

The Plio-Pleistocene terrestrial mammals of Sardinia: Biochronology and Faunal Renewals

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Abstract — From the Pliocene to the Late Pleistocene-Holocene, two main mammalian faunal complexes (FCs) can be recognised in Sardinia: the “*Nesogoral*” (Pliocene-Early Pleistocene) and “*Microtus (Tyrrhenicola)*” (late Early Pleistocene-Early Holocene) FCs. Notable fauna renewal characterises the transition between these two major FCs, while individual appearance (origination/immigration) and disappearance (extinction) bioevents permit the distinguishing, in the sphere of each major complex, of two distinct subcomplexes (sFCs): the Mandriola plus Capo Figari/Orosei 1 and Orosei 2 plus Dragonara sFCs.

1. Introduction

Knowledge of Plio-Pleistocene endemic faunas from Sardinia has significantly increased in the last few decades due to new discoveries that have deepened our understanding of Middle-Late Pliocene fauna (Abbazzi et al., in press; Palombo, in press a) and given new information about Middle-Late Pleistocene faunal complexes (Palombo & Melis, 2005; Palombo et al., 2005), shedding new light on the settlement and evolution of post-Miocene Sardinian terrestrial faunas (Abbazzi et al., 2004; Palombo, in press a and references therein).

Our aim is to provide a concise picture of our knowledge of Sardinian mammal biochronology, as well as to illustrate faunal renewals and shifts in diversity from Messinian colonisation up to the establishment of so-called Late Pleistocene “classic Sardinian fauna”.

2. Biochronological setting: historical background and new evidence

Cenozoic mammals from Sardinia have been known since the 19th or early 20th century. For the most part, fossil mammal remains have been found in cave deposits, karstic fissure fillings cropping out in quarries, or natural sections and isolated pockets whose age is in the main approximate or undefined. Some other remains come from aeolian sediments, palaeosoils or localised fossiliferous fluvial-lacustrine or beach deposits, frequently of limited thickness and extension. Therefore, correlations are difficult, and the chronological framework previously proposed for Middle-Late Pleistocene faunas (mainly based on the evolutionary stage reached by arviculids and murids, or on deer size) have been rather approximate (Kotsakis, 1980; Palombo, 1985; Caloi et al., 1988, and references therein). To date, several issues require

clarification: for instance, what is the taxonomical composition of the faunal assemblages found at the beginning of the last century in Capo Figari’s karstic fissures? How many endemic bovids inhabited Sardinia? Did endemic bovids belonging to the “*Nesogoral*” group coexist with the archaic vole *Microtus (Tyrrhenicola)* n. sp. (Brandy, 1978; Abbazzi et al., 2004)? When did *Chasmaporthetes melei* and bovid ancestors migrate to Sardinia? (cf. for example: van der Made, 1999; Palombo, in press a, and references therein).

Recently, Van der Made (1999), revised Sardinian fauna, provided a few absolute dates placing some chronological constraints on so-called “*Nesogoral*” fauna, and confirmed the presence of an endemic “*Praemegaceros*”, at least during the early Middle Pleistocene. On the other hand, the Dutch scholar Paul Sondaar extensively scrutinised Sardinian mammalian taxa and faunal turnovers, mainly in the perspective of more than one (hypothetical) colonisation by humans throughout the Palaeolithic (Sondaar, 2000; Sondaar et al., 1984, 1986, 1995; Sondaar & van der Geer, 2002). Sondaar (2000) suggested that Early Pleistocene “*Chasmaporthetes-Nesogoral* fauna” (impoverished, endemic but rather balanced) had been replaced at the beginning of the Middle Pleistocene by unbalanced “*Tyrrhenicola-caprid* fauna”. This turnover would have been characterised by the arrival of new settlers (in Sondaar’s opinion, possibly including *Homo erectus*), and the extinction of more than 50% of pre-existing taxa. The arrival of deer and archaic *Homo sapiens*” (Sondaar, 2000, pg. 216), as well as the disappearance of *Macaca* and the caprid, would have led to the transition to late Middle Pleistocene-Early Holocene “*Tyrrhenicola-Megaceros* fauna.” Later, Sondaar & Van der Geer (2005) substantially changed the biochronological scheme already proposed by Sondaar (2000), hypothesizing the occurrence of the following faunas: Pliocene/Early Pleistocene *Rhagapodemus*–

