

The role of coastal areas in the Neogene-Quaternary mammal island populations of the central Mediterranean*

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SUMMARY

The fossil record, even with its severe limitations and uncertainties, provides the only direct access to the chronological and paleogeographical dimension of biological events and processes that took place in ancient insular environments in completely natural conditions.

Terrestrial mammals, unlike other land vertebrates such as reptiles, have a high metabolic rate that requires large amounts of food and water. This would lead one to expect that land mammals could not cross extended expanses of deep water. Differing abilities in colonising islands in large versus small mammals are also expected. One can roughly distinguish three groups of models to explain the occurrence of mammals on islands: 1) Insular mammals are the relics of a previous population (vicariance); 2) Mammals reached the island through filtering barriers of various intensity (dispersals); 3) A third possible dispersal mechanism, is passive

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transport on floating islands or by strong marine currents. This mechanism is poorly realistic for large sized mammals while empirical observations on how this mechanism might operate for small mammals are scant.

Nevertheless, in general, these considerations pose major constraints to the processes responsible for the presence of land mammals in insular domains, and thus to the models that can be employed to explain them.

When the population of islands originates by dispersal, it is likely that those dispersals originated from lands close to the islands, either across direct temporary land connections or by overcoming moderately extended barriers. This model predicts a pattern in which dispersals are not scattered in time but concentrated in precise time zones corresponding to suitable palaeogeographic conditions separated by phases of isolation. Such a pattern can be corroborated or tested by the study of the fossil record and, as will be shown later, can be observed in most cases of populating the Mediterranean islands.

After having traced a synthetic outline of palaeogeographic evolution of the Central Mediterranean area two case histories, Mio-Pliocene Gargano insular domain, and Quaternary Sicilian archipelago are analysed, basing on literature data, searching for confirmation of the expected pattern.

The results can be outlined in a number of issues. A first consideration, is that the complexity of real cases cannot be reduced to classical models (dispersive and vicariant) without unacceptable simplifications. Secondly, the concept of 'polyphasic' populations appears to have great value when applied to unravelling the history of island populations. This term means a faunal population in which, in a given time zone, faunal elements derived from more ancient population phases coexist with elements of more recent events, often with different modalities and processes. Thirdly, there is actually an evident difference in behaviour between large sized and small sized mammals with respect to island colonisation. For small mammals the 'floating islands' model may be important. Fourth, the ecological conditions on islands apparently plays an important role in controlling biodiversity and extinction in insular environments and deserve further and deeper investigations. Last but not least, more investigation on new fossil localities is needed to enhance the quality of models and testing. With regard to model development, model testing and interpretation of case histories, it is evident from the present work that a "cross checking" strategy is the most effective: acquiring as much information as possible from as many sources as possible, and using multidisciplinary information to constrain models and results.

1. THE CONTRIBUTION OF THE FOSSIL RECORD TO ISLAND MAMMALIAN BIOGEOGRAPHY

The nature of the fossil record, particularly of organisms living in continental environments, is strongly discontinuous and incomplete. Fossil assemblages are

distributed as 'points' in time and space and do not represent a continuous record of faunal and palaeobiogeographic changes, but only 'snapshots' of a single moment and situation. Spatial (geographic) discontinuity is related to a variety of intense destructive processes occurring in the continental domain: fossilisation takes place predominantly within particular environments, which are geographically scattered, such as caves, karst fissures, lakes, swamps, lagoons, and soils. Time scattering of fossil assemblages is the result of discontinuities affecting sedimentation and depositional processes in such environments, and of intensely destructive taphonomic and diagenetic processes. Indeed, each step of the taphonomical processes responsible for fossilisation and preservation of fossils requires several favourable conditions to occur at the same time. This co-occurrence cannot be expected to last very long, since environmental conditions are mutable over time.

Moreover, natural fossil assemblages are not usually representative of the whole local faunal population; their composition being deeply influenced by the nature of sedimentation and fossilisation environments and by relevant taphonomic processes. For instance, in deposits formed within a cave or a karst fissure, which often act as concentration traps, small mammals and sometime carnivores tend to be over-represented, while ungulates are more common in limnic and fluvial deposits. The role of stratigraphy is to organise all this scattered information in a coherent space-time frame.

Taxonomy and systematics based on fossils are also problematic since the usual uncertainties and difficulties which affect zoological taxonomy are made worse by the fact that fossils in most cases are represented only by fragmented, incomplete skeletal remains. Only a few of the many potential characters of an organism can be observed, and the available incomplete skeletal material does not always contain suitable information for systematic purposes. In the case of fossil taxa from islands, systematics and especially phylogeny, are affected by additional uncertainties because of endemic evolutionary modification. In the case of long-lasting geographic isolation, the changes in endemic forms may be so great as to make the detection of the ancestral taxon impossible (e.g. *Deinogalerix* from the Gargano paleo-archipelago, *Myotragus* from the Balearics).

