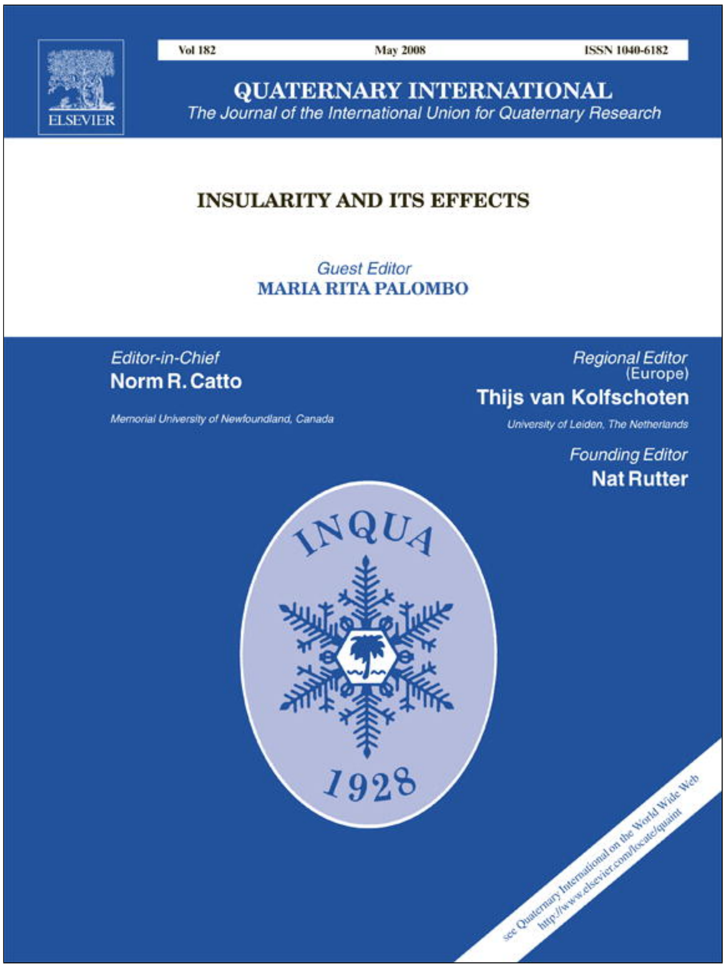
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Origination and extinction patterns of mammals in three central Western Mediterranean islands from the Late Miocene to Quaternary

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Abstract

An overview of the population histories of three insular realms (Gargano palaeo-archipelago, Sardinia–Maritime Tuscany palaeo-bioprovince and the Sicilian insular complex) during the Late Miocene and Quaternary are here presented. The complexity of biodiversity changes in the islands is analysed to propose an interpretation of origination and extinction patterns. The study highlighted several important aspects of insular faunas. Evolutionary radiations were found to contribute significantly only to the Gargano faunal diversity, likely because the area was an archipelago at the time.

Another interesting result is that large and small mammals do not disperse and become extinct all at the same time on each island. In fact, because of their distinct body sizes, large and small mammals have different dispersal ability and therefore different chances to cross-filtering barriers. But distinct body sizes means also different influence on diversity, resistance to environmental changes and likelihood of extinction. Another important point is that large mammalian carnivores at the top of the trophic net are quite more fragile and susceptible to become extinct than other predators.

The study finally shows the clear influence that the intense Middle and Late Pleistocene climate-driven environmental changes had on island communities. The reconstruction of the faunal histories of Sardinia and Sicily shows that without exchanges with the mainland the island system represents a rather stable refuge area not too affected by the changes in the ‘‘physical’’ parameters of the environment. In contrast, if the island is frequently connected with the continent, insular faunal assemblages tend to behave as their mainland counterparts.

1. Foreword

The faunal diversity of an island can be viewed as a balance between origination and extinction processes through time. MacArthur and Wilson (1963, 1967) and their followers Brown and Brown (1977) proposed the renown ‘‘Island Equilibrium Theory’’ to express this concept. The Equilibrium Model predicts that the number of taxa at equilibrium on islands is controlled both by the distance of the island from the mainland and by the carrying capacity of the environment, which is in turn related to the island's extension as well as to several other factors, which include physiography and environmental variety.

The Equilibrium Theory is a very general model which can be applied to the whole spectrum of organisms (plants, invertebrates and mammals). Different kind of organisms, however, have different abilities in dispersing and colonising islands and a different behaviour respect to extinctions. The case of mammalian populations is here considered more in the details with respect to their dispersals and extinctions. Because of their elevated metabolism, mammals, unlike other land vertebrates such as reptiles, need large amounts of food and water. Land mammals are thus not expected to be able to cross-extended deep water expanses. Moreover, large and small mammals are assumed to have different abilities when they colonise islands. Terrestrial mammals are thus expected to reach islands fairly rapidly under favourable palaeogeographic

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circumstances (i.e. the island should be fairly close to the mainland).

Considering the Equilibrium Theory as a starting point, we present here some considerations on how mammalian fauna originate and become extinct in islands. The occurrence of mammals on islands can be roughly explained by four groups of mechanisms.

Firstly, the insular mammals are relics of earlier populations when the island was part of a continental area or of a wider island (vicariance model s.s.). Secondly, mammals reached the island through filtering barriers of various effectiveness (sweepstake dispersals sensu; Simpson, 1940), through moderately wide corridors formed by partially emerged sea floor areas or through lagoons, or through temporary fully terrestrial connections (land bridges sensu; Simpson, 1940). These are the basic mechanisms of the dispersal of the biogeographic model. Another possible mechanism, which can also be assigned to dispersal biogeography, is passive transport on floating islands or by strong marine currents. The former process is obviously not very realistic for large mammals but it could be relevant for small mammals, which, in spite of their very high metabolism and great body surface heat loss, might survive for a while on tangles of vegetation and/or lumps of soil with attached plants. Last but not least, the number of taxa on islands can increase also by in situ speciation events, phylogenesis sensu Heaney (2000) (evolutionary radiation in De Giuli et al., 1986, 1990). This is most likely expected in long-lasting isolated systems as stressed by Heaney (2000).

The first two models are the evident extremes of a whole range of possibilities (Masini et al., 2002b). Vicariance assumes that a barrier appears cuts through a previously continuous geographic region. However, the barrier sets up gradually, so that in the beginning connections grow increasingly more difficult to end into complete isolation. The opposite can be assumed when an insular area gets connected with the mainland. The dispersal mechanisms also represent a continuum, with vicariance at one extreme.

MacArthur and Wilson's theory assumes that extinction rate is controlled by internal factors (i.e. the island's extension and the variety of environmental features) and by interactions with immigrant taxa. More in the details, extinction processes in insular systems may be related to competitive and/or predatory interaction between new comers and residents, to changes in island geography (e.g. reduction or increase of the island area, etc.) in response to geodynamic events (crustal movements), eustatic fluctuations or a combination of both. Global climatic changes and their regional effects may also be a cause of extinction on the insular environment. Eventually, the increasing number of taxa originated by "in situ" speciation events could impact also on the extinction process of other resident taxa. Each factor or process may interact in determining the behaviour of the biological system on each island and in affecting origination and extinction events.

These preliminary considerations represent a theoretical base, which serves as a starting point to analyse and interpret the palaeontological record of insular faunal complexes. In the following sections, the histories of three Mediterranean insular domains are considered. In presenting an overview of the case histories and in the following discussion, we shall focus on the possible mechanisms which gave origin to the population of the three realms, and on those which were responsible of extinction events. A second point regards the question if the differences in ecology and ethology between large and small mammals is also affecting dispersals and survivorship in islands. Eventually, the possible influence of Middle to Late Pleistocene climatic fluctuation on island biodiversity is considered.

2. An overview of three mediterranean case histories

Late Neogene and Quaternary populations of the following insular realms are here considered: the Gargano palaeo-archipelago, the Sardinia–Maritime Tuscany palaeo-bioprovince and the Sicilian insular complex (Fig. 1). The cases discussed below concern sequences of insular populations which can be defined as "polyphasic"—i.e. populations whose faunal components include both ancient elements and more recent ones, which often coexist with different modalities and processes (Masini et al., 2002b). The Miocene and Pliocene palaeogeographic evolution of these three insular domains has been mainly controlled by large and medium scale tectonics, which have modified the geography of the lands (Azzaroli and Guazzone, 1979; Moya Sola et al., 1999; Rögl, 1999; Rook et al., 2006). Such changes also interacted with medium to high order eustatic fluctuations in determining the configuration of lands and their connections.

