

Biochronology of the Plio-Pleistocene Terrestrial mammals of Sardinia: The state of the art*

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ABSTRACT: On the basis of currently available data, two main mammalian faunal complexes can be recognised in Sardinia from the Pliocene to the Late Pleistocene-Holocene: the “*Nesogoral*” and “*Microtus (Tyrrenicola)*” faunal complexes. Notable faunal renewal characterises the transition between the two major complexes, while individual appearance and disappearance bioevents permit the recognition of less important renewals, which however allow one to distinguish, in the sphere of the two major complexes, subcomplexes of biochronologically-distinct fauna.

The occurrence of endemic bovids, suids and archaic micromammals typified the earliest Sardinian LFAs. This faunal complex was present during the Pliocene and the beginning of the Early Pleistocene and was probably characterised by local evolution of some lineages, by a reduced extinction rate and by a moderate immigration rate. Two subcomplexes may be detected within this complex.

In the earliest Mandriola faunal sub-complex, descendants from endemic pre-existing taxa (*Tyrrenoglis*) are associated with new settlers that entered during the Messinian (murids, suids and bovids) and micromammals suggesting an early Middle Pliocene age. Very modest faunal renewal marks the transition to the following faunal subcomplex (“Capo Figari/Orosei 1”) (late Middle?, Late Pliocene-Early Pleistocene). The latter is typified by the occurrence, among others, of micromammals which evolved from pre-existing taxa, of an endemic predator, the Hyaenidae *Chasmaporthetes melei*, and strongly modified bovids, possibly present in Sardinia from the late Messinian, as well as mustelids that may have entered Sardinia during the Middle Pliocene regression.

Marked faunal renewal indicates the transition to the subsequent *Microtus (Tyrrenicola)* faunal complex (?latest Early Pleistocene/Early Holocene), within which two faunal subcomplexes can be recognised. In the older “Orosei 2” faunal sub-complex (latest Early Pleistocene/early Middle Pleistocene), an archaic endemic vole (*Microtus (Tyrrenicola)* sp.), *Cynotherium* sp., a large megalcerine (“*Praemegaceros*” n. sp.) and possibly a new caprine first occurred, together with some pre-existing taxa such as *Rhagamys minor*. The younger “Dragonara” faunal sub-complex (latest Middle Pleistocene-Early Holocene), corresponding to classic endemic Sardinian fauna, is characterised by the presence, among others, of advanced voles (*Microtus (Tyrrenicola) henseli*) and murids (*Rhagamys orthodon*), *Cynotherium sardous*, megacerines more or less reduced in size (“*Praemegaceros cazioti*”) and, occasionally, endemic elephants (*Mammuthus lamarmorai*).

These faunal complexes testify to the evolution of mammalian fauna in the Sardinian insular domain towards progressively more unbalanced and impoverished fauna, and document colonisation phases from the mainland and faunal turnovers/renewals, followed by periods of more notable insularity conditions.

Key-words: Plio-Pleistocene, Sardinia, Mammals.

ΠΕΡΙΛΗΨΗ: Βασίζόμενοι στα πρόσφατα δεδομένα, στη Σαρδηνία μπορούμε να αναγνωρίσουμε δύο κύρια πανιδικά συμπλέγματα από το Πλειόκαινο μέχρι το Ανώτερο Πλειστόκαινο-Ολόκαινο: το πανιδικό σύνολο “*Nesogoral*” και το πανιδικό σύνολο “*Microtus (Tyrrenicola)*”. Η μετάβαση από το ένα πανιδικό σύνολο στο άλλο χαρακτηρίζεται από αξιοσημείωτα γεγονότα ανανέωσης της πανίδας, ενώ ιδιαίτερα γεγονότα εμφάνισης και εξαφάνισης επιτρέπουν την αναγνώριση φάσεων λιγότερο σημαντικής ανανέωσης, τα οποία όμως επιτρέπουν τη διάκριση πανιδικών υποσυνόλων εντός κάθε κύριου πανιδικού συνόλου.

Τα παλαιότερα τοπικά πανιδικά σύνολα της Σαρδηνίας χαρακτηρίζονται από την παρουσία ενδημικών Bovidae, Suidae και αρχαϊκών μικροθηλαστικών. Αυτό το πανιδικό σύνολο ήταν παρόν κατά τη διάρκεια του Πλειοκαινού και κατά την αρχή του Κατώτερου Πλειστοκαινού και χαρακτηριζόταν πιθανόν από την τοπική εξέλιξη ορισμένων φυλογενετικών γραμμών, από το μικρό ρυθμό εξαφάνισης και από το μέτριο ρυθμό μετανάστευσης. Εντός αυτού του συνόλου μπορούμε να διακρίνουμε δύο πανιδικά υποσύνολα.

Στο παλαιότερο πανιδικό υποσύνολο Mandriola, οι απόγονοι ενδημικών προϋπαρχόντων taxa (*Tyrrenoglis*) σχετίζονται με νέους μετανάστες που εισήλθαν κατά τη διάρκεια του Μεσσηνίου (Muridae, Suidae και Bovidae) και μικροθηλαστικά που υποδηλώνουν μία ηλικία κάτω Μέσου Πλειοκαινού. Η μετάβαση στο ακόλουθο πανιδικό υποσύνολο (“Capo Figari/Orosei 1”) (άνω Μέσο; Ανώτερο Πλειόκαινο-Κατώτερο Πλειστόκαινο) χαρακτηρίζεται από τη μέτρια ανανέωση της πανίδας. Αυτό το υποσύνολο χαρακτηρίζεται μεταξύ άλλων από την ύπαρξη μικροθηλαστικών που εξελίχθηκαν από προϋπάρχοντα taxa, από ένα ενδημικό αρπακτικό, την ύαινα *Chasmaporthetes melei*, και έντονα διαφοροποιημένα βοοειδή, πιθανόν παρόντα στη Σαρδηνία από το Ανώτερο Μεσσηνίο, καθώς και από Mustelidae που μπορεί να ήρθαν στη Σαρδηνία κατά τη διάρκεια της θαλάσσιας

* Βιοχρονολόγηση των Πλειο-Πλειστοκαινικών χερσαίων θηλαστικών της Σαρδηνίας: Η κατάσταση προόδου.

απόσυρσης του Μέσου Πλειοκαίνου.

Αξιοσημείωτη πανιδική ανανέωση δείχνει τη μετάβαση στο μεταγενέστερο *Microtus (Tyrrenicola)* πανιδικό σύνολο (ανώτατο Κατώτερο Πλειστόκαινο/Κατώτερο Ολόκαινο), εντός του οποίου αναγνωρίζονται δύο πανιδικά υποσύνολα. Το παλαιότερο πανιδικό υποσύνολο "Orsei 2" (ανώτατο Κατώτερο Πλειστόκαινο-κατώ Μέσο Πλειστόκαινο) χαρακτηρίζεται από την παρουσία ενός αρχαϊκού ενδημικού αρουραίου (*Microtus (Tyrrenicola)* sp.), του *Cynotherium* sp., ενός μεγάλου Megacerinae ("*Praemegaceros*" n. sp.) και πιθανόν ενός νέου Caprinae που απαντά για πρώτη φορά, μαζί με ορισμένα προϊπάρχοντα taxa όπως το *Rhagamys minor*. Το νεότερο πανιδικό υποσύνολο "Dragonara" (ανώτατο Μέσο Πλειστόκαινο-Κατώτερο Ολόκαινο), που αντιστοιχεί στην κλασική ενδημική πανίδα της Σαρδηνίας, χαρακτηρίζεται μεταξύ άλλων από την παρουσία εξελιγμένων αρουραίων (*Microtus (Tyrrenicola) henseli*) και Muridae (*Rhagamys orthodon*), του *Cynotherium sardous*, Megacerinae περισσότερο ή λιγότερο ελαττωμένου μεγέθους ("*Praemegaceros*" *cazioti*) και, περιστασιακά, ενδημικών ελεφάντων (*Mammuthus lamarmorai*).

Αυτά τα πανιδικά σύνολα μαρτυρούν ότι η πανίδα των θηλαστικών της Σαρδηνίας εξελίχθηκε προς διαδοχικά περισσότερο μη ισορροπημένη και πτωχή πανίδα, και πιστοποιούν φάσεις αποίκησης από την ηπειρωτική χέρσο και πανιδικές αναλλαγές/ανανεώσεις, που ακολούθηθηκαν από περιόδους με αξιοσημείωτες συνθήκες απομόνωσης.

Λέξεις-κλειδιά: Πλειο-Πλειστόκαινο, Σαρδηνία, Θηλαστικά.

INTRODUCTION

Cenozoic and Quaternary mammals from Sardinia, which have been known since the 19th century, contribute substantial information to a reconstruction of the complex and still controversial history of Western Mediterranean palaeogeography. For instance, the occurrence of the endemic perissodactyls *Atalonodon monterini* DAL PIAZ, 1929 and *Paralophiodon sardus* (BOSCO, 1902) in the Early and Middle Eocene marine and marsh deposits of Terras de Collu (Sulcis area, southwestern Sardinia) testifies to the existence of ecological or physical barriers between Sardinia and Cantabric plus Provencal regions (MATTEUCCI *et al.*, 2000). At the beginning of the Miocene, isolation was complete, as indicated by the unbalanced fauna from Oschiri (Sassari), including endemic and insular micromammals (DE BRUIJN & RÜMKE, 1974), a suid, an antracothere and *Bachitherium* (VAN DER MADE, 1999). Their ancestors might have reached the island in separate migration phases during the late Oligocene and Early Miocene. On the other hand, the recent discovery of the relatively diversified but notably endemic "*Oreopithecus*" fauna at Fiume Santo (Porto Torres, northwestern Sardinia) (CORDY & GINESU, 1994; CORDY *et al.*, 1995), bears witness that the Tusco-Sardinian paleobioprovince came into existence as an isolated region during the Late Miocene. Moreover, the occurrence of *Eumaicherus* and *Agriotherium* in both Fiume Santo and Baccinello V2 (Tuscany) deposits suggests that Sardinia and Tuscany were connected during the MN 12. Sardinia was possibly isolated from Tuscany before the Messinian, since the new immigrants from Europe recorded in the Baccinello V3 level have not yet been found in Sardinia. Nevertheless, the hypothesis that during the Messinian, Sardinia and the mainland were possibly connected, cannot be ruled out (see below). Post-Miocene faunas have been recorded in the Sinis Peninsula (western Sardinia) in a weathered deposit cropping

out at the top of the Mandriola Formation (Middle Pliocene) and in the palaeosoils at the bottom of the Capo Mannu Formation (Late Pliocene) (PECORINI *et al.*, 1974; CARBONI & LECCA, 1995; MELIS & PALOMBO, 2003).