Nevertheless, even with its severe limitations and uncertainties, the fossil record provides the only direct access to the chronological and paleogeographical dimension of biological events and processes, and thus to the biogeographic history of an area. In some cases, such as very ancient islands, palaeontology is the only possible approach.

Moreover, the fossil record documents processes that took place in completely natural conditions, while the actualistic approach must take into account modification of faunal assemblages due to human activities. Although human modification may be negligible in some geographic areas and environments, such as tropical forests and deserts, in the case of islands anthropogenic disturbance

might have had a dramatic effect given the isolation, limited area and fragility of insular environments (e.g. Fofopoulos and Ives, 1999). In the case of Mediterranean islands, data on the impact of Palaeolithic colonisation are rather scant (Sondaar, 1987). Apparently hunter-gatherer Palaeolithic populations had little impact on insular faunas as shown, for instance by faunal data coeval with the late Palaeolithic (Lateglacial) human occupation of Sicily (Tagliacozzo, 1993). In contrast, the bulk of evidence shows that anthropogenic impact becomes important, starting with the widespread Neolithic colonisation of islands (e.g. Vigne, 1988, Tagliacozzo, 1993). Introduction of alien wild taxa from the European continent, for instance, may cause extinction of endemics by competition and/or predation. The same effect can be produced by human overkill of particular insular species of large mammals. Perhaps even more drastic changes are caused by irreversible environmental modifications and habitat fragmentation related to agriculture and keeping of livestock, including the introduction of domestic animals that in some cases may return to the wild (feral taxa). It is not just a matter of chance that nowadays almost no endemic mammalian taxa are present in the Mediterranean islands and archipelagos, whereas there are several endemics amongst the herpetofauna (Corti et al., 1999a,b) and avifauna.

2. REFLECTING ON MODELS

Terrestrial mammals, unlike other land vertebrates such as reptiles, have a high metabolic rate that requires large amounts of food and water. This would lead one to expect that land mammals could not cross extended expanses of deep water, but there are some exceptions.

It is possible to refine such a very general statement, taking into account also other factors such as body mass, ecological adaptation and ethology (see also Zunino and Zullini, 1995). During the Tertiary, mammals display a wider range of sizes than any other vertebrate group; as size is often a feature strictly linked to the evolutionary history and general adaptations of clades (Kelt and Brown, 1998). Body size could be a discriminating factor when considering ability to cross open-sea barriers. A large-sized mammal is in principle more capable of facing extended periods of stress and actively following a given route than a small mammal. The latter has less reserves, a relatively higher metabolic rate and greater heat loss through the body surface.

Adaptation is another factor that could influence dispersals. For instance, otters and hippos have an aquatic or semi-aquatic way of life and are commonly found in island populations, while, on the contrary fossorial Arvicolidae are very rare.

In addition, last but not least, an important role is played by behaviour. Some non-aquatic mammals are known to be very confident in water. For example,

elephants and deer, which are good swimmers are commonly found in the Quaternary mammalian population of islands. Also in general, large sized taxa tend to have more complex and flexible behaviour than small ones, probably reflecting a relatively larger brain size: ethological flexibility may influence the effective capability of dispersal in many subtle ways.

All these factors play roles of differing importance in determining the ability, and enhancing the probability, for different taxa to disperse through major barriers such as open sea corridors. These factors should be considered when approaching the study of faunal dispersal on islands.

Nevertheless, in general, these considerations lead one to expect differing abilities in colonising islands in large versus small mammals, and pose major constraints to the processes responsible for the presence of land mammals in insular domains, and thus to the models that can be employed to explain them.

Taking the above issues into account one can roughly distinguish three groups of models to explain the occurrence of mammals on islands.

1) Insular mammals are the relics of a previous population phase when the land was still connected to the mainland (vicariance model; Grande, 1990, Zunino and Zullini, 1995).

2) Mammals that reached the island through filtering barriers of various intensity (moderately wide sea corridors, partially emerged sea floor, lagoons), or through temporary fully terrestrial connections ('land bridges').

3) A third possible mechanism, that also belongs to the dispersal models, is passive transport on floating islands or by strong marine currents. This mechanism is obviously not very realistic for large mammals but it could be relevant for small mammals, which, in spite of their very high metabolic rate and heat loss through the body surface, might survive for a while on tangles of vegetation and or lumps of soil with attached plants. However, transport by floating islands requires a series of conditions to be met. These conditions include, for instance: extensive tree cover on the continental area for the formation of a floating island; the presence of large rivers on the coast line in proximity to the islands, and marine currents which are directed so as to allow the 'docking' of these floating islands. Empirical observations on how this mechanism might operate for small mammals are scant.