With regard to Quaternary islands, palaeogeographic control results from the interaction of tectonics, with prevalent uplift and marked semi-periodic glacio-eustatic fluctuations. In the case of Sicily, glacio-eustatic effects appear to have governed late Middle Pleistocene and Late Pleistocene faunal exchanges. Such punctuated pattern, in which short time intervals of favourable conditions for dispersals or connections alternate with long phases of isolation, strongly influences the pattern of origination and extinction which can be effectively observed in the fossil record of islands.

2.1. *Late Miocene–Early Pliocene populations of the Gargano palaeo-archipelago*

Faunal and geological data indicate that during the Late Miocene and Early Pliocene the Gargano area was part of an archipelago (De Giuli et al., 1986, 1987; Abbazzi et al., 1996). In this interval, the configuration of the emerged lands in the palaeo-Adriatic area underwent significant changes that eventually lead to the connection of the Apulian platform to the Apennine chain in the Early

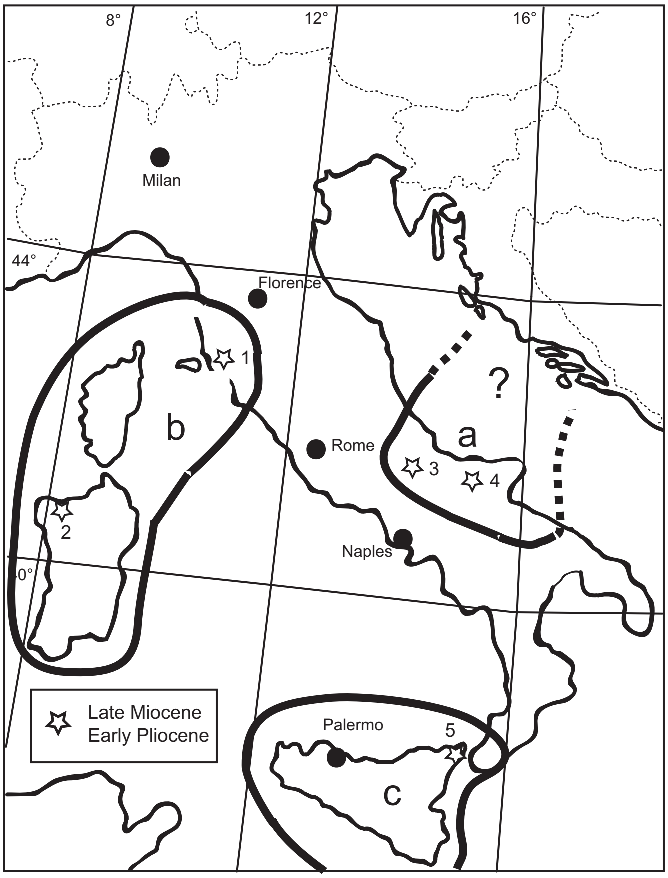


Fig. 1. Location map of the three considered insular domains in the central Western Mediterranean area (a—Apulia–Abbruzzi palaeo-bioprovince; b—Tuscany–Sardinia palaeobioprovince; c—Sicily insular complex). Only Late Miocene/Early Pliocene sites are reported. 1—Maritime Tuscany (Grosseto, Tuscany), various sites, Late Miocene endemic fauna of the Tuscany-Sardinian palaeo-bioprovince; 2—Fiume Santo (Sassari, Sardinia), Late Miocene, endemic fauna of the Tuscany–Sardinia palaeobioprovince; 3—Scontrone (Abruzzo), Late Miocene endemic fauna of the Apulia–Abruzzi palaeobioprovince; 4—Gargano "terre rosse" fissure fillings, (Apricena, Apulia), Late Miocene-Early Pliocene (?) endemic fauna of the Apulia–Abruzzi palaeo-bioprovince. 5—Gravitelli (Messina, Sicily), late Tortonian–early Messinian.

Pleistocene. The occurrence of common faunal elements in the Gargano and at Scontrone (Abruzzo; Southern Central Appennine; Rustioni et al., 1993; Mazza and Rustioni, 1996) shows that the Gargano palaeo-islands might actually represent a late relic of a wider system of isolated lands (De Giuli et al., 1987; Rook et al., 1999, 2000).

The age of the Gargano "terra rossa" faunal assemblages is still debated (cf. Freudenthal and Martín-Suárez, 2006). In the present work the Messinian—Early Pliocene age proposed and discussed by De Giuli et al. (1987), based on both faunal and geological data, is accepted, in agreement with the palaeogegraphic reconstruction of Boccaletti et al. (1990).

The rich endemic vertebrate fauna includes mammals, birds, reptiles and amphibians. The faunal composition is highly unbalanced: the bulk of the assemblage is composed of endemic small mammals (rodents, lagomorphs and insectivores). In the oldest phase of population, however, also some not endemic small mammal taxa occur (Table 1; phase 1a in Fig. 2). Large mammalian taxa are absent and the few middle-sized mammals are represented by strongly endemic ruminants of the family Hoplitomericidae (Leinders, 1984), the strongly endemic gigantic "moon rat" *Deinogalerix* (Freudenthal, 1972; Butler, 1980) and the sea otter *Paralutra garganensis* (Willemsen, 1983) (Table 1). During the time documented by the fissure fillings deposit the faunal diversity changed (Fig. 2) and many taxa underwent significant evolutionary changes and radiations (De Giuli et al., 1986, 1988, 1990).

The Gargano taxa show different degrees of endemism and have potential ancestors of widely different ages (Table 1), so that the origin of the faunal assemblage cannot be reduced to a single event (vicariant and/or dispersive), but rather has a polyphasic origin involving different ages and different mechanisms. The occurrence of the strong endemics Hoplitomericidae and *Deinogalerix* can be interpreted as relics of an older phase, and therefore as a vicariance from a pre-existing and wider bioprovince. The several species of Hoplitomericidae, in fact represent a group of ruminants whose ancestor possibly derived from a Palaeogene "pre Pecora" ruminant stock (Leinders, 1984; Mazza and Rustioni, 2000; Rook et al., 2006), while *Deinogalerix* is an Echinosoricinae whose ancestor also likely dates back to the Oligocene (Butler, 1980; Fanfani and Masini, 1998). The intermediate to moderately endemic "small mammals" found only in the Gargano "terre rosse" area include at least four lineages of different size of the murid *Microtia* (Freudenthal, 1976; Zafonte and Masini, 1992; Abbazzi et al., 1993; Parra et al., 1999), the "normal-sized" moon rat *Galerix* ("*Parasorex*") (Butler, 1980; De Giuli et al., 1988; Masini et al., 2002b), the Crocidosoricinae shrew *Lartetium* (Fanfani, 1999), the dormice *Stertomys* represented by two lineages, one of which very large sized (Daams and Freudenthal, 1985; De Giuli et al., 1990; Freudenthal and Martín-Suárez, 2006, Rinaldi, 2006; Martín-Suárez and Freudenthal, 2007), the hamster *Hattomys* (Freudenthal, 1985b) and two lineages of *Prolagus* (Mazza 1987a, b). The dispersal of the ancestors of these endemics probably is not the result of a single event. Indeed the actual "continental" ancestors of many of these taxa are not yet clearly defined, even if some probably are of Late Miocene European origin (Table 1; Fig. 2). The available information is at present too scant to interpret the underlying mechanism responsible of the presence of these taxa in the Gargano land. On the other side, the origination of two species of *Microtia* (phases 2 and 3 in Fig. 2) and of *Prolagus* (phase 3) is likely due to dispersals from neighbouring islands of the archipelago.