Quaternary localities of particular interest, well-known since the 19th or early 20th century, were Monreale-Bonaria (Cagliari), Capo Figari (northeastern Sardinia), Fontana Morimonta (Gonnesa, southwestern Sardinia) and Monte San Giovanni (see *inter alios* LAMARMORA, 1826; ACCONCI, 1881; LOVISATO, 1884; DEHAUT, 1911, 1914; BATE, 1945; MAJOR 1883, 1905, 1913). During the second half of the last century, new discoveries notably contributed to better defining the distinctiveness of so-called "classic" Sardinian mammal fauna (see, among others, AZZAROLI, 1946; COMASCHI CARIA, 1955, 1956, 1970; MALATESTA 1954, 1970; AMBROSETTI, 1972; CORDY & OZER, 1973; CALOI & MALATESTA, 1974; ENGESSER, 1976; BRANDY, 1978; CALOI *et al.*, 1981; GLIOZZI & MALATESTA, 1982; SPOOR & SONDAAR, 1986; SONDAAR *et al.*, 1988; VAN DER MADE, 1988; EISENMANN, 1990; MINIERI *et al.*, 1995; MEZZABOTTA *et al.* 1996; KLEIN HOFMEIJER, 1997; etc.). This faunal complex, clearly endemic and generally regarded as ranging in age from the late Middle Pleistocene to Early Holocene, includes *Cynotherium sardous* STUDIATI, 1857, *Mammuthus lamarmorai* (MAJOR, 1883), "*Praemegaceros*" *cazioti* (DÉPÉRET, 1897) and micromammals such as *Talpa tyrrenica* BATE, 1945, "*Nesiotites*" *similis* (HENSEL, 1855) (= *Asoriculus similis*, according to VAN DER MADE, 1999), *Microtus (Tyrrenicola) henseli* (MAJOR, 1905), *Ragamys orthodon* HENSEL, 1856 and *Prolagus sardus* WAGNER, 1825. Mustelids such as *Enhydriactis galictoides* MAJOR, 1902 and three Lutrinae were also reported: the large *Megalenydris barbaricina* WILLEMSEN & MALATESTA, 1987, the smaller *Sardolutra ichnusae* (MALATESTA, 1977) and *Algarolutra majori* (MALATESTA, 1978) (WILLEMSEN, 1992 and references therein).

Fossil mammal remains appear mainly in cave deposits,



Fig. 1. Location map of selected Cenozoic localities.

karstic fissure fillings or isolated pockets cropping out in quarries or natural sections, in aeolian sediments, palaeo-soils or in localised fossiliferous fluvial-lacustrine alluvial deposits, frequently of limited thickness and extension. Accordingly, correlations are very difficult and up to now, the chronological framework of middle-Late Pleistocene faunal successions (based principally on the evolutionary stage reached by arvicolid and murids or on deer size) has been rather approximate (KOTSAKIS, 1980; PALOMBO, 1985; CALOI *et al.*, 1988).

Moreover, it was generally supposed that, after the opening of the Tyrrhenian Sea (Early Pliocene), Sardinia remained permanently insular. Therefore, if Sardinia became isolated from the mainland, ancestors of endemic taxa must have reached the island by sweepstake dispersal (*sensu* SIMPSON, 1965: "spread is impossible for the most and very improbable for some, but does occur accidentally") (PALOMBO, 1985). Accordingly, the island of Sardinia should be classified as an oceanic-like island (*sensu* ALCOVER *et al.*, 1998); nevertheless, Sardinian palaeogeographic history is more complex than previously believed, and recent discoveries have opened new windows on the settlement and evolution of post-Miocene Sardinian terrestrial faunas.

Indeed, during the last twenty years, knowledge of

Sardinian Plio-Pleistocene mammal faunas was increased by new finds, such as the discovery of impoverished but quite balanced assemblages, including an active hunter Hyaenidae, in fissure fillings at Monte Tuttavista (Orsei, eastern Sardinia) (GINESU & CORDY, 1997; SONDAAR, 2000; ABRAZZI *et al.*, 2004a), as well as of a large megacerine in Sadali cave (Tacchi di Seulo, Central Sardinia) (PALOMBO *et al.*, 2003). These discoveries led to new concepts in both the biochronology and faunal evolution, as well as the palaeobiogeography of the Sardinian-Corsican massif. For instance, according to SONDAAR & VAN DER GEER (2002), "the presence of a hyaenid in association with a diverse terrestrial mammal fauna, Early Pleistocene in age (GINESU & CORDY, 1997), means that during the Plio/ Pleistocene Sardinia was not colonized overseas, and therefore cannot be considered an oceanic-like island in that time" (SONDAAR & VAN DER GEER, 2002:166) (but see below).

The aim of this paper is to provide an updated list of the Plio-Pleistocene mammalian taxa thus far reported from the island of Sardinia and to highlight the still-unresolved problems concerning their biochronological setting, as well as when and how colonisation took place.

PLIO-PLEISTOCENE MAMMALS FROM SARDINIA: AN OVERVIEW

Terrestrial micromammals (Erinaceomorpha, Soricomorpha, rodentia, Lagomorpha)

Erinaceomorpha and Soricomorpha were not common in Sardinian Plio-Pleistocene local faunal assemblages (LFAs); rodents (Gliridae, Muridae and Arvicolidae) were the most frequent, whereas Ocotonidae belonging to the *Prolagus* genus were the most widespread, persisting with *P. sardus* until proto-historical times (see below).

Talpidae

Erinaceidae were recorded in the Middle Pliocene lagoon deposits (affected by soil processing) cropping out at Mandriola (western Sardinia, PECORINI *et al.*, 1974). Scanty remains from Capo Figari 1 (Early Pleistocene) were assigned to *Talpidae* (VAN DER MADE, 1999), whereas *Talpa* sp. was reported at Nuraghe su Casteddu (?Middle Pliocene) (eastern Sardinia, ESU & KOTSAKIS, 1980). The more advanced endemic species *Talpa tyrrhenica*, established by BATE (1945) on the basis of Monte San Giovanni (Middle Pleistocene) specimens, was cited in a number of Middle and Late Pleistocene localities (COMASCHI CARIA, 1968; GLIOZZI *et al.*, 1986; MELIS *et al.*, 2002). Assuming that *Talpa tyrrhenica* was the descendent of *Mandriola* and Nuraghe su Casteddu taxa, we can hypothesise that the ancestor of the Sardinian mole lineage came to the island during the Late Ruscinian or the Messinian, as already suggested by VAN DER MADE (1999).

Soricidae

At last three species of *Soricidae* occurred in the Plio-

Pleistocene of Sardinia: *Asoriculus* aff. *A. gibberodon* (PETÉNYI, 1864) from the ?Middle Pliocene locality of Nuraghe su Casteddu (ESU & KOTSAKIS, 1980) and two or more species belonging to the “*Nesiotites*” genus. BATE (1944) established the genus for endemic soricids in Sardinia [the small “*Nesiotites*” *similis* (HENSEL, 1855)], Corsica [the larger “*Nesiotites*” *corsicanus*, BATE, 1944] and the Balearic Islands (as far as Balearic soricids are concerned, see REUMER, 1980, 1982). Actually “*Nesiotites*” *corsicanus* also occurred in Sardinia, since it was found in Early Pleistocene fissure fillings at Capo Figari I (ZAMMIT MAEMPEL & DE BRUIJN, 1982; VAN DER MADE, 1999; FANFANI, 2000). “*Nesiotites*” *similis* was more common and has been cited in a number of Middle and Late Pleistocene localities as well as in Early Holocene deposits (BATE, 1844; COMASCHI CARIA, 1968; GLIOZZI *et al.*, 1986; SONDAAR *et al.*, 1988; DELUSSU, 2000). A large soricid (“*Nesiotites*” sp. 1), morphologically similar to but even larger than “*N.*” *corsicanus*, has recently been cited in the more advanced LFAs from Monte Tuttavista (Orosei, western Sardinia), whereas a smaller one, “*Nesiotites*” sp. 2, was found in archaic ones (ABBAZZI *et al.*, 2004).

Gliridae

Among rodents, Gliridae seem to be extremely rare in late Early-Middle and absent in Late Pleistocene LFAs. They belong to the *Tyrrhenoglis* genus, established by ENGESSER (1976) on the basis of large specimens (*Tyrrhenoglis majori*, ENGESSER, 1976) from Capo Figari, belonging to MAJOR’s collection. Some slightly larger remains from Monte Tuttavista have been cited as *Tyrrhenoglis* cf. *T. majori* (ANGELONE *et al.*, in ABBAZZI *et al.*, 2004a); the glirid from Nuraghe su Casteddu, assigned to *Hypnomys* by ESU & KOTSAKIS (1980), can be attributed to *Tyrrhenoglis* aff. *T. majori* (see ZAMMIT MAEMPEL & DE BRUIJN, 1982). A smaller species, *Tyrrhenoglis figariensis* (= *Eliomys* (*Tyrrhenoglis*) *figariensis* ZAMMIT MAEMPEL & DE BRUIJN, 1982) has been established for specimens from type locality Capo Figari I and from Capo Figari II. For the latter LFA, an age of 366,959 +/- 20% years B.p., was obtained using the ESR method (MOTOJI IKEYA, *vide* VAN DER MADE, 1999). Accordingly, *Tyrrhenoglis figariensis* may have survived in the late Middle Pleistocene LFAs together with *Microtus* (*Tyrrhenicola*), *R. orthodon* and “*Praemegaceros*”.

A more primitive species, possibly related to *T. figariensis*, occurred in the Mandriola LFA (RAGE *et al.*, in PECORINI *et al.*, 1974). ENGESSER (1976) suggested that *Antracoglis* from Baccinello V1 and V2 and possibly from Fiume Santo LFAs was the possible ancestor of *T. majori*. If this is correct, we may suppose that, after the separation from Tuscany, *Tyrrhenoglis* survived in Sardinia, giving rise to two different, perhaps ecologically separated species (ABBAZZI *et al.*, 2004a).

Gerbellidae

A second molar of a gerbillid has been found in a fissure at

Monte Tuttavista, from which advanced taxa such as *M. (Tyrrhenicola) henseli*, *Ragamys orthodon* and “*Praemegaceros*” *cazioti* were recovered (ABBAZZI *et al.*, 2004a). Gerbellidae occurred in Miocene and Pliocene European LFAs, as well as in Italian ones (CAVALLO *et al.*, 1993; ROOK *et al.*, 2001a). Accordingly, the Sardinian specimens might constitute the most recent fossil record of this taxon in Europe (but see ANGELONE *et al.*, in ABBAZZI *et al.*, 2004a). Poor knowledge of the actual distribution of Sardinian populations prevents any hypothesis regarding the timing of Gerbellidae migration and extinction.

Arvicolidae

Arvicolidae are represented by the endemic lineage of the large “*Tyrrhenicola*” vole. According to BRUNET-LECOMTE & CHALINE (1990), “*Tyrrhenicola*” may represent an archaic branch of the *Terricola* Mediterranean group, which has been suggested to have derived from the late Villafranchian *Allophaiomys chalinei* ALCADÉ, AGUSTI & VILLALTA, 1981. However, features common to both “*Tyrrhenicola*” and *Terricola* (such as the typical pitomyan rhombus) probably depend only on parallelism, as previously suggested by some authors. In addition, in recent papers, “*Tyrrhenicola*” has been considered a subgenus of *Microtus* (MEZZABOTTA *et al.*, 1995; MINIERI *et al.*, 1995; PEREIRA *et al.*, 2003).

The *Microtus (Tyrrhenicola) henseli* (MAJOR, 1905) species has been well documented in Sardinia during the Middle and Late Pleistocene and occurred until the Bronze Age (Santu Antine de Torralba, MANCONI, unpublished data). This taxon shows great variability, and a number of different morphotypes have been recognised even within a single population (MEZZABOTTA *et al.*, 1995, 1996; MINIERI *et al.*, 1995). Moreover, chronological information on each sample is scanty, and the advanced features shown by *M. (T.) henseli* samples prevent recognition of indisputable apomorphic characters. Consequently, thus far biochronological relationships inferred by the author on the basis of analysis of *M. (T.) henseli* M₁ have been quite contradictory: e.g. according to MEZZABOTTA *et al.* (1995), the Dragonara sample would be more archaic than those from Monte San Giovanni, whereas MINIERI *et al.* (1995), using a larger sample, drew opposite conclusions.

