & Steininger 1983). Evaporation in the Mediterranean was then, and still is, greater than the influx by precipitation and rivers. It is possibly the sea level low stands 6.3 and 5.8 My ago (Haq *et al.* 1987), that caused the isolation of the Mediterranean and triggered what is known as the Messinian Salinity Crisis. The beginning of the Pliocene is marked by the re-establishment of the connection with the Atlantic Ocean resulting in the flooding of the Mediterranean. This happened about 5 My ago.

When, during the Messinan, Tuscany, Corsica and Sardinia became connected to the mainland, these areas became accessible to mainland species, including carnivores. This meant the extinction of the island faunas. When, in the Pliocene, the Mediterranean flooded again, Tuscany remained part of the mainland, but Corsica and Sardinia became islands again. The fauna living on these

islands became isolated. Geologically speaking, species diversity dropped immediately and species acquired island adaptations, such as gigantism in small mammals and dwarfism in large mammals. The Capo Mannu fauna is from shortly after the isolation. Pecorini *et al.* (1973) suggest an age of, in terms of Neogene Mammal Units, MN 14. *Sus* aff. *sondaari* is already dwarfed and *Apodemus mannu* became already large, showing that the fauna was already isolated. A number of animals that are not frequently found in island environment is present in this fauna: Erinaceidae, Talpidae and Bovidae. This is possibly due to the fact that the fauna came walking to the islands, instead of swimming. *Macaca* is possibly no good swimmer either, and may have arrived at Sardinia at this time. *Asoriculus*, *Eliomys* and the ancestor of *Nesogoral* are likely to have reached both Corsica-Sardinia and the Baleares during the Messinian, giving rise to *Nesiotites*, *Hypnomys* and *Myotragus* in the Baleares and to *Asoriculus corsicanus-similis*, *Tyrrhenoglis* and *Nesogoral* in Sardinia and Corsica. Intermittent connections between the latter two islands may have resulted in two lineages in *Tyrrhenoglis*. Possibly stratigraphically interesting evolution occurred in this period in the *Asoriculus, Rhagapodemus-Rhagamys*, *Tyrrhenoglis* and *Sus* lineages. New arrivals from the mainland in Sardinia might be expected during low sea level stands. These occurred about 3.8, 2.9 and 1.6 My ago (Haq *et al.* 1987), allowing for small differences due to advance in dating. There is little evidence for such arrivals, though the arrival of *Mammuthus* 1.6 or 1.8 My ago cannot be ruled out.

The fauna described above is the one indicated by the name '*Nesogoral* fauna' after its most emblematic taxon (Sondaar *et al.* 1984, 1986; Sondaar 1987). The youngest locality of this 'fauna' is Capo Figari I. An ESR date on *Nesogoral* tooth enamel by Dr. Motoji Ikeya (Dpt. of Earth and Space Science, Osaka Univ.) is 1,807,500 ± 20% yBP (pers.

comm. D.S. Reese).

Middle and Late Pleistocene

The younger faunas are characterised by the presence of *Prolagus sardus*, which is interpreted as a new arrival and not a descendant of *P. figaro* (López Martínez & Thaler 1975), *A. similis* and *R. orthodon*, which are interpreted as advanced evolutive stages of lineages that where present already, and *Tyrrhenicola henseli*, '*Megaloceros*' *cazioti* and possibly *Cynotherium*, which are new arrivals. The transition to this new fauna is assumed to have occurred during a regression at the beginning of the Middle Pleistocene, some 0.8 My ago, by Sondaar *et al.* (1986), who also assumed *Homo* to have arrived at this moment in Sardinia. *Mammuthus* may have arrived at this moment in Sardinia, or some 1.6-1.8 My ago, as pointed out above.

The Middle and Late Pleistocene fauna is indicated by the name '*Tyrrhenicola* fauna' (Sondaar *et al.* 1984, 1986; Sondaar 1987). ESR dates on *M. cazioti* tooth enamel by Dr. Motoji Ikeya (Dpt. of Earth and Space Science, Osaka Univ.) are 450,000 ± 20% yBP for Santa Lucia I, 366,950 ±20 % yBP for Capo Figari II, and 15,375 ± 20 % and 14,490 + 20 % yBP for two samples from Corbeddu (pers. comm. D.S. Reese). As suggested by the find from Capo Figari II, *Nesogoral* (as well as *E.* (*Tyrrhenoglis*) *figariensis*) persisted quite some time after the new arrivals. *M. majori* is another large mammal that (if it really arrived at Sardinia during the Messinian), persisted after this faunal turnover event. Alternatively, *Macaca* arrived as part of this event. There is evidence for a faunal phase that could be termed '*Nesogoral - Tyrrhenicola* - fauna', though it is of little practical use, in view of the fact that the older elements in this fauna seem to be rare.