caprid fauna (consisting of a caprid, different from *Nesogoral*, *Sus sondaari*, *Chasmaporthetes*, *Apodemus mannu* and *Prolagus figaro*); early Middle Pleistocene “*Tyrrhenicola*”-*Nesogoral* fauna, and late Middle-Late Pleistocene “*Tyrrhenicola*”-*Megaloceros* fauna. As stated by this scheme, “the ancestor of *Nesogoral* (in the author’s opinion, possibly *Galogoral*) came by sweepstake dispersal during the middle Pleistocene on the island” (Sondaar & Van der Geer, 2005, pg. 248). This statement runs counter to a number of data. For instance, *Nesogoral* has been found at Capo Figari I (estimated age of about 1,8 Ma, *vide* Van der Made, 1999), along with archaic micromammals, as well as at Monte Tuttavista, where archaic micromammals, *Macaca* aff. *M. majori* and *Sus* cf. *S. sondaari* have also been recorded (Abbazzi et al., 2004) (Tab. 1). Moreover, *Galogoral* was last reported in the earliest Pleistocene European faunas.

On the basis of currently available data (Palombo, in press a), two main mammalian FCs should be recognised from the Pliocene to the Late Pleistocene-Holocene (Tab. 1): the “*Nesogoral*” (Pliocene/Early Pleistocene *partim*) and “*Microtus (Tyrrhenicola)*” (?latest Early Pleistocene/Early Holocene) FCs. The occurrence of endemic bovids, suids and archaic micromammals typified the earliest Sardinian LFAs. The disappearance of *Chasmaporthetes*, suids and bovids, and the appearance of *Cynotherium*, “*Praemegaceros*” and *Microtus (Tyrrhenicola)* lineages, mark the transition to the subsequent *Microtus (Tyrrhenicola)* FC. Notable renewal characterises the transition between the two major FCs, while individual appearance and disappearance bioevents and anagenetic evolution within endemic lineages enable us to distinguish, in the sphere of the two major complexes, biochronologically-distinct subcomplexes (SFCs). Within the “*Nesogoral*” FC, two SFCs could be detected. In the earliest one, the Mandriola SFC, descendants from endemic pre-existing taxa (*Tyrrhenoglis*) were associated with new settlers (murids, suids and bovids). The more recent “Capo Figari/Orosei 1” SFC (?late Middle, Late Pliocene-Early Pleistocene) is typified by the occurrence, among others, of micromammals which evolved from pre-existing taxa, of *Chasmaporthetes melei*, and bovids, including *Nesogoral*. Within the “*Microtus (Tyrrhenicola)*” FC, in the older “Orosei 2” sub-complex (latest Early Pleistocene- early Middle Pleistocene), new settlers (the archaic vole *Microtus (Tyrrhenicola)* n. sp., *Cynotherium* sp., a large megacrine and possibly a Caprinae) first occurred, together with some pre-existing taxa, whereas the younger “Dragonara” sub-complex (latest Middle Pleistocene-Early Holocene) corresponds to “classic” endemic Sardinian fauna.

3. Faunal diversity and renewal

3.1. Methods

Standing mean richness has been calculated following Harper (Harper, 1975) and Foote’s (Foote, 2000) methods, standardising the number of taxa potentially occurring at a given time interval by considering species richness at the midpoint of each such interval.

Turnover indices between two successive FCs are calculated by means of first appearance and last appearance percentages, normalised using a running mean, as in Torre et al. (1999). In addition, the per-taxon Origination rate plus the Extinction rate and Origination plus Extinction indexes have been estimated, respectively following Foote (2000) and Palombo’s (in press c) equations.

3.2. Results

The standing richness of species and lineages peaks at the time of the CapoFigari-Orosei 1 SFC. Diversity then gradually declines from that time to the end of the period analysed (Fig. 1). It is worth noting that the decrease in richness of phyletic lineages at the time of the Dragonara SFC is more evident using Foote’s method (Foote, 2000) (Fig. 1 B), due to the underestimation of taxa confined to just one interval (N_{FI}).