In any case, a *Tyrrhenicola* with archaic features and small in size (*Microtus (Tyrrhenicola)* n. sp.) occurs at Capo Figari (collection Thaler, BRANDY, 1978), as well as at Monte Tuttavista (CORDY, 1977; SONDAAR, 2000; ANGELONE *et al.*, in ABBAZZI *et al.*, 2004a), in a faunal assemblage where “*Rhagapodemus*” *minor*, *Oryctolagus* aff. *O. lacosti* and *Pannonictis* sp. were still present, while *Cynotherium* sp. and a new Caprinae (*s e n s u* GENTRY, 1992) appeared for the first time.

The migration time and phylogenetic relationships of the Sardinian endemic vole are uncertain and controversial. For example, MEZZABOTTA *et al.* (1995) and MINIERI *et al.* (1985) hypothesised evolution from the *Allophaiomys ruffoi* – *Allophaiomys burgondiae* lineage, and a late Early

Pleistocene-early Middle Pleistocene migration, whereas VAN DER MEULEN (1973) suggested derivation from *Allophaiomys pliocaenicus* and Early Pleistocene migration.

Ongoing research will clarify these important, still unanswered questions.

Muridae

Sardinian Plio-Pleistocene endemic murids belong to the *Apodemus* genus and *Rhagapodemus*/*Rhagamys* anagenetic lineage.

The “giant” murid *Apodemus mannu* THALER, 1973 is known only in the Middle Pliocene (late MN15) Mandriola LFA. It is a clearly endemic taxon; its ancestor did not reach Sardinian before the Messinian, since the *Apodemus* genus first appeared in Europe in LFAs ascribed to MN13.

The most archaic representative of the endemic *Rhagapodemus*/*Rhagamys* lineage also first appeared in the Mandriola LFA, where ANGELONE & KOTSAKIS (2001) have recently established a new species, *Rhagapodemus azzarolii*, for specimens formerly ascribed to *Rhagapodemus* aff. *R. hautimagnensis* MEIN & MICHAUX, 1970 by PECORINI *et al.* (1974). ANGELONE & KOTSAKIS (2001) suggested that the ancestor of the Sardinian *Rhagapodemus*/*Rhagamys* lineage, *Rhagapodemus balleisioi* MEIN & MICHAUX, 1970, arrived in the Corsican-Sardinian area during the late Ruscinian. *R. azzarolii*'s descendant, “*Rhagamys*” *minor* BRANDY, 1978, occurred at Capo Figari (Capo Figari 1 LFA, THALER and FORSITH MAJOR collections) and Monte Tuttavista, where it was found together with “archaic” taxa such as bovids belonging to *Nesogoral* group and *Sus sondaari*.

The larger and more high-crowned *Rhagamys orthodon* (HENSEL, 1856) has been identified in a number of localities ranging in age from the Middle Pleistocene (e.g. for Santa Lucia an age of about 450 ka +/- 20% has been proposed on the basis of an ESR date on “*Praemegaceros*” tooth enamel, MOTOJI IKEYA, *vide* VAN DER MADE, 1999) to the Neolithic Age (Grotta del Guano (Oliena), SANGES & ALCOVER, 1980; Grotta Punta del Quadro (Alghero), DELUSSU, 2000).

It is noteworthy that MARTEN SUYREZ & MEIN (1998) assigned “*Rhagamys*” *minor* to the *Rhagapodemus* genus, whereas they maintained the generic name *Rhagamys* for *R. orthodon*. Actually, features showed by *R. minor* teeth look more close to *Rhagapodemus* stock than to the advanced *R. orthodon* representatives. Nevertheless, it should be preferable to maintain the same generic name, at least for *R. minor* and *R. orthodon*, taking into account that both species belong to an endemic insular lineage (but see ANGELONE *et al.*, 2003), as indicated by the intermediate evolutive status of some specimens recently described from Monte Tuttavista (quarry “X 3 uccelli”) (ANGELONE *et al.*, in ABBAZZI *et al.*, 2004a).

Ochotonidae

A peculiar feature of Sardinian insular faunas is the occurrence of the ochotonidae *Prolagus*, particularly abun-

dant and frequent from the Pliocene to the Iron Age, whereas during the Plio-Pleistocene, Lagomorpha were not present on any other Mediterranean island.

Three ochotonids have been described to date: *Prolagus sardus* WAGNER, 1985, based on specimens from Bonaria (TOBIEN, 1935) (considered the most advanced and abundant species, occurring in Middle and Late Pleistocene LFAs), *Prolagus figaro* LOPEZ MARTINEZ, 1975, larger than *P. sardus*, which occurred in more archaic faunal assemblages (? Early Pleistocene), and “*Prolagus* cf. *P. figaro*” from Mandriola (LOPEZ MARTINEZ & THALER, 1975) and Capo Figari I (ZAMMIT MAEMPEL & DE BRUIJN, 1982).

More recently, ANGELONE *et al.* (in ABBAZZI *et al.*, 2004a), in analysing Plio-Pleistocene rich samples coming from Monte Tuttavista fissure fillings, have recognised different morphotypes but excluded the presence of different species due to the overlapping of metrical parameters and morphological features. Accordingly, the authors have ascribed whole ochotonid remains to *Prolagus* cf. *P. sardus*, implying the presence of *P. sardus* since at least the Late Pliocene. More recent data attest the occurrence of *P. figaro* in the earliest Monte Tuttavista LFAs as well (TUVERI 2004, personal communication). In addition, ANGELONE (2003), suggested that the Sardinian ochotonid “probably descended from continental species closely related to *Prolagus michauxi* (*P. calpensis* and *P. depereti*)” and considered it possible that the ochotonid from Mandriola belongs to a new species. Accordingly, it seems reasonable to suppose that the ancestor of *Prolagus* sp. *P. figaro* (perhaps *P. depereti* LOPEZ MARTINEZ, 1975, recorded from continental LFAs ascribed to MN15) entered Sardinia during the Early/Middle Pliocene transition, while to date it is difficult to hypothesise a colonisation time for the *P. sardus* ancestor (?*P. calpensis*).

Leporidae

Sardinia is also the only island where Leporidae occurred during the Plio-Pleistocene in endemic faunas: the *Oryctolagus* genus is present in the earliest faunal assemblages from Monte Tuttavista (“*Nesogoral* faunal complex, Capo Figari/ Orosei 1 faunal sub-complex”, see below). The few specimens so far recorded show morphological affinities with the species *Oryctolagus lacosti* (POMEL, 1853), known since the Pliocene in continental European LFAs (ANGELONE *et al.*, in ABBAZZI *et al.*, 2004a and references therein). A Leporidae, very similar to the Monte Tuttavista one, was retrieved from the paleosoils cropping out at the bottom of the Capo Mannu Formation (CARBONI & LECCA, 1995), together with a suid and bovids very similar to those found at Monte Tuttavista (see below).

Large mammals (Primata, Carnivora, Artiodactyla)

Cercopithecidae

Only Sardinian Plio-Pleistocene endemic fauna includes a Cercopithecidae, whose remains were collected at the

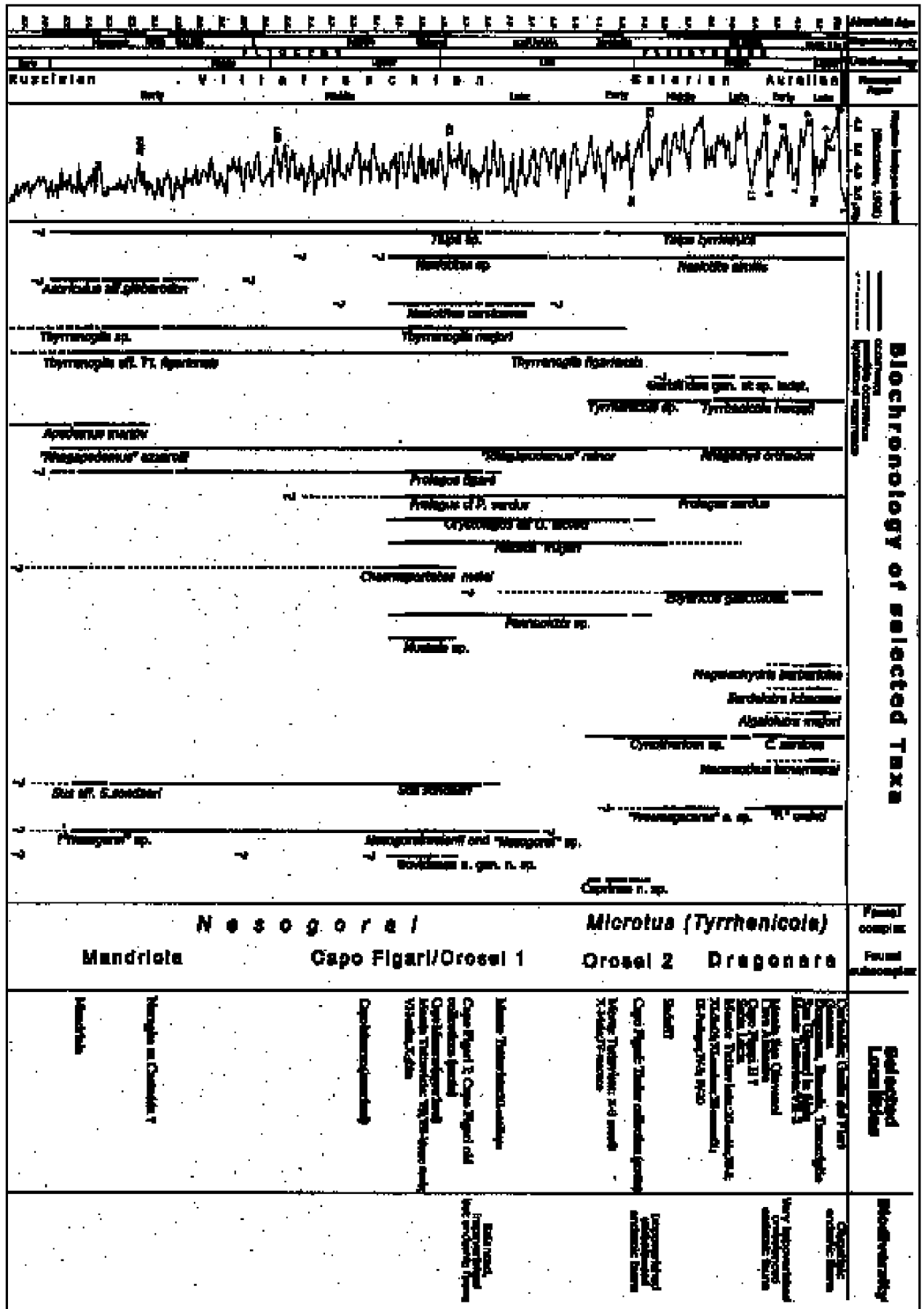


Fig. 2. Chronological range of mammal taxa documented in selected Sardinian deposits.