The occurrence in phase 1 (Fig. 2) of the few not endemic taxa, *Apodemus*, *Dryomys*, *Cricetulodon*, *Cricetus*, which are fully comparable with European Messinian and Early Pliocene mainland counterparts, suggest that these latter dispersals were subject to a severe filtering mechanism. A fully emerged connection or a sweepstake dispersal is not

Table 1
Overall taxonomic composition of the Miocene–Early Pliocene mammalian assemblages of Gargano "terre rosse" (after De Giuli et al., 1990, updated)

Order	Family	Genus	Characteristics	Age of the forerunners	Source
Carnivora	Mustelidae	*Garganolutra*	Rare, endemic.	Late Miocene?	Willemsen, 1983
Arctiodactyla	Hoplitomericidae	*Hoplitomeryx*	Strongly endemic, represented by several species with different size and adaptations. Present in Gargano and Scontrone.	Oligocene–Early Miocene	Leinders, 1984
Insectivora	Erinaceidae	*Deinogalerix*	Strongly endemic, represented by at least two evolutionary lineages (five species). Present in Gargano and Scontrone.	Oligocene–Early Miocene	Butler, 1980; Freudenthal, 1985a, b
	Erinaceidae	*Galerix* (*Parasorex*)	Intermediate endemic. Single lineage.	Late Miocene	Fanfani and Masini, unpublished
	Soricidae	*Lartetium*	Not endemic. Single lineage.	Middle Miocene (?)	Fanfani, 1999
Rodentia	Gliridae	*Stertomys* (*large sized*)	Intermediate endemic, giant size. Represented by three species.	Late Miocene (?)	Daams and Freudenthal (1985); Freudenthal and Martín-Suárez, 2006; Rinaldi, 2006; Martín-Suárez and Freudenthal, 2007
	Gliridae	*Stertomys* (small sized)	Intermediate endemic. Represented by several specie	Late Miocene (?)	De Giuli et al., 1990; Freudenthal and Martín-Suárez, 2006; Rinaldi, 2006; Martín-Suárez and Freudenthal, 2007
	Gliridae	*Dryomys*	Not endemic. Rare.	Messinian–Early Pliocene	De Giuli et al., 1990; Freudenthal and Martín-Suárez, 2006
	Cricetidae	*Hattomys*	Intermediate endemic.	Late Miocene	Freudenthal, 1985a, b
	Cricetidae	*Cricetulodon*	Not endemic.	Messinian–Early Pliocene	Freudenthal, 1985a, b
	Cricetidae	*Cricetus*	Not endemic.	Messinian–Early Pliocene	Freudenthal, 1985a, b
	Muridae	*Microtia*	Intermediate endemic, four lineages.	Late Miocene	De Giuli et al., 1990
	Muridae	*Apodemus*	Not endemic.	Messinian–Early Pliocene	De Giuli et al., 1990
Lagomorpha	Ochotonidae	*Prolagus*	Intermediate endemic, two lineages	Late Miocene	Mazza, 1987a, b

likely, since these mechanisms would be expected to allow also large mammals to enter the insular system. One can suggest that these arrivals occurred via floating islands passageways.

The range chart in Fig. 2 also shows that *Dryomys*, *Cricetulodon* and *Cricetus* were retrieved only in the oldest fissure fillings, thus indicating a precocious extinction (Freudenthal, 1985a; De Giuli et al., 1990). Otherwise some of the endemic small mammals, like *Stertomys*, *Hattomys* and two of the lineages of *Microtia*, which are long-lasting forms, become extinct at the end of phase 3 (Fig. 2). The last phase shows a critical drop in faunal diversity before the breakdown of the insular domain (De Giuli et al., 1990; Fig. 2).

2.2. Late Miocene–Pleistocene populations of Sardinia

The Sardinian–Corsican archipelago has also a very long and complex history, related to the geodynamic evolution of the Western Mediterranean basin (Azzaroli and Guazzone, 1979; Rögl, 1999, 2001) which is reflected by mammal populations. The bulk of data here presented (Fig. 3) derive from the reviews of Van der Made (1999, 2005a), Abbazzi et al. (2004a) and Palombo (2006). These papers contain an exhaustive list of references on mammalian fauna of Sardinia. The assemblage of Fiume Santo, according to Abbazzi et al. (2004c), represents the youngest record of the so called "Tusco-Sardinian palaeo-bioprovince" dating to the Turolian (MN12–13?; Kotsakis et al., 1997; Van der Made, 1999; Gallai and Rook, 2004). The large mammal assemblage is very diversified, particularly ruminants (giraffids, the bovids *Tyrrhenotragus*, *Maremmia*, *Etrutria* and Neotragini indet.; Abbazzi et al., 2004c), and is characterised by the occurrence of the ape *Oreopithecus* (Cordy and Ginesu, 1994) and the suid *Eumaiochoerus* (Van der Made, 1997, 1999; Gallai and Rook, 2004). Among carnivores the ursid *Agriotherium* (Palombo, 2004) is

Stratigraphic sequence	phase 1			phase 2	phase 3			phase 4
	a	b			a		b	
samples	F15	F21b	F21c	F1	F8	F9	SG	F32
taxa								
Cricetus	▨							
Cricetulodon	▨							
Dryomys	▨							
Lartetium	▨	▨	▨					
Microtia (small species 1)	▨	▨	▨					
Microtia (medium species)	▨	▨	▨	▨	▨	▨	▨	
Hattomys	▨	▨	▨	▨	▨	▨	▨	
Stertomys (large species)	▨	▨	▨	▨ >	▨	▨	▨	
Galerix	▨	▨	▨	▨	▨	▨	▨	▨
Apodemus	▨	▨	▨	▨	▨	▨	▨	▨
Stertomys (small species)	▨	▨	▨	▨	▨	▨	▨	▨
Prolagus (species 1)	▨	▨	▨	▨	▨	▨	▨	▨
Microtia (small species 2)				▨	▨	▨	▨	▨
Microtia (large species)					▨	▨	▨	
Prolagus (species 2)							▨	▨
number of taxa	12	9		8	9		10	6

Fig. 2. Distribution of Gargano "terre rosse" small mammals occurrences set in chronological order, from older to younger samples (F15–F32). After De Giuli et al., 1990 modified. Legend: shaded rows indicate the distribution of taxa; the sign ">" indicate a phyletic transition within an evolutionary line.

worthy of note. The giraffids and bovids have marked endemic characteristics.

Virtually all these taxa are present also in Maritime Tuscany, and, according to Thomas et al. (1982) and Thomas (1984) the bovids have African affinity. The Fiume Santo fauna indicates that a major connection was established between Sardinia and Maritime Tuscany, and also indirectly with the African continent. Rook et al. (2006), however, rule out a direct connection with Africa on the basis of faunal and geological evidence and suggest that faunas reached the Tusco-Sardinian bioprovince from Europe through a North-Western pathway. The large mammals assemblage, therefore, tells us a very complex palaeobiogeographic history controlled by wide-scale tectonics, in which dispersal phases (foreshadowing the connection among different bioprovinces) alternate to intervals of isolation and endemism.

After the disruption of the Tusco-Sardinian bioprovince, possibly in the late Messinian (Moya Sola et al., 1999; Van der Made, 1999, 2005a; Rook et al., 2006), faunas changed without any relation to the Fiume Santo assemblage. The oldest Pliocene localities are those of Capo Mannu and Mandriola which are not older than MN15 (Middle to Late Pliocene) according to Abbazzi et al. (2004b). These two localities represent a sort of turning point in the island's fossil record. In fact, from this time on, the fossil record turns much more continuous and richer, thanks also to the Monte Tuttavista fissure fillings (Abbazzi et al., 2004a; Palombo, 2006), which range from the latest Pliocene to the Late Pleistocene (Figs. 3 and 5). Capo Mannu-Mandriola phase (Mandriola Faunal Sub-complex in Palombo et al., 2006) yielded a highly unbalanced fauna, mainly composed of small-sized mammalian taxa, whose descendants will become resident taxa, some of which for the whole Quaternary (*Rhagapodemus*-*Rhagamys*, *Asoriculus*, *Talpa* and *Prolagus*). Other taxa (a hedgehog and *Apodemus*) are on the contrary apparently restricted to this phase. Large mammals are represented only by two artiodactyls: the endemic *Sus* cf. *sondaari*, smaller than the suid from the younger locality of Capo Figari (Van der Made, 1988, 1999; Abbazzi et al., 2004b), and the Sardinian endemic Caprinae, *Nesogoral* (Van der Made, 1999, 2005a; Abbazzi et al., 2004b).The following phase (Capo Figari I—Monte Tuttavista 1, = Capo Figari 1/Orosei faunal subcomplex in Palombo, 2006) documents an important dispersal of large-sized mammalian taxa, which include the running hyena *Chasmaporthetes melei*, the mustelids *Pannonictis* and *Mustela putorius* and the Cercopithecidae *Macaca* (Van der Made, 1999; Abbazzi et al., 2004a; Palombo, 2004; Rook et al., 2004). Among small mammals, the dispersal of *Oryctolagus* is also noteworthy. This phase also records the appearance of the endemic bovid *Asoletragus gentryi*, which, however, according to Palombo et al. (2006), may be a relict from a Late Miocene mammalian population. Some of these taxa do not show strong endemic features and two of them apparently soon became extinct (*Chasmaportetes* and *Mustela*). The bulk of the Capo Mannu-Mandriola small mammal taxa is still present (Fig. 3). After the Capo Figari 1—Monte Tuttavista 1 dispersal phase there were few other dispersals to the island: those of the vole *Tyrrhenicola sondaari* (Marcolini et al., 2006a, b), the canid *Cynotherium* sp. (Abbazzi et al., 2004a; Lyras et al., 2006) and the deer *Praemegaceros* (Van der Made and Palombo, 2006). According to Palombo (2006), these dispersals may have occurred close to the end of the Early Pleistocene. The ancestor of *Mammuthus lamarmorai* (documented by few scattered finds of late Middle Pleistocene–Late Pleistocene