A clue that supports the possibility of this unusual mode of dispersal of small mammals can be found, for instance, in the vertebrate population of the oceanic island of Sao Tome (the major island on a line of volcanic islands in the Gulf of Guinea). Even at first glance, the faunal list reveals an imbalance in biodiversity among reptiles and birds on the one hand and mammals on the other. Reptiles and particularly birds are represented by several endemic species (Schatti and Loumont, 1992) while mammals, apart from taxa directly or indirectly derived by

anthropogenic activity (*Mus*, *Rattus*, *Sus*, *Mustela nivalis*, a monkey), include five bats (three of which are endemics) and a single land mammal – an endemic shrew of the genus *Crocidura* (Heim de Balsac and Hutterer, 1982; Feiler, 1998). Given the volcanic origin of Sao Tome, its considerable distance from any coast mainland and from the nearest volcanic island (about 250 and 150 km respectively), and the depth of the sea floor (more than 2000 m), it is not realistic to invoke a vicariant model for the terrestrial mammals. Dispersal step by step through the volcanic line cannot be excluded *a priori*, even though this is unlikely for small mammals (see second section for discussion). We feel that passive transport on floating islands (rafting) carried by marine currents is the most likely dispersal process (but see also Heim de Balsac and Hutterer, 1982, for a discussion). The presence of the mouths of big equatorial rivers (Niger, Congo) in the Gulf of Guinea and of currents directed towards the islands makes this interpretation very feasible. Therefore, the presence of an endemic species of *Crocidura* on Sao Tome suggests that, even though rather an uncommon mechanism, rafting can transport small mammals to islands across wide expanses of sea.

Reflecting on the models, and taking information on geodynamic evolution into account, it is apparent that the first two models are the extremes of a continuous range of possibilities. Vicariance assumes that a barrier appears and divides a previously continuous geographic region. However, in the case of islands the barrier will develop gradually, so that in the initial phases we shall pass from a situation of increasingly difficult connections (dispersal can occur) to complete isolation. The opposite can be assumed to occur when an insular area becomes connected to the mainland. In contrast, the dispersal models can also be seen as a continuum, with vicariance as one extreme. For instance, if eustatic and/or tectonic lowering of sea level causes the emergence of a coastal area thus connecting an island to the continent, this process should be somewhat gradual. At first, the width of the (sea) barrier will decrease, as the coastlines of the island and the continent approach each other, followed by the formation of a filtering barrier, and eventually the sea floor could emerge completely producing a full connection.

From the above arguments it is apparent that, in principle, island mammalian populations seldom originate by purely random (chance) events (see also Zunino and Zullini, 1995, on this topic). With “random events” we mean events evenly distributed in time, such as those assumed as determining colonisation (origination) rates in the classical biogeographical island biodiversity model of Mac Arthur and Wilson (1963). Therefore, when the population of islands originates by dispersal from elsewhere, it is likely that those dispersals originated from lands close to the islands, either across direct temporary land connections or by overcoming moderately extended barriers. This model predicts a pattern in which dispersals are not scattered in time but concentrated in precise time zones corresponding to suitable palaeogeographic

conditions separated by phases of isolation. A sort of 'punctuated' succession – to paraphrase evolutionary theories. Such a pattern can be corroborated or tested by the study of the fossil record and, as will be shown later, can be observed in most cases of populating the Mediterranean islands.

3. MEDITERRANEAN PALEOGEOGRAPHIC EVOLUTION IN THE NEOGENE AND QUATERNARY

The Mediterranean area has been characterised, since the beginning of Mesozoic, by very active geodynamics, since it forms a belt in which two large lithosphere plates interact (African and Eurasian plates). This complex interaction has determined the formation of several highly mobile micro-plates, a sort of mutable mosaic.

In the Neogene and the Quaternary the palaeogeography of the Central Mediterranean insular realms underwent an intense evolution related to the opening of the Tyrrhenian Basin and the folding and uplifting of the Apennine chain.

Considering paleogeographic data strictly derived from geology and the relevant paleogeographic reconstructions, two phases characterised by different behaviour can be recognised. During the Oligo-Miocene and in the early Pliocene the main role is performed by large scale tectonics, prevalently translational, which have modified the geography of the land above sea level, forming and interrupting connections between the various areas. Such changes interacted with medium to high order eustatic fluctuations (for details see Vail et al., 1977, Vail and Hardenbol, 1979). Perhaps during the Messinian tectonic events triggered off important eustatic sea level changes because of the unbalanced evaporation regime in the Mediterranean (Salinity Crisis). Large scale paleogeographic maps available to date give rather broad indications of the land configuration, but lack the detail necessary for detailed reconstruction of the extension and connections of insular domains. The maps concerning the palaeogeographic evolution of the Mediterranean during the Miocene (from ~23 to ~10 my) reported in Fig 1, give a good idea of the broad changes, but are, however, deficient in the details.