beginning of the XX century from Capo Figari breccias (DEHAUT, 1911, 1914; MAJOR, 1913). DEHAUT (1911) first mentioned a macaque, but established his new species *Ophthalmomegas lamarmorae* based on a skull fragment actually belonging to an endemic owl (see PAVIA, 1999 and references therein) and did not apparently take into account some post-cranial macaque bones. As a result, DEHAUT's species is invalid. Then AZZAROLI (1946) established the species *Macaca majori* on the basis of Capo Figari material, including an incomplete skull collected by MAJOR (1913), who already recognised the occurrence of a macaque. A second skull was recovered from breccias cropping out in Santa Lucia mine (Is Oleris, Iglesiente, southwestern Sardinia) (COMASCHI CARIA, 1970), and a very rich sample has recently been found in fissure fillings at Monte Tuttavista (Orosei, eastern Sardinia) (ABBAZZI *et al.*, 2004). The Monte Tuttavista specimens, although dimensionally and morphologically similar to the type of the species *Macaca majori*, show, along with the Is Oleris skull, some peculiar maxillary features that suggest they should be ascribed to *Macaca* aff. *M. majori* (ABBAZZI *et al.*, 2004a and references therein). In any case, *Macaca majori* and *Macaca* aff. *M. majori* share characteristic features such as an inflated molar row and an allometric increase in molar dimensions (AZZAROLI, 1982; ABBAZZI *et al.*, 2004a). The latter feature might confirm the insular dwarfism of *Macaca majori* (GOULD, 1975). On the other hand, cranial dimensions appear reduced in relation to postcranial bones; this allometry seems to be unusual in dwarfed mammal taxa, but a similar feature also characterises the extensively-modified bovid *Myotragus balearicus* BATE, 1909 from the Balearic Islands (KÖHLER & MOY-SOLY, 2004). Some authors have debated the insular dwarfism of Sardinian macaques: e.g. SZALAY & DELSON (1979) and JABLONSKI (2002) regard the Sardinian macaque as a subspecies of *Macaca sylvanus* LINNAEUS, 1758. Indeed, the size of *Macaca majori* falls within the dimensional range of the smallest extant insular and peninsular South East Asia macaques, but is smaller than the Plio-Pleistocene representative of the *Macaca* genus. Accordingly, the process of rendering the Sardinian macaque endemic led to a reduction in size and to some allometries supporting attribution to a distinct species.

Dates for the arrival of the *Macaca* ancestor and macaque disappearance in Sardinia are uncertain. Sardinian macaques were undoubtedly present in Late Pliocene/Early Pleistocene Monte Tuttavista LFAs belonging to "Nesogoral faunal complex, Capo Figari/Orosei 1 faunal sub-complex" (see below). The species also occurred in renewed, possibly late Early Pleistocene LFAs, where *Tyrrhenoglis* cf. *T. major*, "*Rhagapodemus*" *minor*, *Oryctolagus* aff. *O. lacosti* and *Pannonictis* sp. were still present, but newcomers such as *Tyrrhenicola* sp., *Cynotherium* sp. and a new "goat" occurred (*M. (Tyrrhenicola)* faunal complex": see below). Furthermore, if the skull from Santa Lucia/Is Oleris actually belongs to "*Tyrrhenicola* fauna" (still unproven), *Macaca majori* may have survived during the Middle Pleistocene, as already suggested by some authors (e.g. KOTSAKIS,

1980; GLIOZZI *et al.*, 1986; CALOI *et al.*, 1988; VAN DER MADE, 1999).

Macaca genus first appeared in Europe in MN 13 (ANDREWS *et al.*, 1996); accordingly and taking into account the poor swimming ability of macaques, the ancestor of the Sardinian lineage may have reached the island during the Messinian, even if a later migration (perhaps during the Pliocene sea level low standing, cf. HAQ *et al.*, 1987; MILLER *et al.*, 1996) cannot be excluded. Ongoing research and a detailed comparison with the Ruscinian and Villafranchian mainland *Macaca* will answer open questions.

Hyaenidae

In 1995 a cranium belonging to a large hyaenid was found by Dr. G. Mele, along with other fossil bones, in a fissure opening up in the Monte Tuttavista quarry area (Orosei, eastern Sardinia) (GINESU & CORDY, 1997; SONDAAR 2000; Rook *et al.*, 2004b). Unfortunately, *Chasmaporthetes* cranium has been found as an erratic element, and despite the huge number of fossil remains thus far retrieved from Monte Tuttavista fissures, no other hyaenid specimen has been found to date. Thus, the composition of the accompanying fauna may be inferred but not unquestionably defined.

The morphology of skull, mandible, canines, teeth and the peculiar symmetrical shape of the P₄ shown by the Monte Tuttavista specimen are typical of the *Chasmaporthetes* genus and similar to *Chasmaporthetes lunensis* (DEL CAMPANA, 1914), but undeniably smaller than European Plio-Pleistocene hunting-hyaenas (FICCARELLI & TORRE, 1967a; GALIANO & FRAILEY, 1977; KURTÉN & WERDELIN, 1988). This reduction in size might be the result of adaptation to an insular ecosystem and were considered sufficient to justify the creation of the new species *Chasmaporthetes melei* ROOK, FERRETTI, ARCA & TUVERI, 2004 (see ROOK *et al.*, 2004b). We assume that the endemic hyaena belongs to the "Nesogoral faunal complex", although the list of accompanying taxa unfortunately remains unknown.

The time when *Chasmaporthetes* entered Sardinia can be inferred, considering the presence of bovids possibly belonging to the *Nesogoral* group in Mandriola fauna (VAN DER MADE, 1999), as well as the peculiar features of *Nesogoral* limb bones, suggesting competition with large predators (PALOMBO *et al.*, this volume).

Chasmaporthetes was widespread in the Old World from the Late Miocene to the earliest Pleistocene. Moreover, during the Miocene, *Chasmaporthetes bonisi* was recorded in Greece, whereas *Chasmaporthetes lunensis* was present in Western Europe (France, Spain) at the end of the Ruscinian. Accordingly, we can hypothesise that *Chasmaporthetes* and bovid ancestor entered Sardinia during the Messinian salinity crisis. Nonetheless, on the basis of available data, a more recent migration of the hyaenid, even if improbable, cannot be totally excluded (?Middle Pliocene sea low standing, cfr.

HAQ *et al.*, 1987).

Mustelinae

Three distinct Mustelinae displaying different degrees of endemisation were present in Plio-Pleistocene Sardinian LFAs.

The best-known species is *Enhydriactis galictoides*, established by MAJOR (1902) on material from Monte San Giovanni (?Late Pleistocene). Peculiar features are a strongly marked postorbital constriction and a profile of cranial vault-frontals-nasals. *Enhydriactis galictoides* may have had greater aquatic aptitudes than its possible ancestor *Enhydriactis ardea* (BRAVARD, 1828) (FICCARELLI & TORRE, 1967b). Continental fossil records were infrequent: *Enhydriactis ardea* was recorded in the middle Villafranchian San Vallier (France) LFA (VIRET, 1954) and in late Villafranchian Olivola (Italy) LFA, while specimens from Villany (MN 17) and Beremend (Hungary), ascribed to *Enhydriactis ardea* by VIRET (1954), actually belong to *Pannonictis pilgrimi* KORMOS, 1933. Accordingly, arrival in Sardinia from the mainland might have occurred during the Middle Pliocene, when a sea level low standing reduced the distance between island and mainland coasts.

Two other mustelids have recently been identified at Monte Tuttavista (Orosei, eastern Sardinia) in association with “*Nesogoral* fauna”: a large mustelid very similar to *Pannonictis pliocaenica* KORMOS, 1931, ascribed to *Pannonictis* sp., and a smaller one very similar to *Mustela putorius* LINNAEUS, 1758 (see ABBAZZI *et al.*, 2004a).

Pannonictis was widespread in Europe during the Plio-Pleistocene (SOTNIKOVA, 1980 and references therein) and has been reported in China since the Late Miocene (Mustelid gen. indet. in ZDANSKY, 1927), whereas *Mustela* fossil remains are rather infrequent before the Late Pleistocene. Sardinian specimens might represent one of the earliest known fossil records.

Lutrinae

Even if otter remains are rather rare, lutrines are found in many unbalanced faunas of Mediterranean islands (WERDELIN, 1992 and references therein). Their morphological variations and different types of adaptation seem to emphasize the different characteristics already present in ancestral forms. As far as Sardinia is concerned, three species have been recorded from Late Pleistocene deposits: *Megalenhydris barbaricina* WILLEMSSEN & MALATESTA, 1987 (probably coming from the Aonchini group), was extremely large and actively preyed on large fish, even shellfish; *Sardolutra ichnusae* (MALATESTA, 1977) was smaller, very aquatic and preyed on fish; *Algalolutra majori* (MALATESTA, 1978), from the Dragonara LFA, was not very large and had a mixed diet (WILLEMSSEN, 1992). Competition might have led to different ecological specialisation and perhaps to their more or less marked endemic features.

Canidae

Two canids have been recorded in Sardinian Heistocene LFAs: *Cynotherium sardous* STUDIATI, 1857, the best-known species from the Middle and Late Pleistocene of Sardinia and Corsica, and *Vulpes vulpes ichnusae* MILLER, 1907, the extant subspecies recorded in Dragonara Late Pleistocene deposits by MALATESTA (1970).

Cynotherium sardous, one of the more debated taxa, is a small canid with peculiar dentition, a depressed, elongated skull and short limb bones; it was not a good runner and probably preyed on micromammals such as *Prolagus sardus* (the conformation of the acropod might also suggest fossorial capability) and perhaps birds (MALATESTA, 1970; EISENMANN & VAN DER GEER, 1999; PALOMBO, in prep.).

The species *Cynotherium sardous* was erected by STUDIATI (1857) on the material recovered by LAMORMORA from Monreale di Bonaria (Cagliari). Some specimens were also retrieved from breccias cropping out at Tramariglio (FORSITH MAJOR collection), whereas the richest sample comes from Dragonara Cave (MALATESTA, 1970). Some interesting remains, including a smaller skull, have been found in late Glacial deposits in Corbeddu Cave (Nuoro) (EISENMANN, 1990). The species is also cited in some other localities (Nurra, Porto Conte, Regione Carreras, Monte San Giusta, COMASCHI CARIA, 1968; Cava Grande, GLIOZZI *et al.*, 1986; Grotta dei Cervi, ANTONIOLI *et al.*, 1998; Grotta dei Fiori, MELIS *et al.*, 2003). Remains exceeding the dimensional variability range of the Dragonara sample have been recorded at Capo Figari (FORSITH MAJOR collection, VAN DER MADE, 1999), and Monte Tuttavista (Orosei, eastern Sardinia, ABBAZZI *et al.*, 2004a). In the latter locality, ?*Cynotherium* sp. is present in the Cava X uccelli LFA, together with some species also recorded from so-called “*Nesogoral* fauna” (“*Rhagapodemus*” *minor*, *Oryctolagus* aff. *O. lacosti*, *Macaca* cf. *M. majori* and *Pannonictis* sp.), as well as newcomers such as an archaic vole (*M. (Tyrrenicola)* n. sp.) and a new Caprinae (CORDY & GINESU, 1997; SONDAAR, 2000; ABBAZZI *et al.*, 2004a). Accordingly, the specimen from the Cava X uccelli LFA might represent the oldest evidence of this endemic canid in Sardinia.