Chronology	Tortonian-early Messinian	Midlle-Late Pliocene		latest Pliocene - Early Pleistocene		Early-Middle Pleistocene											Late Pleistocene									
Biochronology	Fiume Santo phase	Capo Mannu phase		Capo Figari 1 - Tuttavista 1 phase		a				b							c									
Taxa	Fiume Santo	Capo Mannu/Mandriola	Nuraghe su Casteddu	Monte Tuttavista Ass.1	Capo Figari I	Capo Figari Thaler	Monte Tuttavista Ass.2	Capo Figari F. M.	Sadali	Capo Figari II	Santa Lucia	Campo Giavesu	Monte Tuttavista Ass.3	Monte San Giovanni	Cava Alabastro A	Cava Alabastro B	Dragonara	Monte Tuttavista Ass.4	Cava Grande A	Cava Grande B	Buggemu	San Giovanni in Sinis	Tramariglio	Fontana Marimenta	Bonaria	Corbeddu 2-3
Small Mammals																										
Gliridae indet.	x																									
aff. *Huerzelerimys turoliensis*	x																									
Erinaceridae indet.		x																								
Apodemus mannu		x																								
Prolagus sp. - *P. figaro*		cf		>	cf	x		x																		
Eliomys (*Tyrrhenoglis*) *figariensis*		aff		cf	x					x																
Talpidae indet.-*Talpa* sp.- *tyrrhenica*		x	x	x	x	>	x			x			x	x	x	x			x							
Rhagapodemus azzarolii-Rhagamys minor-orthodon		x		>	x	x	x	x		>	x		x	x	x	x	x	x		x					x	x
Eliomys (*Tyrrhenoglis*) *majori*			aff	cf		x		x																		
Asoriculus aff. *gibberodon* - sp.-*similis*			x	>	x	x	x				x		>	x	?	x	x	x			x				x	x
Asoriculus corsicanus				x																						
Oryctolagus aff. *O. lacosti*				x			x																			
Prolagus sardus				cf		x	cf			x	x		cf		?	x	x	cf	x	?	?	x				?
Tyrrhenicola sondaari - henseli						x	x	>		x	x		x	x	?	?	x	x	?	?	?			x	x	x
Gerbillidae indet.											?		x			?										
Large Mammals																										
Oreopithecus cf. *bambolii*	x																									
Agriotherium anthracites	x																									
Eumaiochoerus	x																									
Giraffidae indet. (small)	x																									
Giraffidae indet. (medium)	x																									
Tyrrhenotragus gracillimus	x																									
Bovidae indet.	x																									
Maremmia lorenzi	x																									
Neotragini indet.	x																									
Etruria viallii	x																									
Sus aff. *sondaari- sondaari*		x		>				x																		
Nesogoral sp.-*melonii*		x		>	x		aff	x																		
Chasmaporthetes melei				x																						
Mustela putorius				x																						
Sus sp.				x																						
Asoletragus gentryi				x																						
Pannonictis sp.				x			x																			
Nesogoral sp.-*cenisae*				x			>																			
Macaca majori				cf			cf	x								x										
Caprinae gen. et sp. n							x																			
Cynotherium ? sp.-*sardous*							x	x					x				>	x	x						x	x
Praemegaceros sp.- *sardus* - *cazioti*								x	x	>	x		x				>	x	x			x			?	x
Enhydrictis ? - *E. galictoides*								x					sp	x			>									
Mammuthus sp. - *lamarmorai*												x							>			x	x	x		
Algarolutra majori						?											x									
Sardolutra ichnusae						?											x									
Megalenhydris barbaricina						?											x									

Fig. 3. Distribution chart of mammalian taxa in the Sardinia island (after Van der Made 1999; Abbazzi et al. 2004a and Palombo 2006; showing small and large mammals separately. The scheme is updated according to Marcolini et al. (2006a, b), Palombo et al. (2006), Van der Made (2005a), Van der Made and Palombo (2006). Only some of the localities are reported. The major gap in the documentation between Fiume Santo and Capo Mannu phases is indicated by a white column. In the second row the Pleistocene populations phase "a" roughly corresponds to the "Orosei 2" faunal Subcomplex of Palombo (2006); phases "b" and "c" to "Dragonara" faunal Subcomplex of the same author. Legend: shaded rows indicate the range of taxa; sign " × " indicate the occurrence of a taxon in a given locality; sign ">"indicate a phyletic transition within an evolutionary line; the question mark indicate a doubtful occurrence.

age) may have also entered the island during this dispersal phase (Palombo et al., 2005). Meanwhile, the extinction of several taxa caused a drop in faunal diversity and during most of the Middle Pleistocene and the Late Pleistocene the fauna was mainly composed of endemic taxa and no other dispersals seem to have occurred. Instead, some phyletic evolution occurred (eg, the appearance of *Thyrrenicola henseli*, *Rhagamys orthodon*, *Praemegaceros cazioti*, *Cynotherium sardous*, etc.) which indicates a long-lasting isolation of the insular complex. In biogeographical terms during the Middle Pleistocene–Holocene, the Sardinian system became a sort of "oceanic" island. Endemic taxa last occurred in the Holocene. They include only small mammals (e.g. *Tyrrhenicola*, *Prolagus* and probably *Asoriculus*) from Meso-Neolithic anthropogenic deposits. The increasing impact of Neolithic and post-Neolithic

Chronology	late Miocene (MN12-13)		Early Pleistocene	early Middle Pleistocene	late Middle Pleistocene-early Late Pleistocene	early Late Pleistocene	Pleniglacial-Late Glacial	Late Glacial-Holocene	early Holocene
Extimated age of the beginning of each phase			1.6	0.9	0.3	0.07	0.02	0.011	0.01
Extimated duration of the phases			0.7	0.6	0.23	0.05	0.009	0.001	0.005
Taxa	**Gravitelli locality**		**M.Pellegrino F. C.**	***Elephas falconeri* F. C.**	***Elephas mnaidriensis* F. C.**	**Grotta San Teodoro-Pianetti F. C.**	**Castello F. C**	**transition Castello-Holocene**	**Holocene Fauna**
Small mammals									
Asoriculus burgioi			▨						
Hypolagus peregrinus			▨						
Apodemus maximus			▨						
Pellegrinia panormensis			▨						
Maltamys sp.-gollcheri-wiedincitensis			▨	>	>				
Crocidura esuae				▨	▨				
Leithia melitensis				▨	▨				
Erinaceus europaeus						▨	▨	▨	▨
Microtus (Terricola) savii						▨	▨	▨	▨
Crocidura cfr. *sicula*						▨	▨	▨	▨
Apodemus cfr. *sylvaticus*						▨	▨	▨	▨
Lepus europaeus							▨		
Oryctolagus cuniculus								▨	▨
Arvicola terrestris									▨
Glis glis									▨
Large mammals									
Mesopithecus monspessulanum	x								
Machairodus ogygia	x								
Ictitherium hipparionum	x								
Ictitherium orbignyi	x								
Hexaprotodon siculus	x								
Propotamochoerus sp.	x								
"Gazella deperdita"	x								
Bovidae indet.	x								
Parabos ? sp.	x								
Dicerorhinus sp.	x								
Zigolophodon turicensis	x								
Diceros pachygnatus	x								
Mustelercta arzilla			▨						
Vulpes sp.				?					
Ursus sp.				?					
Elephas falconeri				▨					
Lutra trinacriae				▨	▨				
Panthera leo spelaea					▨				
Hippopotamus pentlandi					▨				
Elephas mnaidriensis					▨	▨			
Crocuta crocuta spelaea					▨	▨			
Cervus elaphus siciliae					▨	▨			
Dama carburangelensis					▨	▨			
Bison priscus siciliae					▨	▨			
Bos primigenius siciliae					▨	▨			
Ursus arctos					▨	▨			
Canis lupus					▨	▨	▨	▨	▨
Vulpes vulpes					▨	▨	▨	▨	▨
Sus scrofa					▨	▨	▨	▨	▨
Equus hydruntinus						▨	▨	▨	▨
Equus ferus							?		
Lynx lynx							▨		
Martes sp.							▨	▨	▨
Mustela cfr. *nivalis*							▨	▨	▨
Cervus elaphus							▨	▨	▨
Bos primigenius							▨	▨	▨
Capreolus capreolus								?	
Felis silvestris								▨	▨
Lutra lutra									▨