With regard to Plio-Quaternary islands, palaeogeographic control results from the interaction of tectonics, with prevalent uplift and marked semi-periodic glacio-eustatic fluctuation (Shackleton, 1995) that characterise the Bipolar Cryosphere (Fig. 2). Glacio-eustatic effects appear to have dominated in controlling faunal exchanges during the late Middle and Late Pleistocene (Fig. 3)

4. STUDIED CASES

The cases discussed below concern insular populations that can be defined as 'polyphasic'. By this term we mean a faunal population in which, in a given time

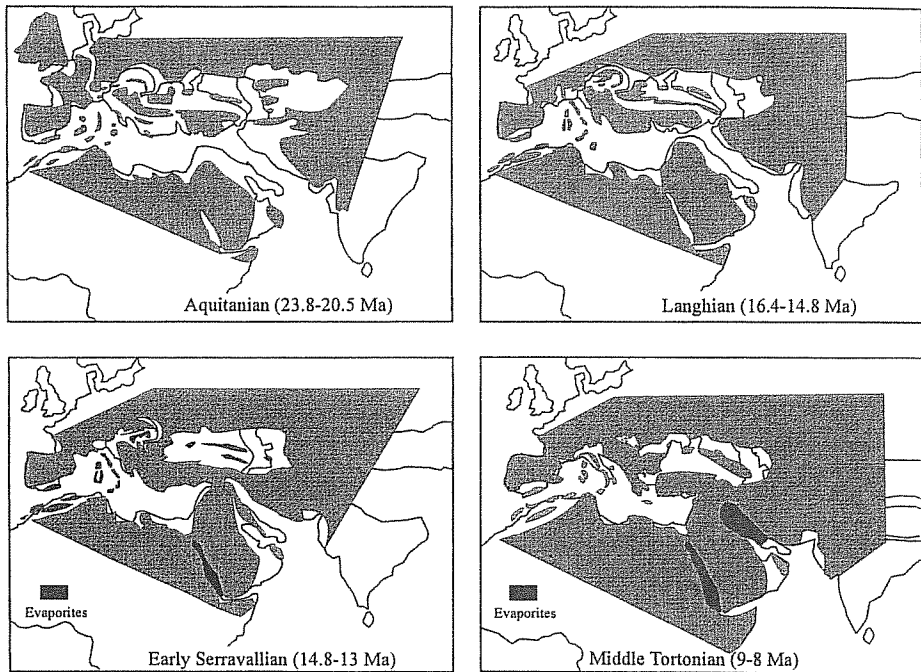


Fig. 1 - Miocene paleogeographic evolution of the Mediterranean area. From Rögl (1999) modified

zone, faunal elements derived from more ancient population phases coexist with elements of more recent events, often with different modalities and processes. Polyphasic faunal populations are common in all Mediterranean islands which have a rather long and complex history, e.g. Sardinia-Corsica, Balearics, Sicily-Malta and Gargano.

We present here two cases in which historical reconstruction has been worked out in some detail, and we discuss the predominant mechanisms that have determined the succession of population phases.

a) Neogene populations of the Gargano insular domain

The Gargano “terra rossa” faunal assemblages, late Messinian-early Pliocene in age, are found in sediments derived from soils which filled an extensive karst system (*Kluftakarren*) developed within Mesozoic carbonates over a significant period of time (Abbazzi et al., 1996). Some scattered finds of this assemblage also occur near Trani (Freudenthal, 1971).

The rich endemic vertebrate fauna collected in the Gargano area includes mammals, birds, reptiles and amphibians. The faunal composition is highly unbalanced; large sized mammalian taxa being absent. Mammalian carnivores