A peculiar feature of *Cynotherium* is the unicuspidate talonid of M₁. This characteristic persuaded some previous authors to refer *Cynotherium* to *Cuon* (see MALATESTA, 1970 for a discussion). Nonetheless, the occurrence of a unicuspidate talonid should represent a case of “iterative evolution” among canids (see VAN VALKENBURGH, 1991). Although the Sardinian canid is currently considered linked to Villafranchian dogs, phyletic relationships with Plio-Pleistocene continental representatives of the Canidae family [such as *Canis “senezensis”* MARTIN, 1973, *Canis etruscus* MAJOR, 1877, *Canis arnensis* DEL CAMPANA, 1913, *Lycan falconeri* (MAJOR, 1877)] have not yet been established. Indeed, the study of *Cynotherium sardous* from Dragonara (MALATESTA, 1970) and from Corbeddu Cave

(EISENMANN, 1990; EISENMANN & VAN DER GEER, 1999) pointed out the difficulties in identifying the continental ancestor of this taxon. This endemic dog needs to be revised to clarify whether its peculiar cranial morphology is due to allometric factors linked to size reduction or to morphofunctional adaptive changes related to a particular diet (PALOMBO, unpublished data).

Moreover, even if the skull of the adult *Cynotherium sardous* displays some juvenile features (see EISENMANN & VAN DER GEER, 1999), precocious stunting of ontogenetic growth does not seem to have induced any important brain changes in this small endemic predator (PALOMBO & GIOVINAZZO, 2004) contrary to it was already demonstrated for the Sicilian dwarf elephant *Elephas falconeri* (PALOMBO, 2001).

Elephantidae

The extremely scanty elephant remains recorded to date in Sardinia provide quite contradictory information. At the end of the 19th century, ACCONCI (1881) described some tarsal, carpal and long bones recovered from the last Glacial eolian deposits cropping out at Fontana Morimonta (Gonnesa, southwestern Sardinia). On the basis of these remains, MAJOR (1883) erected the new species "*Elephas Lamarmorae*", considered similar in size to *E. mnaidriensis*, from which the Sardinia species possibly differs in the peculiar morphology of its carpal and tarsal bones.

Later, during the second half of the 20th century, two molars were found, the first one in the post-Tyrrhenian (post-MIS, 5) breccias at Tramariglio (Alghero), and the second one in pre-Tyrrhenian (pre-MIS 5, ?MIS 6) continental deposits at S. Giovanni in Sinis (AMBROSETTI, 1972; MELIS *et al.*, 2001). The morphological and biometrical characteristics of the more complete but very worn molar from San Giovanni in Sinis suggest attribution to a species having features similar to those of an advanced representative of *Mammuthus trogontherii* (POHLIG, 1885). More recently, two specimens belonging to a less size-reduced *Mammuthus* have been recorded in alluvial deposits outcropping at Campu Giavesu (northwestern Sardinia, Sassari). In accordance with the enamel thickness, hypsodonty index, lamellar frequency and enamel loop morphology, the Campu Giavesu M³ are more archaic than the San Giovanni in Sinis one (PALOMBO *et al.*, in press). Due to uncertainty regarding the actual chronostratigraphic setting of Campu Giavesu specimens, this hypothesis needs

to be confirmed by more consistent geological data.

The ancestor of endemic elephants [an advanced representative of *Mammuthus meridionalis* (NESTI, 1825) or an archaic *Mammuthus trogontherii*] might have entered Sardinia at the Early to Middle Pleistocene transition. Nevertheless, due to scarcity of data, this hypothesis has yet to be fully substantiated.

Suidae

In Sardinia, an endemic suid, *Sus sondarii* VAN DER MADE, 1999 (= *Sus nanus* VAN DER MADE, 1988), was reported from the bone-breccia at Capo Figari (FORSITH MAJOR collection, VAN DER MADE, 1988) and from the paleosoils cropping out at the bottom (CARBONI & LECCA, 1995) and top of the Capo Mannu Formation (= *Sus scrofa* ssp., dwarfed, AMBROSETTI *et al.*, 1980), as well as from Monte Tuttavista fissure fillings from which taxa belonging to "Nesogoral fauna" have also been retrieved (ABBAZZI *et al.*, 2004a). This endemic taxon is characterised by small size, simplified molar structure, especially the talon of M₃, as well as by shortening of the anterior part of the mandible. According to VAN DER MADE (1988), *Sus sondaari* lacks P₁. Nonetheless, at Monte Tuttavista, along with a skull belonging to a young individual ascribed to *Sus sondaari*, a larger hemimandible with an erupting third molar also occurs. This specimen shows simple, smooth enamel and a very short diastema, like *Sus sondaari*, but retains P₁ (ABBAZZI *et al.*, 2004a). All things considered, the hypothesis that this specimen belongs to the endemic Sardinian species *Sus sondaari* cannot be ruled out, and the presence of P₁ may reflect population variability within this species.

In VAN DER MADE's (1999) opinion, the ancestor of the endemic suid (*Sus arvernensis*) entered Sardinia during the Messinian Salinity Crisis.

It is worth noting that *Sus scrofa meridionalis* MAJOR, 1883 has been reported in Dragonara Cave (MALATESTA, 1970). The actual occurrence of this subspecies in the Late Pleistocene still awaits confirmation.

Cervidae

In the Pleistocene of Sardinia, cervid remains, generally ascribed to "*Megaceroides*" or "*Megaloceros*" or "*Praemegaceros*" *cazioti* (DEPÉRET, 1897)¹, are relatively common, mainly in eolianites or cave deposits, attributed for the most part to the Late Pleistocene (cf *inter alios* DEHAUT,

1. The problem concerning the nomenclature of the genera referring to the so-called Megacerini tribu (type genus *Megaloceros* BROOKE, 1828) is still unresolved. Assuming that the species ascribed to the *Megaloceros giganteus* group and those to "*verticornis*" group belong to two distinct lineages, what is the correct generic name to choose among those used thus far for the giant deer belonging to the "*verticornis*" group? From one hand it seems more correct to maintain the name *Megaceroides* (proposed by Joleaud in 1914 as *Cervus* subgenus, with the type species "*Cervus*" *algericus*, established for a fragmentary maxillary from Late Pleistocene Algerian deposits) only for the North African species (see e.g. HADJOUUDIS, 1990; ABBAZZI, 2004). On the other hand, the name "*Praemegaceros*", though not formally correct (see e.g. AZZAROLI, 1979; CALOI & PALOMBO, 1996), was frequently employed, whereas other names, such as "*Ortognoceros*" or "*Psekupsoceros*", have not been *de facto* utilised in more recent times. For this reason, waiting for a formal revision, I provisionally prefer to use the generic name "*Praemegaceros*" for European megacerine as well as, of course, for the Sardinian and Corsican ones (but see also VAN DER MADE & PALOMBO, this volume).

1911; COMASCHI CARIA, 1955, 1956; AZZA-ROLI, 1962; CORDY & OZER, 1973, CALOI & MALATESTA, 1974; CALOI *et al.*, 1981, KLEIN HOFMEYER, 1997; ANTONIOLI *et al.*, 1998; GINESU *et al.*, 1998; MELIS *et al.*, 20023; PALOMBO, *et al.*, 20023; ABBAZZI *et al.*, 2004a; PALOMBO & MELIS, in press).

Initial reports date back to the second half of the 19th century (e.g. STUDIATI, 1857; DEHAUT, 1911); however, it was only in 1935 that Tobien ascribed cervid remains from the Alghero area to the “*Cervus*” *cazioti* species already established by DEPÉRET in 1897 on the cervid remains found at Nonza (Corsica). In more recent times, knowledge of the morphological and biometric characteristics of “*Praemegaceros*” *cazioti* has been increased by the detailed studies carried out by CALOI & MALATESTA (1974), KLEIN HOFMEIJER (1997) and PEREIRA & BONIFAY (1998), based respectively on the large cervid samples coming from the Late Pleistocene deposits of Dragonara and Corbeddu Caves (Sardinia), as well as those in Coscia Cave (Corsica). Other reports from Sardinia and Corsica refer for the most part to sporadic isolated remains (cf. *inter alios* DEHAUT, 1911; COMASCHI CARIA, 1955, 1956; SIGOGNEAU 1960; AZZAROLI, 1961; CORDY & OZER, 1973; CALOI *et al.*, 1981; MELIS *et al.*, 2003) or samples not yet analysed.

Megacerines are absent in the “*Rhagapodemus*” *minor* fauna coming from the Capo Figari I karst fissure, whose age has been hypothesized at approximately 1.8 +/- 20% Ma (ESR on a *Nesogoral* molar, MOTOJI IKEYA, fide VAN DER MADE 1999), whereas scanty remains of a rather large cervid are present at the same locality in the fissure called Capo Figari II, where an archaic arvicolid also occurs. An age of 366,959 +/- 20% years B.p. was obtained using the ESR method applied to cervid tooth enamel (MOTOJI IKEYA, fide VAN DER MADE, 1999).

Large specimens (“*Praemegaceros*” sp.) associated with an archaic vole (*M. (Tyrrhenicola)* n. sp.) have also been reported in the karst fissures opening up at Monte Tuttavista (Orosei, western Sardinia) and tentatively attributed to the early Middle Pleistocene (ABBAZZI *et al.*, 2004), at Santa Lucia (Iglesias, southwestern Sardinia, estimated age about 450 ka, MOTOJI IKEYA, fide VAN DER MADE, 1999) and in the FORSYTH MAJOR collection from Capo Figari. The size of deer from Capo Figari, Santa Lucia and Monte Tuttavista (smaller than their presumed continental ancestor, but much larger than their descendant, “*Praemegaceros*” *cazioti*), suggest they should be attributed to a new taxon (cf. VAN DER MADE & PALOMBO, this volume).

More recently, large deer specimens have been discovered at Su Fossu de Cannas Cave (Sadali). The specimens thus far analysed show some morphological affinities with the endemic Sardinian megacerine “*Praemegaceros*” *cazioti*. However, the Sadali cervid differs from the latter in its larger size, exceeding the variability range calculated for the endemic species, and in some morpho-

logical features (such as the deep, curved *corpus mandibulae*), as well as in its proportionally smaller teeth and particularly its elongated, slender metacarpal (PALOMBO *et al.*, 2003; PALOMBO & MELIS, in press). Tooth proportion would suggest the occurrence of a “non-insular species” (cfr. GOULD, 1975); however, the peculiar morphology of *angulus mandibulae* might be an apomorphic characteristic. The peculiar features of the Sadali specimens suggest their attribution to a new species that should be regarded as the most primitive representative of the “*Praemegaceros*” genus in Sardinia and the ancestor of the endemic Sardinian “*Praemegaceros*” lineage.

The lack of any micromammal remains in both the Monte Tuttavista fissure fillings and in Su Fossu de Cannas Cave deposits makes it difficult to hypothesize the actual date of the earliest occurrence of megacerini in Sardinia. The above-mentioned occurrence in about 450ka of a cervid, possibly intermediate in size between Sadali deer and “*Praemegaceros*” *cazioti*, indicates earlier colonisation (? late Early Pleistocene). The hypothesis that the Sardinian cervid belongs to the “*Praemegaceros*” group is currently widely accepted, as supported by some skull, mandible and tooth features shared by continental and endemic taxa. Megacerine representatives [“*Praemegaceros*” *obscurus* (AZZAROLI, 1953) and related forms] were first reported in Europe in late Villafranchian LFAs. However, on the basis of available data and due to the different opinions expressed by authors regarding the possible ancestor of the large deer endemic lineage of Sardinia and Corsica, migration time cannot be reliably inferred.