Fig. 4. Range chart and chronology for the Pleistocene–Holocene of Sicily showing separately small and large mammals (after Bonfiglio et al., 2002a modified. Gravitelli site after Sequenza, 1902, 1907; Thomas et al., 1982; Kotsakis, 1986a; Rook, 1999; Gallai and Rook, 2006). The numerical age estimations in the second row are based on data reported in the Appendix. The ages and durations are expressed in Ma. Legend: shaded rows indicate the distribution of taxa; sign "×" indicate the occurrence of taxa in Gravitelli locality; the question mark indicate a doubtful occurrence; the sign ">" indicate a phyletic transition within an evolutionary line. The major gaps in the documentation between two subsequent phases are represented by white columns.

human colonisation of the island wiped away all the original endemic taxa (Sondaar, 1987, 2000).

2.3. Late Miocene–Pleistocene populations of sicilian insular complex

Sicily's mammalian fossil record is also scattered in time and marked by long stratigraphic gaps (Fig. 5). The Quaternary is the best documented interval, but its record is uneven because of the disproportionate amount of Middle and Late Pleistocene deposits (Masini et al., 2006). Excluding sporadic finds of the mastodon *Gomphotherium* from Burdigalian marine sediments (Kotsakis, 1986a), the oldest Sicilian mammal assemblage is that from Gravitelli (Messina; Figs. 1 and 4). The Gravitelli fauna, which is not endemic, includes Eurasian taxa such as the Colobinae *Mesopithecus* (Rook, 1999), the sabre-toothed *Machairodus*, the suid *Propotamochoerus* (Gallai and Rook, 2006) and the hyaenid *Ictitherium*, alongside two African taxa, e.g. the hippopotamus *Hexaprotodon*, and the bovid "*Gazella*" *deperdita*, which likely belongs to the African subfamily Reduncinae (Thomas et al., 1982; Kotsakis, 1986a). The assemblage was found in a lignite deposit overlain by the Messinian diatomite and gypsum marls of the Sicilian "Gessoso-Solfifera" Formation; it is therefore dated to the late Turolian (MN12–13). Rook et al. (2000) affirm that the Gravitelli fauna attests to the existence of a Late Miocene Calabrian—Peloritan non-endemic palaeo-bioprovince, which is, however, still poorly defined.

After a long late Messinian to Late Pliocene gap, the mammal record starts again in the Early Pleistocene with the Monte Pellegrino (Palermo; Bonfiglio and Burgio, 1992; Bonfiglio et al., 2002a) endemic fauna (Figs. 4 and 5). The poorly diversified fauna is mainly composed of small mammals with different degrees of endemism and of different geographical affinity, which is indubitably of polyphasic origin. *Asoriculus burgioi*, "*Apodemus*" *maximus* and *Maltamys* sp. are endemic taxa, probably relics of an older and unknown fauna (Masini and Sarà, 1998; Petruso, 2003). In contrast, the strongly endemic *Pellegrinia panormensis*, has the typical advanced characters of the African Ctenodactilids, thus indicating a dispersal from that region (Thaler, 1972). *Hypolagus peregrinus*, but even more *Mustelercta* (= *Pannonictis*) *arzilla*, are moderately endemic (Burgio and Fiore, 1988a, 1997; Fladerer and Fiore, 2002). Standing knowledge indicates typical European forms as potential ancestors of these taxa; none were ever found so far in Northern Africa.

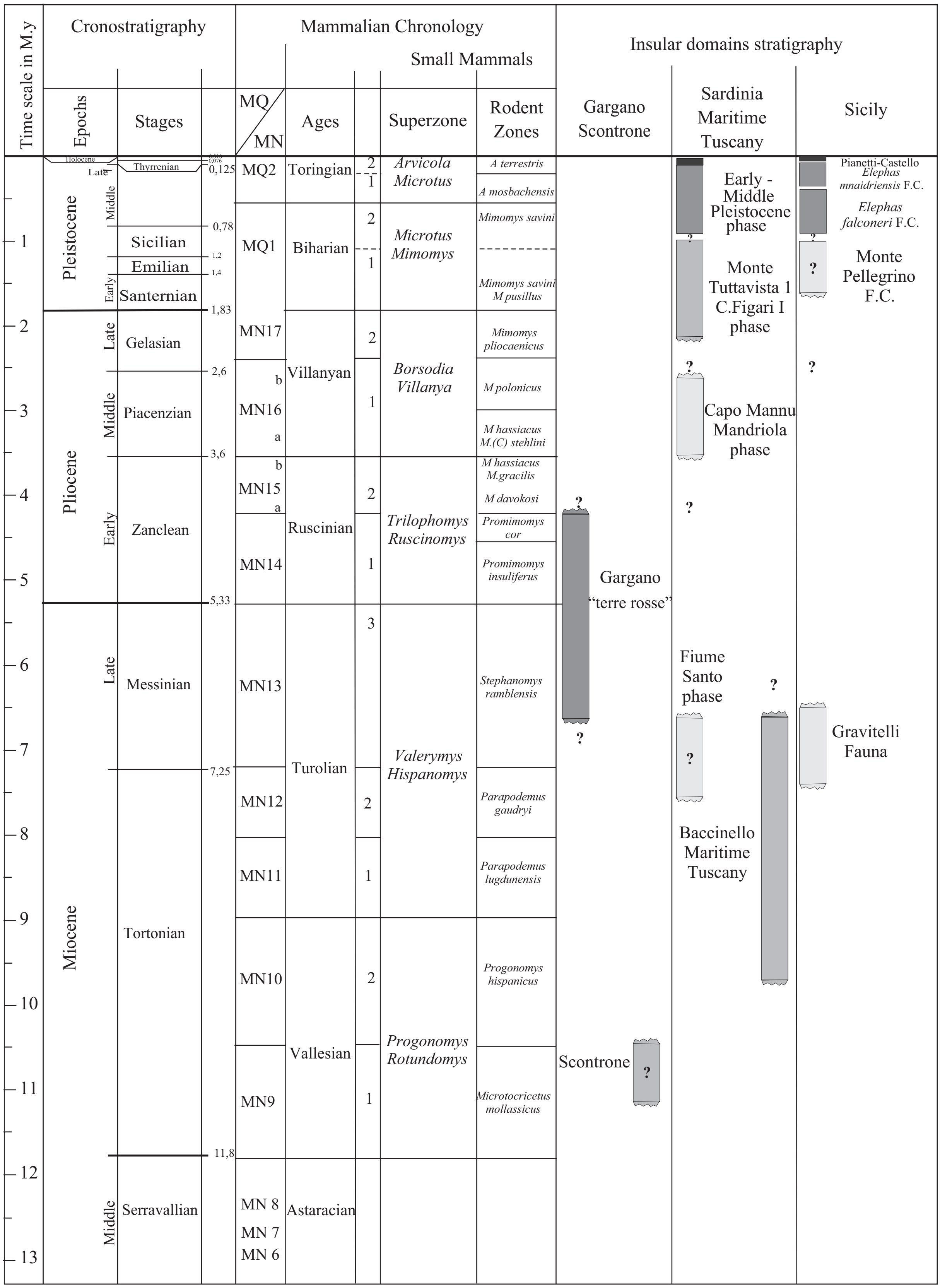
The following *Elephas falconeri* Faunal Complex is also poorly diversified. The only taxon shared with the Monte Pellegrino assemblage is the endemic dormouse *Maltamys*. The assemblage is very unbalanced, as it includes mostly small mammals. The shrew *Crocidura esuae* is an endemite of uncertain biogeographic, African or European, affinity (Kotsakis, 1986b). The Gliridae occur with three species, the giant *Leithia melitensis*, the smaller and very rare *Leithia cartei*, and *Maltamys gollcheri*, which is the probable descendant of the Monte Pellegrino dormouse (Petruso, 2003). Large mammals include the "pigmy" elephant *E. falconeri*, as well as *Nesolutra* (Burgio and Fiore, 1988b). The occurrence of a small bear, as well as that of "*Vulpes*", are considered uncertain and deserve further investigation. The composition of this Faunal Complex reveals a polyphasic origin; one taxon probably is a relic from the preceding phase (*Maltamys*), while the others are "newcomers" which probably entered the island through a strongly filtering barrier. Overall, this F.C. denotes the occurrence of an insular system consisting of very isolated small islands, with difficult and sporadic connections with the mainland (Bonfiglio, 1992; Bonfiglio et al., 2002b).