ENDEMIC ISLAND FAUNAS ORIGINATING *IN SITU* FROM A BALANCED FAUNA

Paul Sondaar is the person who most contributed to the model of island evolution that we are familiar with now (for instance, Sondaar 1986). Though the model is of course much more complex, the most characteristic features are mentioned here. Proboscideans, cervids and hippos are the most common endemic large mammals on Mediterranean islands, as well as on many other islands elsewhere. This is because they are good swimmers. Large mammals become dwarfed in such environments and small animals become giants. Apart from their size, the animals have other typical adaptations, that evolved parallel on many islands: 'low gear locomotion" (short legs, changes in posture), stereoscopic view etc. Since carnivores do not get to the islands (they are not such good swimmers), high gear locomotion is no advantage, nor is a wide visual field; instead the economy and stability of low gear locomotion and stereoscopic view are advantageous. The absence of carnivores leads to overpopulation, which is the cause for adaptations in the dentition (extreme hypsodonty, reduction of premolars etc.). Thus, the typical endemic island fauna, as on Cyprus and Crete, results largely from the fact that carnivores could not reach the island. But in the case of Sardinia, two times (in the Late Oligocene and in the Early Pliocene) the island started as part of the mainland, only later to become isolated. It is to be expected that a balanced mainland fauna became isolated on the island. So carnivores and all other kind of animals were present that are not commonly found in endemic island faunas. Still impoverished island faunas developed. Why?

Herbivore biomass is much bigger than carnivore biomass, because carnivores need large populations of herbivores to maintain themselves. Therefore, the carnivore biomass supported by a certain land surface is much smaller than the herbivore biomass supported. Carnivores need huge territories. Moreover, populations need a certain size to be viable;

small populations tend to be genetically less diverse and are more vulnerable (for instance an epidemic might wipe out the entire population). Some examples of carnivore population densities are (in numbers per km2): Lion 0.38-0.06, *P. pardus* 0.03-0.05, *L. lynx* 0.02-0.10, *Crocuta* 0.12-0.24, *U. arctos* 0.007-0.67; *Canis lupus* 0.002-0.04, *Nyctereutes* 0.1-2, *Cuon alpinus* 0.35-0.90, *Vulpes vulpes* 1-2, *Gulo* 0.002-0.005, *Mustela erminea* 10 (Nowak 1991). The higher densities may well be due to artificial circumstances. It can be observed that felids tend to have low densities and that within each family, population densities increase with decreasing body size.

Not all islands can support a population of large carnivores. The surface of Malta is 246 km², of Mallorca some 3600 km² and of Sardinia some 24000 km². Malta might support about 10 panthers, Mallorca 144 and Sardinia 960. Sardinia might support some 4320 hyenas, some 25200 raccoon dogs, some 15000 dholes or 5040 wolves. Populations of these sizes will not all be viable. Population sizes frequently fluctuate and one of the reasons for that may be the interaction between predator and prey. Mathematical models and experiments in limited environments may show increasing amplitude of fluctuation, leading to the extinction of the predator (Hassel 1976). Such fluctuations seem to be more common to small or poor ecosystems. All this suggests that not all islands are able to support populations of large carnivores. The larger the island, the larger the carnivore that may survive on it. Carrying capacity might be the reason that on Mallorca no large carnivore survived, while on Sardinia the canid *Cynotherium*, but no larger carnivores, nor felids could survive.

In the absence of carnivores, competition between the herbivores becomes more accentuated. This may be the reason why island faunas, starting as balanced faunas, become impoverished in herbivores as well. Islands with a single carnivore might be relatively rich in herbivore species. These species would then not change to 'low gear locomotion' and lack a

number of other typical island adaptations, such as stereoscopic view etc. There seem thus to exist two ways in which an endemic island species can originate: (1) it arrives on an island and becomes isolated (generally by 'sweepstake route'), (2) a population lives on a piece of land that becomes an island, isolating the population. It is of interest to note that proboscideans, deer and hippos are common in the first group, whereas the cases of the Baleares and Sardinia suggest that bovids, anthracotheres, primates, hedgehogs, moles and possibly pigs and dogs may be among the second group. Soricids, glirids and murids seem to be present in any case and perissodactyla and carnivores never or rarely survive in insular environments. Cyprus, Crete and many of the smaller Greek islands were colonised by animals that used the sweepstake route. The faunal composition of the Baccinello faunas suggests, that the area was originally connected to the mainland or became connected to islands with such faunas.

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