Moreover, it is worth noting that during the evolutionary process, Sardinian “*Praemegaceros*” underwent proportional reduction in metapodial length, but acquired a more agile gait on both hard and uneven ground (CALOI & PALOMBO, 1989, 1995) and increased its consumption of dry grass as compared to its possible ancestor (PALOMBO, in press).

Bovidae

In Sardinia, bovids belonging to an endemic taxon have been recognised since the last century, when in 1911 DEHAUT established the new species “*Antilope (Nemorhaedus?)*” *melonii* on an incomplete skull found at Capo Figari (northeastern Sardinia). During the 20th century, FORSYTH MAJOR and Miss BATE collected other bovid specimens at Capo Figari, but it is doubtful that such bones came from the same pocket yielding the holotype. More recently, GLIOZZI & MALATESTA, (1982) have studied new specimens and revised the material belonging to the Bate and FORSYTH MAJOR collections, establishing the new *Nesogoral* genus, described as a small nemorhedine (*sensu* GLIOZZI & MALATESTA 1982). According to VAN DER MADE (1999), *Nesogoral* sp. was present in bone breccias filling the karstic fissure called Capo Figari I (ESR age of 1.807.500 +/- 20%, obtained on a bovid tooth MOTOJI IKEYA, fide VAN DER MADE 1999), along with archaic micromammals such as *T. figariensis* and *P. figaro*. Bovid

remains were also reported from deposits cropping out at the top of the Mandriola Formation (Capo Mannu, west-central Sardinia, late N15 – basal MN16?; PECORINI *et al.*, 1974; ANGELONE & KOTSAKIS, 2001) and in the palaeosoils interbedded within the dune complex outcropping at Capo Mannu (CARBONI & LECCA, 1995; VAN DER MADE, 1999).

More recently, bovid specimens have been collected from six fissures at Monte Tuttavista (Orosei, western Sardinia), where archaic micromammals (such as *Tyrreno-glus* cf. *T. majori*, *Tyrreno-glus* cf. *T. figariensis*, “*Rhagapodemus*” minor, *Prolagus figaro* and *Oryctolagus* aff. *O. lacosti*), carnivores (*Chasmaporthetes melei*, *Mustela* sp., *Pannonictis* sp.), *Macaca* aff. *M. majori* and *Sus* cf. *S. sondaari* have also been recorded. After preliminary analysis, three different morphotypes (“A”, “B” and “C”) have been described by PALOMBO & VALLI (in ABBAZZI *et al.*, 2004), essentially on the basis of horn-core position and shape, frontal bone morphology, pterygo-palatine fossa extension, palate width, tooth-row arrangement and the development and shape of the palatine and pre-maxillary bones in front of the P². Morphotypes “A” and “B” belong to the Caprinae subfamily (*sensu* GENTRY, 1992) and can be ascribed to the “*Nesogoral*” genus. The morphotype “C”, represented by only one incomplete skull, probably belongs to a new genus, distinct from all the Plio-Pleistocene Bovidae previously known in the Western Mediterranean (PALOMBO *et al.*, in prep.). Moreover, it is worth noting that these three morphotypes occur in the same fossiliferous deposit (Cava VI, 3 antica). Moreover, it seems that also bovid remains found in Capo Figari fissure fillings may actually belong to different taxa. Accordingly, the new diagnosis given by GLIOZZI and MALATESTA (1980) for *Nesogoral* genus, as well as for *Nesogoral melonii* species, on the basis of specimens coming from different fissures, has to be reconsidered after a revision of all Sardinian bovid remains previously ascribed to the *Nesogoral* genus.

Plio-Pleistocene endemic bovids were not frequent in insular Mediterranean faunas; the most interesting are Sardinian bovids of the “*Nesogoral*” group and the highly peculiar species belonging to the *Myotragus* lineage from the Balearic Islands. Contrary to findings in *Myotragus*, in Sardinian bovids the face was elongated, orbits were quite large and positioned laterally, no premolars were missing, incisors were not significantly modified and the proportion of metapodials did not differ greatly from that of continental Caprinae species. Indeed, the main morphofunctional modifications exhibited by *Myotragus* representatives are possible only in a carnivore-free environment, whereas the presence of a large predator prevented any reduction in speed or vision system vigilance capability in Sardinian bovids (PALOMBO *et al.*, in press b).

DISCUSSION

The characterisation of islands in relation to colonisation pathways and the evolutionary processes undergone by island settlers has been widely debated. Faunal complexes of terrestrial taxa dwelling in geographically and/or ecologically isolated districts generally include a limited number of species, are less diversified, and are compositionally unbalanced with respect to faunas inhabiting similar, but not isolated, continental biotopes. The low diversity often characterising communities populating isolated geographic areas is the result of interaction among various factors; particularly in the case of terrestrial mammals, the broadness and nature of the barriers and their changes through time are particularly important. The manner and possibility of migration, the filtering and canalization action effected by the barrier may differ greatly according to the ecological flexibility of taxa.

As claimed by several authors (see e.g. SIMPSON, 1965; DERMITSAKIS & SONDAAR, 1978; ALCOVER *et al.*, 1981; LOMOLINO, 1985; PALOMBO, 1985; SONDAAR, 1986; SONDAAR *et al.*, 1996 etc.), the composition of insular fauna, and its variation with the passing of time, depends strictly on the dispersal mechanism, e.g. : 1) balanced fauna lacking or with irrelevant endemic features (thus more or less similar to mainland ones) is the consequence of a broad link to the mainland, acting as a two-way corridor with reduced or no filter action; 2) rather balanced but impoverished fauna, including few endemic taxa, may be related to the occurrence of ecological barriers acting as a filter, avoiding the dispersal of some taxa; 3) unbalanced fauna, including both endemic and mainland taxa, may be related to a pendel route, such as a narrow sea strait, easily crossed by selected taxa (e.g. good swimmers); 4) oligotypical, strongly endemic fauna indicates the presence of persistent rigorous barriers, occasionally crossed (sweepstake dispersal) by a reduced number of selected taxa.

As far as islands are concerned, two zoogeographical types can be distinguished: 1) continental islands, in the past part of a continent to which they were connected by an isthmus or peninsula later submerged by the sea and 2) oceanic islands believed to have arisen beneath the sea and to have never been connected to the mainland (DARLINGTON, 1975). Also taking into consideration the origin of insular faunal communities, a third type of island can be added; 3) oceanic-like islands (*sensu* ALCOVER *et al.*, 1998 and references therein) connected to the continent in the distant past, but then separated from the mainland by a persistent, wide sea barrier.

Depending on different colonisation pathways, terrestrial fauna on continental islands is balanced, although possibly impoverished and including some endemic taxa; fauna on oceanic-like islands is unbalanced and characterised by low diversity and a high degree of endemisation; fauna on oceanic islands is oligotypic and includes a few strongly endemic, very specialised taxa.

Moreover, in the past few decades, several authors have emphasised the role played by different factors in explaining the evolution patterns of unbalanced or impoverished faunas in isolated areas. Nevertheless, no model as yet seems to adequately explain the problems related to the origin and evolution of insular species: this process is actually the result of interaction between several factors whose dynamics vary from island to island or even within a single island. Some authors have attributed major importance to the host-island surface, territoriality, genetic segregation and endogamy, etc., although a lack of selection pressure by large terrestrial predators was considered one of the most important factors affecting population dynamics and evolution in island ecosystems. Indeed, each island has its own faunas; according to the palaeogeographic context, different types of fauna might have inhabited the same island at different times, giving each insular fauna its own history. This is especially true for Sardinia. The discovery of a large hyaenid with a strictly carnivorous diet in the karst fissure of Monte Tuttavista (Orosei, eastern Sardinia) forces one to analyse both the palaeogeographic evolution of the island and the dynamics of processes affecting Sardinian faunas, which became more and more impoverished and ecologically unbalanced during the Pleistocene, in a new light.

As mentioned above, during the late Miocene, Sardinia and Tuscany constituted an isolated paleobioprovince that ceased to exist during the Messinian salinity crisis. Nonetheless, Sardinia was perhaps isolated from Tuscany before the Messinian, since the new immigrants from Europe recorded on the Italian peninsula (see e.g. Brisighella, Emilia Romagna and Baccinello V3, Tuscany, MN13-14 LFAs, KOTSAKIS *et al.*, 1997) have never been found to date in Sardinia. Accordingly, migration routes from the mainland to Sardinia may have been more selective than those in the direction of the Italian peninsula.

The question is: after the Messinian, was Sardinia ever joined to the neighbouring continent, or did new settlers enter by sweepstake dispersal, perhaps crossing a small sea arm separating temporarily-emerged lands?

Data thus far available enable us to single out different biochronologically separate faunal complexes but provide no adequate answer to this question.

From the Pliocene to the Holocene, two Sardinian faunal complexes are better delineated: an earlier, impoverished but balanced complex marked by the occurrence of bovids, suids, glirids, leporid and carnivores (called “*Nesogoral*” fauna above), and a younger, highly impoverished and unbalanced one in which cervids and arvicolids are the symbol taxa (previously called “*Praemegaceros*” - *M. (Tyrrenicola)* fauna). Nonetheless, the fact that some LFAs with bovid and suid (e.g. Mandriola LFAs) belong to the former group is at present only hypothetical. On the other hand, some other lower-rank complexes may be recognised within the latter one.

On the basis of available data, the following faunal complexes may be identified:

“*Nesogoral*” faunal complex

The occurrence of endemic bovids, suids and archaic micromammals typified the earliest post-Miocene Sardinian LFAs. As discussed below, this faunal complex was present during the Pliocene and the beginning of the Early Pleistocene and was probably characterised by local evolution of some lineages, a reduced extinction rate and a moderate immigration rate. This complex may be divided into two subcomplexes.