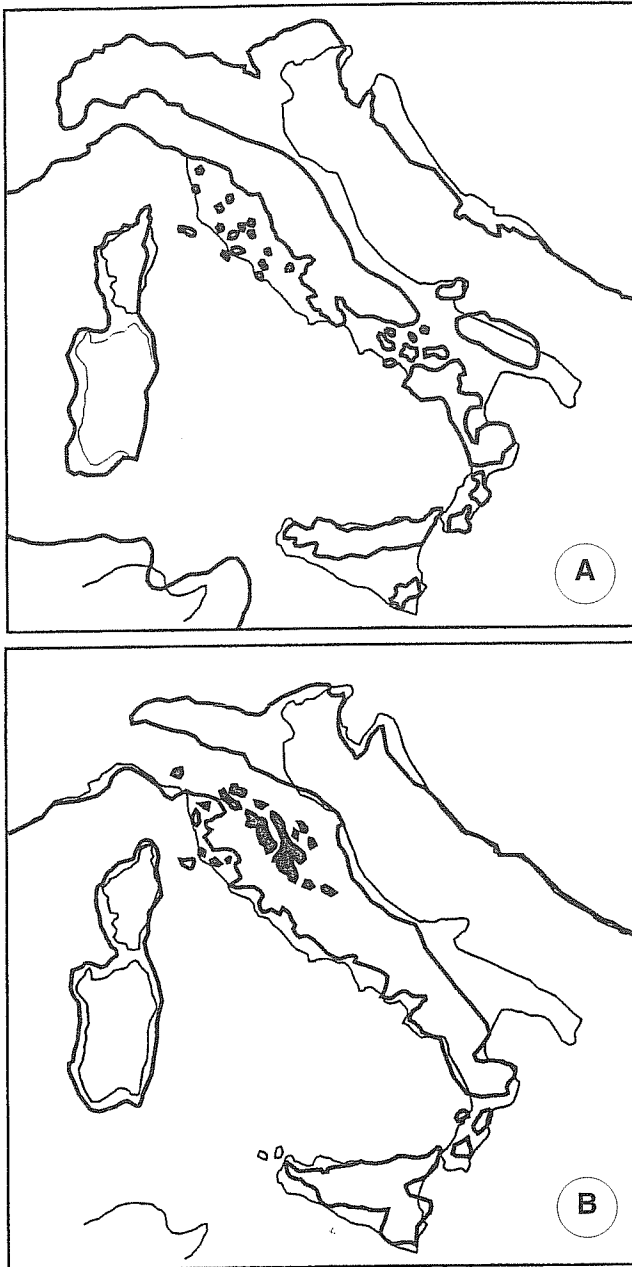


Fig. 2 - Tentative reconstruction of the distribution of emerged lands during the Early Pliocene (A) and Early Pleistocene (B). From Landini and Tanfi (1997) modified. Lakes are in grey, ancient coast lines are in bold line

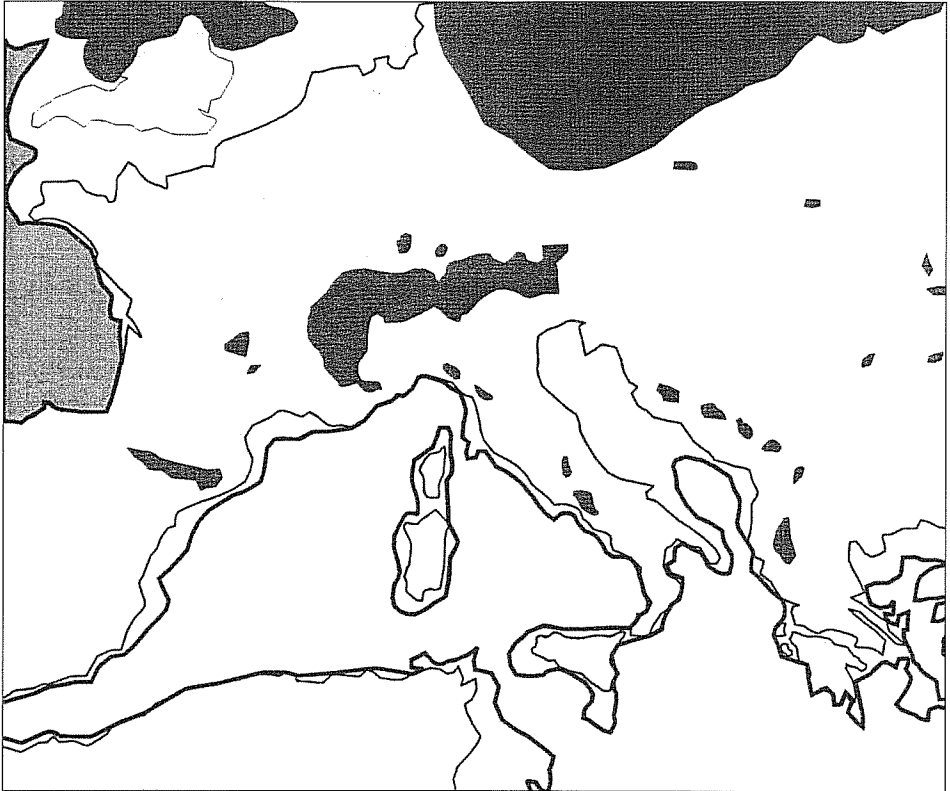


Fig. 3 - Coast line reconstruction during the last glacial maximum (sea level drop ~130 m). From Agnesi et al. (1998) Continental ice is in dark grey, marine ice in light grey, bold line indicates coast line profile at glacial maximum

are limited to a sea otter (*Garganolutra*), and possibly to the strongly endemic 'moon rat' *Deinogalerix*. Top predators are found among reptiles (crocodiles, large sized snakes) and birds ('giant' barn owl and eagle; Ballman, 1973, 1976) while the bulk of the assemblage is composed by endemic small mammals (Rodents, Lagomorpha and Insectivores). During the time documented by the fissure fillings many taxa underwent significant evolutionary changes and radiations (De Giuli et al., 1986, 1988, 1990).