The *E. falconeri* F.C. is followed by the deeply renewed *Elephas mnaidriensis* Faunal Complex, late Middle Pleistocene–early Late Pleistocene in age (Figs. 4 and 5). *E. falconeri* becomes extinct and is replaced by the larger *E. mnaidriensis*. The large mammal assemblage is more balanced, as it includes carnivore (lion, spotted hyena, wolf) and herbivore taxa (elephant, bison, aurochs, fallow deer, red deer, boar, hippopotamus) which, apart *E. mnaidriensis*, are just moderately modified from the congeneric/conspecific taxa of the Italian Peninsula. The small mammal assemblage includes survivors of the *E. falconeri* F.C. (*L. melitensis*, *Maltamys wiedincitensis* and *C. esuae*). The characteristics of the assemblage suggest that the large mammal fauna dispersed from the Italian Peninsula through a sort of filtering barrier such as a partially emerged sea floor or a swampy lagoon system, which likely has prevented small mammals from entering the island.

The two younger Faunal Complexes (Grotta di San Teodoro–Contrada Pianetti and Castello; Fig. 4), which

Fig. 5. Tentative stratigraphic correlation and distribution of the record of the three insular domains with mammalian chronology (after Fejfar et al., 1998) and chronostratigraphy (after Berggren et al. (1985); Rio et al. (1991), with the following updates: base Piacenzian stage after Castradori et al. (1998); base Zanclean stage after Van Couvering et al. (2000); base Gelasian stage after Rio et al. (1998); base Messinian stage after Hilgen et al., 2000). Legend: the grey columns approximate the estimated duration of the population phases; the lighter grey indicates a reduced number of deposits, the darker grey a richer documentation. The "zig zags" at the extremities of the columns represent the occurrence of major stratigraphic gaps. The question marks highlight the uncertainties of the stratigraphic position and/or of the duration of the population phases.
The age of the Gargano "Terra Rossa" fauna is according to De Giuli et al. (1987) and Abbazzi et al. (1996). The estimated age for the Scontrone fauna is according to Rook et al. (2006). The age of Gravitelli fauna is according to Kotsakis (1986a) and Rook et al. (2000, 2006). The age of the Fiume Santo fauna (MN12–13?) is according to Kotsakis et al. (1997), Abbazzi et al. (2004c) and Gallai and Rook (2004). Baccinello Maritime Tuscany chronological range is according to Rook et al. (2006).

are dated to the last glacial cycle and to the Late Glacial, respectively, show that faunas dispersed more frequently: in fact, the mammalian assemblages of Sicily turn very similar to those of Southern Italy, though less diversified (Bonfiglio et al., 1997, 2001; Masini et al., 2002b). Many taxa disappear (large predators, elephant, fallow deer,



endemic dormice and shrew), while "continental" small mammals (*Microtus* (*Terricola*) gr. *savii*, *Crocidura* cf. *sicula*, *Apodemus* cf. *sylvaticus*, *Erinaceus europaeus*) as well as large mammals such as equids (*Equus hydruntinus* and possibly *Equus ferus*), red deer, aurochs, etc., arrive. The extinction of the endemic small mammals that had survived the whole Middle Pleistocene is probably due to the combination of the Last Glacial severe climatic deterioration with the arrival of small-sized terrestrial predators (for instance *Mustela* and *Vulpes*) via land bridge connection. The only taxon that shows a certain degree of endemism is *C. sicula* (Sarà, 1995). The dispersal to Sicily of the *savii* ground vole, which has a fossorial habit, and of horses, which prefer open landscapes, suggests that a fully exposed connection (a temporary land bridge generated by eustatic low-stand) formed perhaps recurrently during the last glaciation. There was a step-wise replacement of the fauna: in fact, the Grotta di San Teodoro–Contrada Pianetti F.C. still contains several endemites, whilst the Castello F.C. has a completely renewed fauna (Fig. 4).

Between the Late Glacial and the Holocene climatic optimum *Glis* and *Arvicola* disperse on the island, the latter becoming soon extinct during the climatic deterioration that follows the Holocene's climatic optimum (Agnesi et al., 2000; Bonfiglio et al., 2000; Masini et al., 2002a). The dormouse, in contrast, becomes a resident taxa. The extinction patterns of large mammals that had survived from the Castello phase are not well known in the details. The "wild ass" *E. hydruntinus* was widespread in Southern Italy during the Late Glacial and probably became extinct both in Sicily and in the southern Italian Peninsula in Mesolithic times, likely due to the spread of a dense arboreal cover during the Holocene climatic optimum. At last, the red deer and the wild boar were still hunted by Neolithic human populations in Sicily (Tagliacozzo, 1993).

3. Results and discussions

The numerous examples described so far show different aspects of mammalian island biogeography and illustrate the complexity of biodiversity changes in insular domains. Each island's peculiar palaeogeographic history has important consequences on the origination and extinction patterns of its fauna.

1. The distribution and the consistency of the fossil record in the three insular domains seen so far are shown in Fig. 5. The episodic Sicilian and Sardinian Late Miocene–Early Pliocene record consists of "snapshot" (e.g. Gravitelli and Monte Pellegrino in Sicily; Fiume Santo and Capo Mannu in Sardinia) which give the misleading impression of drastic faunal renewals, while they conceal the actual patterns of extinctions and originations and thus prevent from a clear view of the real underlying processes. In the Gargano palaeoarchipelago domain, Scontrone also represents a "snapshot" documentation. In contrast, the Late Pliocene–Pleistocene records of Sardinia and Sicily and probably the Gargano "terre rosse" deposits are more continuous and therefore permit a more reliable interpretation of the origination and extinction of the taxa. Many significant lines of evidence that could permit a deeper understanding of the response of insular systems to originations and extinctions (i.e, changes in vegetation, island physiography and several ecological parameters) are either overlooked by researchers or are simply lacking from the fossil record. The inferences and issues here presented, especially those about the ecological aspects of the islands, are therefore fairly speculative.
2. The Gargano "terre rosse" has the most peculiar faunal succession of all those examined here. It documents the late part of a very long history of endemisation. One of the most important characteristic of the Gargano fauna is its in situ radiation. Gargano is the only case which therefore fits well into Heaney's (2000) theoretical definition. In the other islands here considered, on the contrary, speciation is very rare, perhaps with the only exception of the genus *Leithia*. The Gargano's adaptive radiation was likely the side-effect of the animals' distribution in an archipelago-like ensemble of islands, as stressed by De Giuli et al. (1986). Another aspect enlighten by the Gargano history is that its fauna seems to have benefited of the so-called "advantage of the resident taxa". The prolonged existence of many of its taxa shows that they were very strong endemites. This implies that they had excellently adapted to the peculiar conditions on each of the Gargano's islands. In other instances, the Gargano endemic insular ecology was probably very integrated and coevolved (De Giuli and Torre, 1984). The non-endemic small mammals, which dispersed and precociously became extinct in the oldest phase of the Gargano's fossil record (Masini et al.'s, 2002a, "snapshot extinctions"), were likely latest incomers in the insular system which had not integrated as had the resident taxa. On the other hand, the drastic drop in faunal diversity in the last phase of the endemic population, which also effected the highly endemic small mammalian taxa, may have been triggered by external geodynamic forces which shrank the Early Pliocene Gargano island short before its definitive disruption (De Giuli et al., 1990).
3. The Gargano case history involves mainly small mammalian taxa. Yet we can learn some more comparing the patterns of diversity of small- and large-sized mammals in the other islands examined here. Body size differences influence both ethology and ecology. Large and small mammalian taxa have distinct dispersal ability and therefore different chances to cross-filtering barriers, unlike species diversity, dissimilar resistance to environmental disturbances and therefore different liability of becoming extinct.