Mandriola faunal subcomplex

The earliest post-Miocene faunal complex (Early/Middle Pliocene) is characterised by the presence of artiodactyls (small bovids and a suid, *Sus* aff. *S. sondaari*) and archaic micromammals (Erinaceidae, Talpidae, *Tyrrenoglis* aff. *T. figariensis*, *Apodemus mannu*, *Rhagapodemus azzarolii*, *Prolagus* sp. aff. *P. depereti*). We can ascribe the vertebrate remains recorded from a weathered deposit cropping out at the top of the Mandriola Formation (?Early/Middle Pliocene) (CARBONI and LECCA, 1995; MELIS & PALOMBO, 2003), as well as the soricids (*Talpa* p., *Asoriculus* aff. *A. gibberodon*) and a glirid (*Tyrrenoglis* sp. ? aff. *T. majori*) from Nuraghe su Casteddu (Dorgali, Nuoro) (ESU & KOTSAKIS, 1985; ZAMMIT MAEMPEL & DE BRUIJN, 1982; VAN DER MADE, 1999) to this complex. The age of the Mandriola LFA (Erinaceidae and Talpidae indet., *Apodemus mannu*, *Tyrrenoglis* aff. *T. figariensis*, *Rhagapodemus azzarolii*, *Prolagus* aff. *P. depereti*, Bovidae gen. et spec. indet. (?*Nesogoral*), *Sus* aff. *S. sondaari*) has been discussed by a number of authors (cfr. *inter alios* PECORINI *et al.*, 1974; ZAMMIT MAEMPEL & DE BRUIJN, 1982; LOPEZ MARTINEZ & THALER, 1975; ESU, 1986; VAN DER MADE, 1988, 1999). The hypothesis that the endemic species *R. azzarolii* derived from the Early Pliocene continental species *R. ballesioi* leads one to consider this LFA no older than the MN 15 (ANGELONE & KOTSAKIS, 2001), as supported by stratigraphic data (LECCA & CARBONI, 1995; MELIS personal communication, 2003). Therefore, the dispersal of some taxa occurring in this locality (*Rhagapodemus*, *Prolagus*) may be linked to the lowering of the sea level recognised at the Zanclean/Piacenzian transition (HAQ *et al.*, 1987; ANGELONE & KOTSAKIS, 2001). On the other hand, *Tyrrenoglis* possibly represents an advanced form belonging to a Tusco-Sardinian endemic lineage persisting from the Miocene (Fiume Santo, Sardinia, and BaccinelloV2, Tuscany, LFAs); the ancestor of *Apodemus*, as well as the forerunners of bovids and suids, probably entered Sardinia during the Messinian. Moreover, if the cursorial features displayed by the Sardinian suid (VAN DER MADE, 1999) and bovids belonging to the *Nesogoral* group (PALOMBO *et al.*, in press) are actually related to selective pressure by a large predator, we have to hypothesize that the ancestor of *Chasmaporthetes melei* might also have reached the island during the Messinian. Actually, *Chasmaporthetes bonisi* was recorded in Greece during the

Miocene, whereas *Chasmaporthetes lunensis* was present in Western Europe (France, Spain) at the end of the Ruscinian. Nonetheless, no carnivores have thus far been reported from LFAs belonging to the Mandriola faunal subcomplex.

In any case, except for the *Tyrrhenoglis* species, the Mandriola faunal subcomplex seems completely renewed, and its taxa possibly represent the nucleus of the faunal complex that will be present and enriched by new settlers during the Pliocene. In fact, only *Apodemus* seems to have generated no descendants.

Capo Figari/Orosei 1 faunal subcomplex

The Capo Figari/Orosei 1 faunal subcomplex is characterised by the occurrence of new taxa, including some carnivores (the Hyaenidae *Chasmaporthetes melei* and two different mustelids, *Pannonictis* sp. and *Mustela* sp.), *Macaca* aff. *M. majori*, small bovids (Bovidae gen. spec. nov.) and a leporide (*Oryctolagus* aff. *O. lacosti*), whereas micro-mammals (*Talpa* sp., “*Nesiotites*” *corsicanus*, “*Nesiotites*” sp., *Tyrrhenoglis figariensis*, *Tyrrhenoglis majori*, “*Rhagapodemus*” *minor*, *Prolagus figaro*, *Prolagus* sp.), *Sus sondarii* and bovids belonging to the *Nesogoral* group (*Nesogoral melonii*, *Nesogoral* sp.) evolved from mammals already present in the “Mandriola subcomplex”. The Capo Figari/Orosei 1 faunal complex is typically represented by remains found in karstic fissure fillings cropping out at Capo Figari and Monte Tuttavista (Orosei), and by palaeosoils, alternating in the dunes of the Capo Mannu Formation (see *inter alios* CARBONI & LECCA, 1995; GINESU & CORDY, 1997; VAN DER MADE, 1999; SONDAAR, 2000; ABBAZZI *et al.*, 2004a and references therein). Some bovid remains from an unknown locality in the Campidano area (southwestern Sardinia) (VAN DER MADE, 2003) probably belong to the same complex.

The age of the Capo Figari/Orosei 1 faunal complex is questionable. Based on present data, it would appear that the faunal subcomplex took full shape between the end of the Pliocene and the beginning of the Pleistocene, although already identifiable in the late Middle Pliocene. Indeed, at Capo Mannu (Sinis peninsula, west-central Sardinia), a section about 50 m high is visible. This cliff was continuously formed starting from the regressive phase of the Middle Pliocene by sequences of eolianites, calcretes and buried soils (*Formazione di Capo Mannu*) (CARBONI & LECCA, 1995), in arid or humid climatic conditions with either warm or low temperatures (MELIS & PALOMBO, 2003). According to CARBONI & LECCA (1995), the Capo Mannu dune system was probably completed by the end of the Pliocene. At the bottom of the sequence, some remains of *Chelonii*, a leporid, *Sus* aff. *S. Sondaari* and two bovids of different size (perhaps belonging to the “*Nesogoral*” group) were retrieved from buried soils which developed during semi-arid conditions (CARBONI & LECCA, 1995; ABBAZZI *et al.*, 2004b). The larger bovids are slightly superior in size to the samples of *Nesogoral*; ABBAZZI *et al.* (2004 b) considered these bovids as having an endemisation degree

lower than that displayed by Monte Tuttavista specimens. Nonetheless, this hypothesis requires validation due to the dimensional variability of bovids found in Monte Tuttavista deposits. On the other hand, the fragmentary palate and partial mandible of a small suid, found by PECORINI in the buried soil which developed in warm, wet conditions at the top of the section (previously ascribed to *Sus scrofa* LINNAEUS, 1758, cfr. AMBROSETTI *et al.*, 1980), belong to a *Sus sondaari* specimen smaller than those from Capo Figari (ABBAZZI *et al.*, 2004b). Due to limited knowledge of the dimensional range of this primitive endemic suid, one cannot hypothesize a greater degree of endemisation, and consequently a younger age, for the Capo Mannu cranium, with respect to the Monte Tuttavista specimens.

As far as Capo Figari is concerned, it is worth noting that the lists of taxa belonging to old collections are unreliable, since each list possibly includes taxa coming from several fissures, with doubts as to whether these fissures are the ones we know today. In any case, an ESR date of 1.807.500 +/- 20% years B.p. (on bovid tooth enamel by MOTOJI IKEYA, fide VAN DER MADE, 1999) is available for the Capo Figari I LFA, (where *Talpa* sp., “*Nesiotites*” *corsicanus*, *Tyrrhenoglis figariensis*, “*Rhagapodemus*” *minor*, *Prolagus* cf. *figaro*, *Macaca* cf. *M. majori* and *Nesogoral* sp. were present). Thus, the persistence of several taxa belonging to Capo Figari/Orosei 1 is confirmed in the Early Pleistocene.

On the other hand, ABBAZZI *et al.* (2004a) considered the most primitive faunal assemblages from Monte Tuttavista as attributable to the Early Pleistocene, although they did not exclude an older date (late Pliocene?).

Based on the data available, it may be hypothesized that the bovid, suid and carnivore faunal complex took shape over a long time period during which the initial nucleus of taxa that had entered during the Messinian (ancestors of the insectivores, murids and artiodactyls present in the Mandriola LFA as well as possibly *Chasmaporthetes*) was enriched, in the regressive phase of the Middle Pleistocene (about 2.9 Ma, HAQ *et al.*, 1987), by ancestors of *Macaca* (if indeed they had not entered even earlier), *Pannonictis*, *Oryctolagus* and *Mustela*. Several entrances of these taxa, with a migration at the end of the Pliocene as well, cannot be excluded.

If this reasoning is correct, the Mandriola and Capo Figari/Orosei 1 faunal subcomplexes should represent the earliest and youngest subset of that long, persistent faunal complex, the most intriguing and anomalous “insular” complex known thus far.

Actually, this faunal complex is highly distinctive with respect to classic “insular” fauna, as it includes a number of unusual taxa or ones not frequently found in island environments: fauna is impoverished but balanced, although some taxa display a great degree of endemism. Following the model for island evolution, murids and glirids became larger, whereas no important size difference characterised insectivores and macaques.

Apart from their size (changes in bovid size are not assessable), suids and bovids maintain high gear locomotion, contrary to the typical "low gear locomotion" of artiodactyls inhabiting insular carnivore-free environments, but Sardinian bovids show significant hypsodonty and reduction in premolars, as is usual in insular endemic taxa. The reduced size of *Chasmaporthetes melei* should be an effect of insularity, even if dwarfing is usually present in middle-size endemic carnivores (MEIRI, 2004 and references therein), whereas large carnivores become larger in insular environments (e.g. *Ursus arctos middendorffi* bear population, from the Kodiak Archipelago, see e.g. McNab, 2002 and references therein).

Pannonictis, possibly related to the large species *Pannonictis pliocenica*, shows no apparent endemic traits (ABBAZZI *et al.*, 2004a); this absence of modifications is presently difficult to interpret, even if its dependence on a shorter isolation period cannot be excluded.

It is therefore evident that, given the information available at present, many points need clarification before being able to define how Sardinian Pliocene fauna was established and evolved.

The transition to the subsequent faunal complex was characterised by the disappearance of 80 % of taxa, 65 % of lineages, and considerably decreased diversity (PALOMBO, in prep.).

***Microtus (Tyrrhenicola)* faunal complex**

The occurrence of arvicolid belonging to an endemic lineage, *Microtus (Tyrrhenicola)*, characterises the following faunal complex, probably present in Sardinia from the late Early Pleistocene to the Holocene. Actually, during this time, faunal composition progressively changed due to the extinction of taxa persisting from the Pliocene and the arrival of new settlers. This permits the singling out of subcomplexes tending to become more and more unbalanced and impoverished with the passing of time.

Orosei 2 faunal subcomplex

A small arvicolid with relatively archaic features and belonging to a new species, *Microtus (Tyrrhenicola)* n. sp., is reported from Cava X uccelli at Monte Tuttavista, Orosei (GINESU & CORDY, 1997; SONDAAR, 2000; ABBAZZI *et al.*, 2004a; MARCOLINI *et al.*, 2003). Among others, *R. minor*, *O. lacosti*, *Macaca* cf. *M. majori* and *Pannonictis* still occur in the same LFA. Faunal renewal is confirmed by the disappearance of a glirid (*Tyrrhenoglis majori*), the hyaenid, the suid and bovids, the latter substituted by a Caprinae clearly different from those present in "Nesogoral faunal complex" (PALOMBO, in prep.). Moreover, some remains probably belonging to *Cynotherium* also occur.

The existence of a new, primitive species of *Microtus (Tyrrhenicola)* in Sardinia has already been suggested by BRANDY (1978) on the basis of a few molars found at Capo Figari (THALER collection). Even if the actual list of accompanying fauna cannot be definitively clarified, it is

worth noting that *R. minor* and *T. majori* have been reported from the same locality (VAN DER MADE, 1999).

As far as the Orosei 2 faunal subcomplex is concerned, the main question is the actual presence of a megacerine in Sardinia at the time of the first appearance of *M. (Tyrrhenicola)* n. sp.

As mentioned above, deer specimens larger than the cervid found at Santa Lucia and Monte Tuttavista have been discovered at Su Fossu de Cannas Cave (Sadali). The specimens thus far analysed differ from "*Praemegaceros*" *cazioti* in their proportionally smaller teeth and slender and more elongated metacarpal (PALOMBO *et al.*, 2003; PALOMBO & MELIS, in press). Hence, the Sadali deer should be regarded as the most primitive representative of the "*Praemegaceros*" genus in Sardinia and the ancestor of the endemic Sardinian lineage. The ancestor of the megacerine may have entered Sardinia in the same migratory phase as the new bovid and *Cynotherium*.

Nonetheless, the lack of any micromammal remains in Su Fossu de Cannas Cave deposits makes it difficult to hypothesise the actual age of the first occurrence of megacerines in Sardinia. Two different scenarios could be hypothesised: the megacerine and the goat coexisted or the megacerine entered Sardinia later, causing the disappearance of the goat. More data are needed to solve this problem.