Both the faunal and geological data indicate that during the Late Miocene and Early Pliocene the Gargano area was part of an island, possibly an archipelago, inhabited by faunas belonging to a distinct Central-Eastern Mediterranean endemic palaeo-bioprovince (De Giuli et al., 1987). The integration of faunal data with geological, tectonic, geophysical and biostratigraphic data, shows that the configuration of emerged lands in the palaeo-Adriatic area underwent significant changes that eventually lead to the connection of the Apulian platform to the Apennine chain. Some faunal elements have been found also in southern

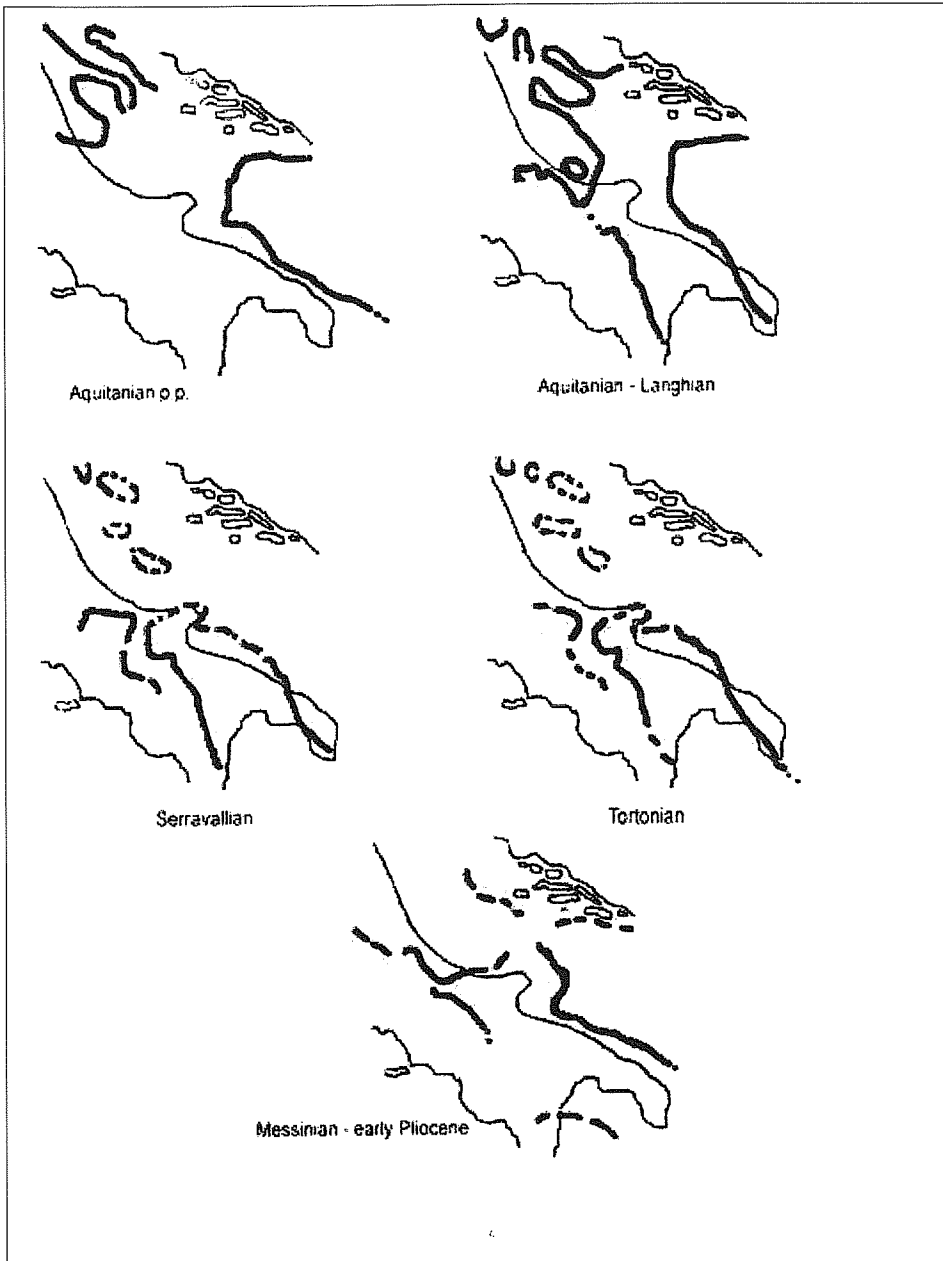


Fig. 4 - Evolution of South eastern Adriatic configuration of emerged lands. Redrawn from an original of Cristina Andreani. (from Rook et al., 2000, modified)