Sardinia and Sicily provide us the most evident examples of non-coinciding dispersal and extinction of large and small mammals. In Figs. 3 and 4, one can observe that endemic small mammals usually tend to survive longer than large-sized mammalian taxa which are more "dynamic" as they tend to disperse and to become extinct at a higher rate. One can observe that four of the mammalian taxa which were present in Sardinia in the Middle Pliocene (*Asoriculus*, *Prolagus*, *Rhagapodemus–Rhagamys* and *Talpa*) survive until the Holocene, while none of the large mammalian taxa present in the island in the Pliocene did survive. In Sicily, the glirids and *C. esuae* have the longer survivorship time than any other large mammal (see also Fig. 6).

A tentative representation of taxon survivorship in Sicily, for both small and large mammals, is given in Fig. 6. The duration of the taxa is computed from the age estimate of the phases of population reported in Fig. 4. The date of the beginning of each phase according to the current literature is reported in Appendix. The upper limit of each phase is given by the beginning of the following phase, with the assumption that during the resulting interval the faunal composition remains unchanged. The beginning of the oldest population phases is derived from the estimated age of the deposits which contain the mammal assemblage characteristic of the phase itself. Such dating underestimate the dating of the dispersal events of the single faunal elements of the oldest considered phase. Such methodological choice, however, seems the most reasonable as the beginning of the oldest phases is preceded by a major stratigraphic gap. The compiled data indicates that in Sicily the average duration of small mammals is about 0.4 Ma, more than one third longer than that of large mammals (about 0.25 Ma). Such result must not be considered as definitive, but simply as a first positive clue, subject to be refined by further work. One should note, however, that the obtained duration for the taxa of the oldest complex is a "minimal estimate" and therefore it is expected that future changes hardly will reverse the result.

The longer survivorship of micromammals might be due to the equilibrium they establish with predators such as reptiles and bird raptors, which are always present and abundant in island faunas (Balmann, 1973; Balman, 1976; Delfino, 2002, 2003; Mourer-Chauviré et al., 2001; Pavia and Mourer-Chauviré, 2002; Pavia and Bedetti, 2003; Pavia, 2004a, b; Louchart et al., 2005). Another possible explanation is that small mammals are more prolific and need less food than large mammalian taxa. Hence, the population is less liable to extinction, however drastic an environmental deterioration can be. Conversely, large mammal communities are more

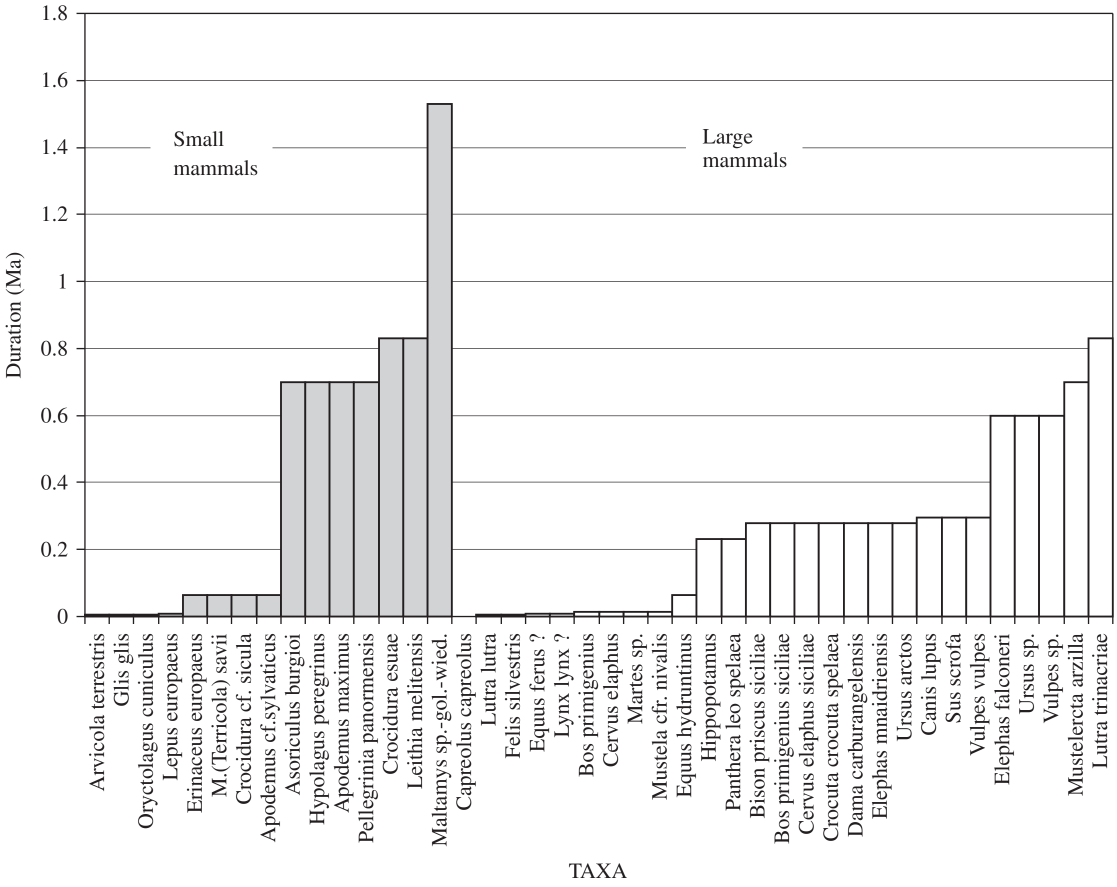


Fig. 6. Histogram illustrating the estimate interval of survivorship of small and large mammals in the Pleistocene of Sicily. The bars of the histogram represent the time duration of the taxa. The numerical data are derived from the duration of the population phases reported in the chronological scheme of Fig. 4 and discussed in Appendix.

sensitive to fluctuations in food availability caused by environmental changes and develop a less stable equilibrium on islands. Moreover, herbivore taxa interact with predators of the same mammalian community, but these are usually very rare in insular assemblages. In this context large-sized herbivores can also become extinct for the dispersal of predators, but also for the arrival of potential competitors from the mainland. The endemic dwarf elephant *E. falconeri*, possibly became extinct because of the immigration of two "top predators" (lion and spotted cave hyena, Masini et al., 2002a) or because of the competition with other larger herbivore taxa of the *E. mnaidriensis* Faunal Complex.