On the other hand, a cervid very similar to "*P.*" *cazioti*, clearly larger than that from Dragonara (Sardinia, CALOI & MALATESTA, 1974) and Grotta Coscia (Corsica, PEREIRA & BONIFAY, 1998), considered typical "*Praemegaceros*" *cazioti*, occurs in the Santa Lucia LFA, together with *R. orthodon* and a vole apparently more advanced than *M. (Tyrrhenicola)* n. sp. (VAN DER MADE, 1999). The deer from Santa Lucia is smaller than the Sadali remains and is closer in size to material from Monte Tuttavista, in particular the specimens from the "XI canide", "XI mar2002" and "IX cervo" fissures (ABBAZZI *et al.*, 2004; VAN DER MADE & PALOMBO, this volume; PALOMBO, ARCA & TUVIERO, unpublished data), where *M. (Tyrrhenicola)* *henseli* occurs. Accordingly, the Santa Lucia, "XI canide", "XI mar2002" and "IX cervo" LFAs should be more recent than LFAs with *M. (Tyrrhenicola)* n. sp., and might belong to a different subcomplex. However, it is difficult to formulate any hypothesis regarding the biochronological setting of these faunas, above all when we take into account that the Capo Figari II LFA, with an archaic arvicolidae, *T. majori*, and a bovid smaller than *Nesogoral* (cfr. VAN DER MADE, 1999, fig. 6), has a proposed ESR age of 366,959 +/- 20% years B.p, therefore more recent than the one obtained for the Santa Lucia LFA (450 ka +/- 20% years B.p.) using the same method (MOTOJI IKEYA, *vide* MADE, 1999).

On the basis of the evolutionary trends of micromammals, it would be rational to hypothesize the existence of two distinct faunal assemblages: an earlier containing some taxa pre-existing in the "*Nesogoral* faunal complex", and a

younger more renewed. Nonetheless, awaiting more informative data, we prefer not to propose any subdivisions.

Dragonara faunal subcomplex

This faunal subcomplex, unbalanced and clearly endemic, includes “classic” Sardinian taxa: among large mammals, evolved populations of both *Cynotherium sardous* and “*Praemegaceros*” *cazioti* occur, together with more advanced small mammals (*T. tyrrhenica*, “*N.*” *similis*, *M. (Tyrrhenicola) henseli*, *R. orthodon* and *P. sardus*). The new settler *Mammuthus lamarmorai* is also part of this classic fauna; unfortunately, it is very poorly represented and, moreover, only by isolated remains, never found in association with any other taxa. A characteristic of this Late Pleistocene faunal complex is the sporadic appearance of three highly endemic Lutrinae: *Megalenhydris barbaricina*, *Sardolutra ichnusae* and *Algarolutra majori*. Their high degree of specialisation might have been achieved immediately after immigration; in effect, modifications induced by isolation, such as a decrease in size, can occur in endemic taxa only thousands of years after isolation (see eg. LISTER, 1986). Consequently, it is possible that ancestors of Sardinian Lutrinae arrived on the island when the Middle Pleistocene low sea standing reduced the distance to the continental coast.

LFAs belonging to the Dragonara faunal subcomplex have been found mainly in cave deposits, e.g. at Dragonara, Grotta dei Cervi, Nurighe, Is Oresis, Grotta dei Fiori, Corbeddu and Siniscola, as well as in fissure deposits at Orosei, Capo Figari, Bonaria, Monte San Giovanni, Tramariglio, etc; it is poorly documented in alluvial deposits, e.g. at San Giovanni in Sinis and Gonnese, whereas isolated remains, mainly cervids, have been found in eolianites, e.g. at Alghero, Gonnese, Maritza, Porto Paglia, Porto Vesme, Riola, etc. (cf. *inter alios*: COMASCHI CARIA, 1968; CORDY & OZER, 1973; MALATESTA, 1970; CALOI & MALATESTA, 1974; CALOI *et al.*, 1981; GLIOZZI *et al.*, 1986; MEZZABOTTA *et al.*, 1995; KLEIN HOFMEYER, 1997; ANTONIOLI *et al.*, 1998; GINESU *et al.*, 1998; MELIS *et al.*, 2003; ABBAZZI *et al.*, 2004a, etc).

This faunal subcomplex was present in Sardinia from the latest Middle Pleistocene to the beginning of the Holocene. Actually, during this time, successive evolutionary stages can be detected in some taxa: e.g. “*Praemegaceros*” shows a decrease in size and proportional shortening of metapodials from the Dragonara to the Corbeddu population (CALOI & MALATESTA, 1974; KLEIN HOFMEYER, 1997; PALOMBO, in press), and in *M. (Tyrrhenicola) henseli*, the frequency of advanced morphotypes becomes more and more important (MARCOLINI *et al.*, 2003; PALOMBO, unpublished data). Moreover, elephant remains seem to occur only in the latest Middle or early Late Pleistocene deposits (PALOMBO *et al.*, in press). Consequently, two different groups of LFAs may be identified, respectively typified by the Dragonara and Corbeddu

LFAs.

During the Early Holocene, the number of endemic Sardinian taxa progressively decreases, substituted by mammals accompanying or introduced by the Mesolithic human population. Among the most common large mammals, *Cynotherium sardous* seems to be the first to disappear (latest occurrence at Corbeddu cave, about 14 ka Bp, SONDAAR *et al.*, 1986), followed by deer (latest occurrence at Giuntu cave, west-central Sardinia, about 7000ka, ABBAZZI personal communication). The disappearance of small mammals is curiously related to the relative frequency and abundance of each taxon in Late Pleistocene LFAs: *Talpa tyrrhenica* and *Nesiotites henseli* first disappeared in the Early Holocene, followed by *Ragamys orthodon*, still present during the Neolithic (Grotta del Guano (Oliena), SANGES & ALCOVER, (1980); Grotta Punta del Quadro (Alghero, DELUSSU, 2000) and *M. (Tyrrhenicola) henseli*, recorded from the late Bronze Age (Nuraghe Is Paras de Isili, DELUSSU, 2000). *Prolagus sardus* survived until historical times (DELUSSU, 2000) and seems to have played an important role as an edible resource for the Mesolithic people of Sardinia (VIGNE, 1998; SONDAAR, 2000).

CONCLUSIONS

Currently available data confirm that from the Messinian to the Late Pleistocene-Holocene, several episodes of colonisation from the European bioprovince affected Sardinian, marking more or less important faunal changes that enable us to recognise successive biochronological complexes.

Two main faunal complexes can be recognised: the Pliocene/Early Pleistocene “*Nesogoral* faunal complex” and the latest Early?+Middle Pleistocene/Holocene “*Microtus (Tyrrhenicola)* faunal complex”.

The majority of taxa belonging to the most primitive “*Nesogoral*” faunal complex are clearly endemic Fauna is diversified but impoverished and structurally unbalanced in respect to the Early Pliocene continental faunas. For example, perissodactyls and proboscideans are lacking, as well as taxa highly dependent on humid forest environments. In fact, fauna is made up of a nucleus of species descending from taxa colonising the island in the Messinian via selective routes. Since Hyaenids and bovids cannot swim or float, we should assume that even the ancestors of the chief endemic predator, modified but quite cursorial bovids and the suid, did not colonise overseas or by sweepstake dispersal. Accordingly, we can suppose that *Chasmaporthetes* also reached the islands during the Messinian. In any case, Sardinia was possibly peopled by sweepstake or overseas dispersal by some small mammals at the Zanclean/Piacentian transition. It is difficult to establish whether the occurrences of some other taxa such as *Macaca*, *Pannonictis*, *Mustela* and *Oryctolagus* depend on further Late Pliocene migration. In any case, the

disappearance of the large *Apodemus*, occurrences of more advanced species within pre-existing lineages and the presence of new settlers are bioevents that permit recognition of two distinct faunal subcomplexes (the Mandriola and Capo Figari/Orosei 1 faunal subcomplexes).

As far as palaeobiogeographic history is concerned, one main point requires explanation. At the time of the “*Nesogoral* faunal complex”, should Sardinia be regarded as a continental (as suggested by SONDAAR, 2000 and SONDAAR and VAN DER GEER, 2002) or an oceanic-like island? Actually, some taxa belonging to this faunal complex reached Sardinia when the island was connected to the mainland; thus fauna could be considered a highlyly endemicised “continental” fauna. On the other hand, some other taxa could have reached Sardinia after its isolation by sea routes, or by way of fragmented and temporarily emerged territories. Accordingly, the composition of Plio-Early Pleistocene Sardinian fauna appears absolutely unique with respect to the other faunas from Mediterranean islands known to date.

The second, the “*Microtus (Tyrrhenicola)*” faunal complex, is characterised by the occurrence of new immigrants such as *Tyrrhenicola*, *Cynotherium* and “*Praemegaceros*”, which will remain present during the whole period, or less persistent taxa such as a new Caprinae or *Mammuthus* and lutrines.

The Caprinae is present in the oldest “*M. (Tyrrhenicola)*” LFA, in which primitive voles and archaic populations of *Cynotherium* and “*Praemegaceros*” coexist with some taxa already present in “*Nesogoral* faunal complex” LFAs, such as *Macaca majori* and some small mammals. The ancestors of the vole, canid and caprine might have migrated during the latest Early Pleistocene, probably when periods of lower sea levels led to the temporary emergence of limited areas of the platform, notably reducing the width of eventually-persistent sea-arms (PALOMBO, 1985). Consequently, for this subcomplex, we assume an early Middle Pleistocene age, although a late Early Pleistocene age cannot be ruled out. Therefore, the islands were oceanic-like.

The sporadic faunal migration occurring after this period may be related to occasional spreading. *Mammuthus* and lutrines belong to the more advanced latest Middle-Late Pleistocene faunal subcomplex characterised by the occurrence of typical Sardinian representatives of *Praemegaceros*, *Cynotherium* and small mammals. Their ancestors arrived in Sardinia by overseas colonisation, while later faunal turnovers were strictly linked to human colonisation.

The proposed faunal complexes and relative subcomplexes testify to the evolution of mammalian faunas in the Sardinian insular domain, moving towards progressively more unbalanced and impoverished faunas. Two main colonisation phases and one main faunal turnover are documented, followed by periods of more noticeable isolation during which, however, some settlers entered Sardinia, producing faunal renewal which in some case led temporary

to increased richness.

Nonetheless, these considerations may be confirmed only when new data clarify the numerous doubts remaining, as, for example, the hypothesized entrance in the Messinian of *Chasmaporthetes*, the actual time when *Macaca* appeared and the survival of the primate in the Middle Pleistocene. It is indeed difficult to establish possible times for the migration stages of some taxa, particularly when represented by isolated remains. For example, the coexistence of the first megacerines with archaic forms of *Microtus (Tyrrhenicola)* still needs verification, as well as when cervids arrived on the island, even in view of the doubts relative to their possible ancestor, which could be sought among the continental megacerines reported in Italy in primitive forms in the late Villafranchian [“*Praemegaceros*” *obscurus* (AZZAROLI, 1953)] or among the more highly evolved “*Praemegaceros*” *ex gr. “P.” verticornis* (DAWKINS, 1872) present in faunas correlated with the Jaramillo event.

Ongoing research will contribute to more clearly defining the biochronology of Plio-Pleistocene Sardinian fauna.

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