Apennine deposits dated to Early Tortonian (Late Miocene), at the Scontrone locality (Abruzzo; Rustioni et al., 1992). The Gargano palaeo island might actually represent a late relic of a wider system of isolated emerged lands which was in existence from at least the Early Oligocene (Fig. 4).

The Gargano taxa show different degrees of endemism (here characterised as: strong; intermediate/moderate; absent) and have potential ancestors of widely different ages, 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 probable models (or mechanisms), Tab. I.

Tab. I - Faunal composition of the Gargano 'Terre Rosse' assemblage. Updated from De Giuli et al., 1990

order	family	genus	characteristics	age of the forerunners	source
Carnivora	Mustelidae	<i>Paralutra</i>	Rare, endemic	Late Miocene ?	Willemsen, 1983
Arctiodactyla	Hoplitomeriidae	<i>Hoplitomeryx</i>	Strongly endemic, represented by several species different with size and different adaptations	Oligocene Early Miocene	Leinders 1984
Insectivora	Erinaceidae	<i>Deinogalerix</i>	Strongly endemic, represented by at least two evolutionary lineages	Oligocene Early Miocene	Butler 1980
		<i>Galerix (Parasorex)</i>	Intermediate endemic. A single lineage.	Late Miocene	Fanfani and Masini unpublished
Soricidae	<i>Larhettium</i>	Not endemic	Middle Miocene (?)	Fanfani 1999	
Rodentia	Gliridae	<i>Stertomys</i>	Intermediate endemic	Late Miocene (?)	Daams and Freudenthal, 1985
		<i>Peridymomys</i>	Moderate endemic	Late Miocene (?)	De Giuli et al., 1990
		<i>Eliomys</i>	Not endemic	Messinian- Early Pliocene	De Giuli et al., 1990
	Cridetidae	<i>Hattomys</i>	Intermediate endemic	Late Miocene	Freudenthal, 1985
		<i>Cricetulodon</i>	Not endemic	Messinian- Early Pliocene	Freudenthal, 1985
		<i>Cricetus</i>	Not endemic	Messinian- Early Pliocene	Freudenthal, 1985
	Muridae	<i>Microtia</i>	Intermediate endemic, 4 lineages	Late Miocene	De Giuli et al., 1990
		<i>Apodemus</i>	Not endemic	Messinian- Early Pliocene	De Giuli et al., 1990
Lagomorpha	Ochotonidae	<i>Prolagus</i>	Moderate endemic, 2 lineages	Late Miocene	Mazza, 1987a,b

Endemic modifications are related to several factors among which the most important are: the availability of resources; the extent and physiography of the island and the duration of insularity (see Sondaar on this topic). One might expect that a long period of insularity in a small island would result in the most marked modifications. Although this idea is realistic in a broad sense, the actual rate of endemic modification is not at all constant among different species, since it is essentially related to adaptive changes, resulting from the interaction of taxa with the peculiar insular environment. Some species may be more 'conservative' in the sense that they maintain a morphology and adaptation closer to that of the ancestor, while others may be more "progressive", since they are forced to enter new ecological niches that in turn drive morphological changes. Furthermore, one might also expect that once an adaptive modification has occurred in a phyletic line or within a clade, the species may enter a stasis phase, unless further environmental disturbances occur. For instance, the two endemic dormice of Sicily appear to have remained rather static, at least regarding dental morphology and size, during the last 400-300 ka before their extinction.

The models

Group A - Strongly endemic Hoplitomericidae and Deinogalerix

Hoplitomericidae have been found in Gargano and in the Scontrone area (Leinders, 1983; Rustioni et al., 1992). They are the most endemic taxa of the Gargano faunal assemblage. Hoplitomericidae are true ruminants, small to medium sized with a peculiar morphology. Their characteristics do not allow placement within any group of "higher ruminants" (Cervidae, Giraffidae, Bovidae). They are so phylogenetically isolated among the ruminant group that they have been considered as a different family by Leinders (1983), possibly related to the Gelocidae. An even more cautious opinion is expressed by Mazza and Rustioni (1996), who consider Hoplitomericidae as generically derived from a very primitive, indeterminate, ruminant clade. A discussion on the processes responsible for the presence of these forms in the wider and older insular realm, including both the Gargano area and the Scontrone locality is beyond the limits of this contribution. However, it is important to stress here that the potential ancestors of this family can be traced back to the Oligocene (Mazza and Rustioni, 1996).