4. The scarcity of large carnivores on islands has long been connected with carnivores' inability to disperse on islands (Sondaar, 1977, 1987). Surviving and adapting to the island ecosystems may be particularly demanding for predators (Van der Made, 1999). Large carnivore populations are normally less numerous than herbivores' and rely primarily on herbivorous prey to survive. Because of the precarious equilibrium of ungulates in insular settings, carnivores, and particularly top predators, are ecologically most vulnerable, and thus more susceptible to become extinct (Van der Made, 1999; Masini et al., 2002a). *Panthera leo*, in Sicily, and *C. melei*, in Sardinia, are good examples. *C. melei* occurs only in a single deposit (Monte Tuttavista Assemblage 1), foreshadowing an early extinction of this running hyena soon after its arrival on the island. Large carnivores which are under-represented in fossil island assemblages, were likely those susceptible to rapid extinction (Van der Made, 1999, 2005b; Masini et al., 2002a). However, sicilian *Crocuta*, which became extinct towards the end of the Late Pleistocene, probably represents a different case. In fact, the spotted hyena survives longer in Sicily than the cave lion likely for its more opportunistic behaviour. The hyaena-formed bone-accumulation at San Teodoro Cave has virtually the same taphonomic characteristics of other similar bone heaps in African and European continental caves. This shows that the ecological conditions under which lived the mammals of the Grotta di San Teodoro–Contrada Pianetti F.C. were not the ones typical of an isolated island. Sicily was therefore connected with mainland areas when the San Teodoro Cave deposits were accumulated (Bonfiglio et al., 2001).
5. This permits some final considerations on the response of these Mediterranean insular systems to climatic-driven extinction. During the Middle to Late Pleistocene, while mainland communities were disrupted by extensive faunal turnovers, the populations of Sardinia enjoyed a period of considerable stability, with only minor morphological changes in its endemic taxa. Sicilian Late Pleistocene faunas, in contrast, experienced the changes and extinction events roughly tracking major faunal events of the Italian Peninsula (hippopotamus, wild ass and spotted hyena; "nearly synchronic extinctions" discussed by Masini et al., 2002a). There is a clearly similar response of the faunas on the two sides of the Messina Strait to the major climatic changes of the time. Of course, also Upper Palaeolithic to Mesolithic human hunter-gatherers contributed to these large mammal extinctions. During the Holocene the ultimate extinction of both islands' endemites was caused by the increasing impact of anthropogenic activities, which include the introduction of predators, competitors, domestic species, stock-rearing and alteration of the vegetation cover. Sicily and Sardinia are placed at medium latitudes and might have experienced climatically driven changes fairly similar to those that occurred in Central-Southern Italy, particularly on the Tyrrhenian side (Masini and Sala, 2006). The reconstruction of the faunal histories of these two islands shows that without faunal exchanges with the mainland, and/or without severe anthropogenic disturbances (as in Sardinia), island systems are fairly stable refuge areas, protected from the climatically induced environmental changes of the Middle and especially of the late part of the Pleistocene. In contrast, if an island is frequently connected with the continent (as was Sicily), its faunal assemblage is fatally doomed to the same fate as its mainland counterparts, even though taxa with temperate affinities tend to survive for slightly longer time (see Masini et al., 2002a).

4. Conclusions

The stratigraphic distribution of mammal assemblages in the three considered insular domains shows that the oldest population phases are separated by long stratigraphic gaps thus preventing deeper insight on mechanisms responsible for the extinction and origination of the faunas. Nevertheless, some general palaeobiogeographic considerations can be carried on. The analysis revealed that almost all the phases of populations recorded in the three systems are of polyphasic nature, and that vicariance episodes alternate to sweepstake dispersals and possibly floating island mechanisms in determining the originations and indirectly influencing also the extinction of insular taxa.

The Gargano "Terre rosse" faunas, the Pliocene–Pleistocene populations of Sardinia and the Pleistocene populations of Sicily are more continuously distributed and are more suitable for a deeper insight. The Gargano sequence of population phases enlighten at least three important aspects. First, the contribution of in situ speciation events to biodiversity in island archipelagos. This process, which has been exhaustively discussed by Heaney (2000) mainly on theoretical and actualistic basis finds in the Gargano an evident fossil example. Secondly, the population history of Gargano gives a fairly convincing example of so-called "advantage of resident taxa". Such phenomenon causes precocious extinction of non-endemic taxa which disperse into a long time coevolved and biologically integrated system of islands. The Gargano also provides indirect evidences of the drop in diversity due to area reduction driven by geodynamical forces. It can be concluded that this cluster of fossil islands, variable in connections and surface, represent an ancient Mediterranean parallel to better known and studied nowadays archipelagoes and deserves further careful investigations.

Another conclusion comes out from the comparisons of dispersal and extinction pattern of large and small mammals in Sicily and Sardinia. The compiled data show that small sized mammals tend to survive for longer time, particularly in systems that remained isolated for long time intervals. Large-sized mammal on the other hand tend to disperse more easily and also more frequently tend to became extinct. The greater stability is expected in small mammals, which, thanks to their limited requirements in quantity of food and a greater fertility, are advantaged in isolated environments which can undergo severe environmental crises. This result also shows that the ecological perspective is crucial for understanding changes in taxonomic diversity in islands. More theoretical and field work is required to develop further insight into these questions. In the same direction is the observation that large carnivores tend to extinguish rapidly in insular environments. Such issue have been first presented by Van der Made (1999) and later by Masini et al. (2002a) and gives a valuable response to why large mammalian carnivores are so rare in islands.

The last conclusion regards the question if and how the island faunas of Sardinia and Sicily are affected by glacial–interglacial climatic fluctuations of the Middle-Late Pleistocene. The result on this topic is not fully expected and opens also new perspectives on the causes of dispersals and extinctions. It appears that in isolated systems no apparent correlation occurs between climatic oscillations and changes of faunal diversity. On the other hand, if an island is close to the continent and separated by a rather shallow sea corridor, the combined effect of climatically forced dispersals and glacio-eustatic controlled formation of land bridges may cause dramatic effects on faunal diversity and composition. This result foreshadows that, at medium latitudes, changes in the environment's "physical" parameters, such as average temperature, precipitation etc., do not impact so strongly on mammalian populations in isolated systems. In contrast, major changes occur when the system is only partially isolated. Such changes are therefore related to the effects of faunal and floral dynamics on the mainland. Such behaviour has important theoretical implications on the responses of the biological systems to climatic–environmental changes, which deserves further investigations.

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Appendix. Estimated ages of Pliocene and Pleistocene mammal phases of Sardinia and Sicily

Sardinia: The age of the beginning of Capo Mannu/Mandriola population phase is assumed at about 3.6 Ma approximating the base of MN16a Zone, according to Palombo (2006). A possible older age for this phase is 4.2 Ma, approximating the base of MN15 Zone, according to the stratigraphical indication of Abbazzi et al. (2004b). The beginning of Capo Figari I/Monte Tuttavista 1 population phase is tentatively placed at about 2.2 Ma according to Palombo (2006). The age of the dispersals that characterise this phase, however, could be older (2.6 Ma ?), as suggested by Abbazzi et al., (2004a). An ESR date on *Nesogoral* remains from Capo Figari I yielded an age of 1.807 ± 0.36 Ma (data reported in Van der Made, 1999). The beginning of the Early-Middle Pleistocene faunal complex as defined by Abbazzi et al. (2004a) (= Orosei 2 Faunal Subcomplex in Palombo 2006) is affected by major uncertainties. The occurrence of *Tyrrhenicola* can provide indirect arguments for a dating, as this vole should be derived from an advanced *Allophaiomys* species. The occurrence of *Allophaiomys* with primitive morphology at Pietrafitta, Cava Pirro and at Soave Cava Sud (Masini and Sala, 2006; Sala and Masini, 2006) suggest that the arrival of *Tyrrhenicola* should be younger than 1.3–1.2 Ma. According to Palombo (2006), it is tentatively assumed that the dispersal of *Tyrrhenicola* and the other taxa characteristic of this faunal complex may have occurred during the low stand of IOS22, referred to at about 0.9 Ma.

Sicily: The age of Monte Pellegrino F.C. is affected by major uncertainties. It is considered here as an Early Pleistocene fauna to which a tentative age of about 1.6 Ma is assigned based on a comparative morphological study of the mustelid *Mustelercta* (= *Pannonictis*) *arzilla* (Burgio and Fiore, 1988a, 1997). The estimated age of the beginning *E. falconeri* F.C. is assumed at about 0.9 Ma. This age estimate corresponds to IOS22, and is indirectly based on correlations of marine terraces bearing fossils of this F.C. with the MIS curve (Di Maggio et al., 1999). The beginning of the *E. mnaidriensis* F.C. is tentatively assigned to an age of 0.3 Ma on the base of ARD by Bada et al.

(1991) and ESR by Rhodes (1996) integrated with correlations to marine isotopic curve in Di Maggio et al. (1999) and Bonfiglio et al. (2003, 2004). The age of 0.07 Ma (IOS4) assigned to the beginning of Grotta di San Teodoro-Contrada Pianetti F.C. is according to Bonfiglio et al. (2003). Recently. a preliminary radiometric ^{230}Th/^{234}U dating carried on a speleothem within a fossiliferous level in San Teodoro cave yielded an age of 32.000 ± 4.000 yr (Bonfiglio et al., 2006). The dispersals that gave origin to the Castello F.C. most likely took place during the Late Glacial Maximum (IOS2) dated 0.020 Ma. However, radiometric ^{14}C dating on Epigravettian levels insist on 0.014–0.011 Ma (Martini, 1997). The age of 0.011 Ma corresponds to the transition between Castello and Holocene fauna. The beginning of the Holocene Fauna is estimated about 0.010 Ma.

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