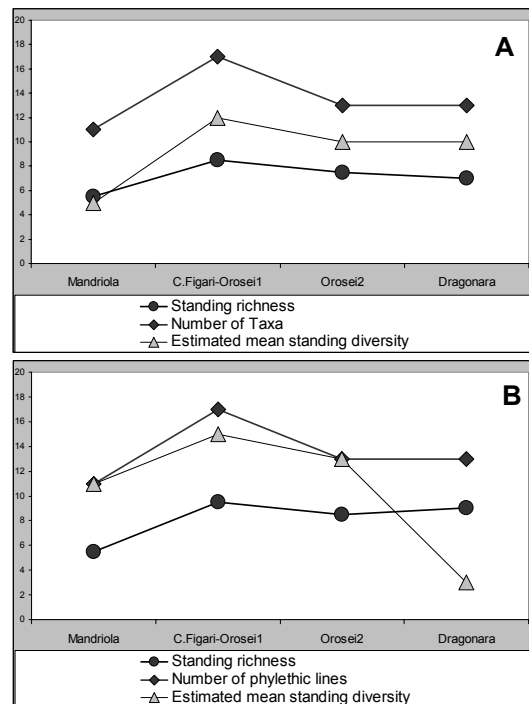


Fig. 1 — Scatter diagram of species (A) and phyletic line (B) total richness, standing richness (as in Harper, 1975) and standing mean richness (as in Foote, 2000), calculated for each faunal subcomplex.

The richness trend is consistent with the origination and extinction indexes calculated at the transition between the two major FCs, since new appearances fail to balance the number of extinctions. Calculation of origination and extinction rates (calculated within each interval and taking into account the probable time span during which bioevents of appearance and disappearance occurred) gives analogous indications. However, it is worth noting that appearances of new taxa, both for immigration (*Mammuthus* and otters) or evolution within phyletic lineages (for example, *Microtus benseli*, *Cynotherium sardous* and *Praemegaceros cazioti*) characterise the Dragonara SFC, despite its low diversity and unbalanced composition (Fig. 2).

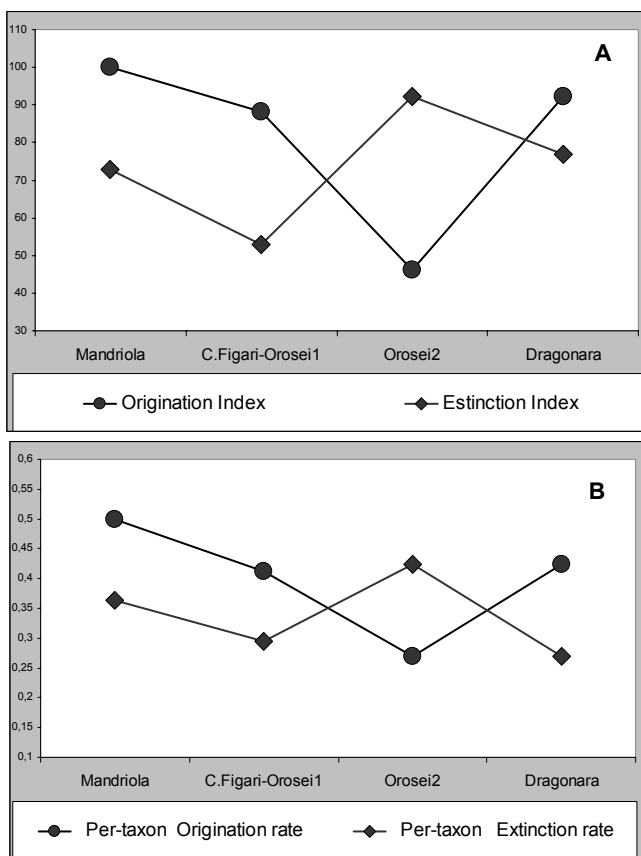


Fig. 2 — Scatter diagram of species origination and extinction indexes (as in Palombo, in press), (A) and origination and extinction indexes (as in Foote, 2000) (B) calculated for each faunal subcomplex.

Notable fauna renewal characterises the transition between the two major FCs: about 47% of the genera and 76% of the species of the “*Nesogoral*” FC disappeared, while the appearance of about 58% of genera and 71% of species typifies the “*Microtus (Tyrrenicola)*” FC. The turnover index is also high (78.26), and the percentage of last appearances slightly higher (%LA=82.60) than that of first appearances (%FA=73.91). Nonetheless, at the transition from

the Capo Figari-Orosei 1 to the Orosei 2 SFC, only genera had a high turnover index. On the other hand, as regards species turnover, the highest index corresponds to the transition between the Orosei 2 and Dragonara SFC, due to the above-mentioned appearance of otters and *Mammuthus lamarmorai*. Nonetheless, these taxa are documented in only a few or only one locality, and are represented by very scanty remains (Fig. 3).

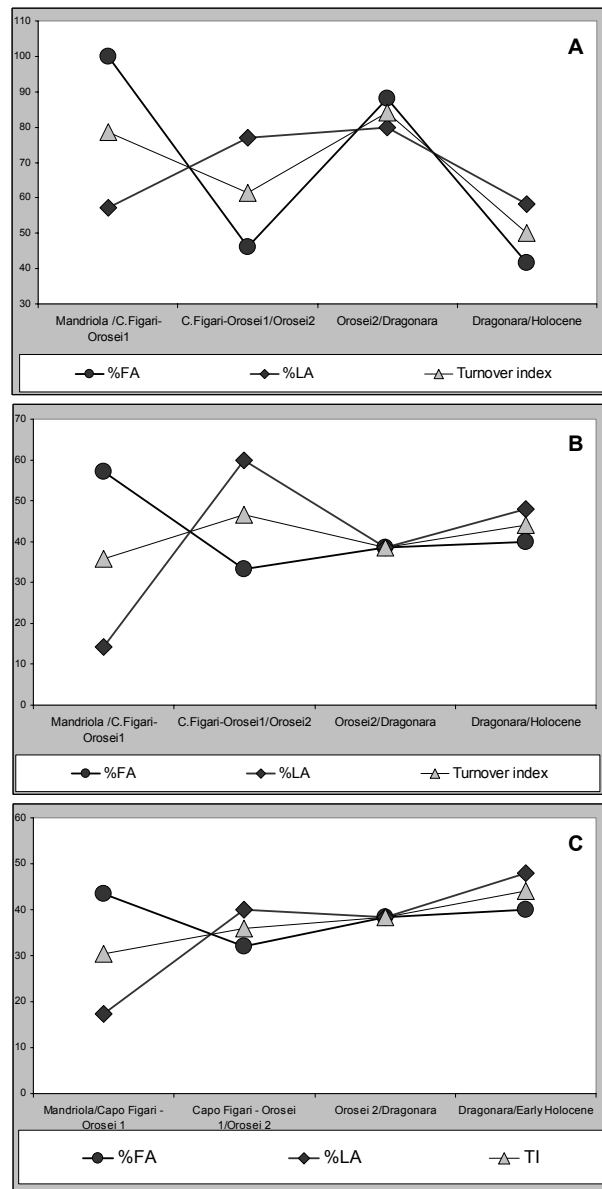


Fig. 3 — Scatter diagram of percentages of first (FA) and last (LA) appearances and Turnover Index (TI) (as in Palombo, in press), (A) calculated at the transition from one faunal subcomplex to the successive one. Species (A), genera (B), phyletic lines (C).

In any case, during the Pleistocene, the number of phyletic lineages progressively decreased, along with, possibly, biodiversity.

4. Discussion and Conclusions

In the past few decades, scholars have for the most part debated on and emphasised the role played by different factors affecting biodiversity, the immigration/extinction rate, evolution and turnovers of extant fauna in isolated areas. In particular, a new conceptual framework for island biogeography stresses differences in speciation, colonisation and extinction among taxa, as well as differences among islands, not only area and isolation, and points out the existence of renewal dynamics that may depart from equilibrium. Actually, especially for terrestrial mammals, the broadness and nature of barriers and their changes in the course of time, long-term island stability, confinement, isolation, and protection from continental invasion and disturbance are particularly important (Walter, 2004 and references therein). Moreover, physical attributes of the island itself, the biological characteristics of settlers, the presence and variety of vacant ecological niches, as well as species interaction (intra- and interspecific competition) and coevolution (allowing origination/extinction bioevents even during periods of complete isolation) play a considerable role in determining the composition and structure of insular fauna over time (Palombo, in press b and references therein).

Actually, we analyse faunal renewals and shifts in diversity as if FCs and SFCs are “blocks of static coordinates”, and consequently in “equilibrium”. Nonetheless, recognising a new species (the so-called chronospecies) within an endemic lineage poses additional difficulties in evaluating faunal renewals, because a new taxon might be only an artificial taxonomic representation, not necessarily representing a true new appearance bioevent. Moreover, it is worth noting that ecologists and evolutionists have been mainly concerned with the question of whether climatic influence or internal dynamics principally drives faunal turnovers. As regards the renewal of insular faunas, and in particular Sardinian ones, we would presume them to be more dependent on colonisation changes than on climate. Nonetheless, geodynamic processes, as well as major changes in climatic conditions (producing sea level oscillations) should produce high turnover rates due to migration and equilibrium disruption. Data thus far available enable us to single out different biochronologically-separate FCs but provide few satisfactory answers regarding colonisation times.

It is well known that during the late Miocene, Sardinia and Tuscany constituted an isolated palaeo-bioprovince that ceased to exist during the Messinian

salinity crisis. Nonetheless, Sardinia was possibly isolated from Tuscany before the Messinian, since the new immigrants from Europe recorded on the Italian peninsula have never been found to date in Sardinia. Accordingly, migration routes from the mainland to Sardinia may have been more selective than those to the Italian peninsula. Nonetheless, the forerunners of some taxa belonging to the Mandriola SFC (*Apodemus*, bovids and suids) probably reached Sardinia during the Messinian. Moreover, if the cursorial features displayed by the Sardinian suids and bovids belonging to the *Nesogoral* group (Van der Made, 2005; 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. *Tyrrhenoglis* possibly represents an advanced form belonging to a Tusco-Sardinian endemic lineage persisting from the Miocene (Fiume Santo, Sardinia and BaccinelloV2, Tuscany, LFAs), while the dispersal of some taxa occurring in this locality (*Rhagapodemus*, *Prolagus*) might have occurred during the lowering of the sea level documented at the Zanclean/Piacenzian transition (Haq et al., 1987; Angelone & Kotsakis, 2001).

In any case, except for the *Tyrrhenoglis* species, the Mandriola SFC was completely renewed, and its taxa possibly represent the nucleus of the *Nesogoral* FC, later enriched by the arrival of new settlers (ancestors of *Macaca*, if indeed they had not entered even earlier, *Pannonictis*, *Oryctolagus* and *Mustela*) during the Middle Pleistocene regressive phase (about 2.9 Ma, Haq et al., 1987). Nonetheless, several migratory phases, including migration at the end of the Pliocene as well, cannot be excluded.

The occurrence of arviculids belonging to an endemic lineage, *Microtus* (*Tyrrhenicola*), characterises the following FC, probably present in Sardinia from the late Early Pleistocene to the Holocene. Actually, during this time, faunal composition changed progressively, due to the progressive extinction of Pliocene taxa and the arrival of new settlers (Tab. 1). The configuration and evolution of Pliocene and Pleistocene Sardinian FCs was probably mainly affected by intra-guild competition. In addition, climatic and environmental changes, negatively affecting the most specialised endemic taxa, should have favoured taxa having a broader niche (the most “flexible” ones).

It seems, however, that during the Middle and Late Pleistocene, internal dynamics drove the evolution of faunal complexes. Colonisation by the ancestor of *Mammuthus lamarmorai* was possibly not successful, giving rise to populations encompassing

only a few individuals that could scarcely compete with deer, the only other large herbivore present on the island.

Sardinian Lutrinae (whose ancestors possibly arrived on the island when the Middle Pleistocene low sea level reduced the distance to the continental coast) could hardly compete with other settlers, due to their peculiar dietary adaptation.

From the latest Middle Pleistocene to the beginning of the Holocene, successive evolutionary stages can be detected in some taxa. For example “*Praemegaceros*” shows a decrease in size and proportional shortening of metapodials from the Dragonara to the Corbeddu population. In addition, within *M. (Tyrrhenicola) henseli* populations, the frequency of advanced morphotypes becomes more and more important (Palombo, in press a and references therein). Moreover, it is not a simple task to determine to what extent faunal evolution might have been affected by the arrival of Upper Palaeolithic human settlers. Actually, a noticeable turnover followed the arrival of Neolithic man and his accompanying fauna, which altered pre-existing equilibriums during a time interval characterised by important climatic oscillations.

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