Deinogalerix is a genus of very large-sized 'giant' Echinoloricinae (about the size of an otter), and includes several species with different adaptations compared with Echinoloricinae from the mainland. As in the case of Hoplitomericidae,

this taxon is at present exclusively known from the Gargano area. This ‘moon rat’ is difficult to link to any of the known fossil and extant genera of the Echinosoricinae (Butler 1980; Fanfani and Masini, 1998). According to Butler (1980) the ancestor of *Deinogalerix* must be traced back to the Early Miocene or Oligocene.

The presence of these mammals in the Messinian-Early Pliocene assemblages from Gargano can be seen as a relic of an older phase of population, and therefore as vicariance from a pre-existing and wider bioprovince.

Group B - Intermediate to moderate endemic ‘small mammals’

This group includes Muridae, Cricetidae, Gliridae, Erinaceidae and Ochotonidae. These forms actually show a variable degree of endemic modification that is always less extreme than that observed in the mammals of group A.

The murid *Microtia*, is represented by at least 4 species, some of which are large to very large in size (for instance, *Microtia magna*, about the size of a rabbit). They display a marked modification and evolutionary trends in dental morphology (Freudenthal, 1976; Torre, 1986; De Giuli et al., 1988; Zafonte and Masini, 1992; Abbazzi et al., 1993), possibly in part related to the acquisition of a fossorial habit (Parra et al., 1999). The oldest murids appear in the European fossil record at the beginning of the Late Miocene (dated at about 12.5 my BP). Therefore, even though the ancestor of *Microtia* has still not been precisely identified (cf. Freudenthal 1985), it is evident that it cannot have entered the insular domain before the Late Miocene.

The moon rat *Galerix* (“*Parasorex*”) is reduced in size compared with the continental representatives of the genus, and displays a modified dental morphology, which may justify its classification in a separate subgenus (Fanfani and Masini, 1998, in prep.). This erinaceid is closely related to *Galerix* (*Parasorex*) *iberica*, a species from the mainland which is recorded from the Vallesian (Late Miocene) to the early Pliocene.

A Crocidosoricinae shrew occurs rarely in the fissure assemblages from the older phase of the Gargano. It has been described by Fanfani (1999) as belonging to the genus *Lartetium* and apparently does not show evident morphological differences respect to *Lartetium debmi* a species occurring in European regions in the Middle Miocene (Rzebik-Kowalska, 1998). The Crocidosoricinae family is present in Europe until at least the Messinian (Reumer, 1994; Rzebik-Kowalska, 1998; e.g., Fanfani, 1999).

The dormouse *Stertomys laticrestatus* is very large, the largest endemic glirid so far known, and characterised by an extremely complicated occlusal dental

pattern (Daams and Freudenthal, 1985). According to these Authors, this genus could be directly related to *Glis* (edible dormouse). *Glis* is recorded from the Early Miocene, even though it is a rather uncommon faunal element in the Pliocene and Quaternary. Another smaller sized glirid, referred to *Peridyromys* by De Giuli et al. (1990), is far more common than its giant relative, but has never been studied in detail. Although the precise origin is uncertain, Freudenthal (1985) considered the lineage of endemic large hamster (Genus *Hattomys*) to be most likely related to *Cricetus kormosi*, of Late Miocene, Messinian age.

The Ochotonid *Prolagus* is represented by two endemic lineages described by Mazza (1987a,b). The smaller-sized lineage (*Prolagus apricenicus*) is present in all the assemblages. The larger species (*Prolagus imperialis*) is apparently derived from the former by a well documented cladogenetic process which occurred within the insular realm. Mazza (1987a) suggests that *Prolagus apricenicus* can be derived from the Middle-Late Miocene continental lineage *Prolagus oenigensis*-*P. michauxi*-*P. crusafonti*.

None of these taxa has been found so far in the Scontrone locality. However we cannot conclude that they were definitely absent from this area, since the coastal deposits from which the Scontrone fauna comes from are not particularly suitable for the concentration, fossilisation and recovery of small-sized vertebrates. In fact, small mammal remains are mostly derived from owl pellets and are common only in concentration or condensation traps (fissures, caves; see Seilacher, 1990). Furthermore, the high degree of cementation of the sediments from Scontrone makes any attempt to recover small mammal fossils (i.e. sieving hundreds of kilos, or even tons, of loose sediment) very time consuming.

Even though this group of "small" mammals probably does not represent a single dispersal event, and some uncertainties still occur in detecting the actual 'continental' ancestor of some of the taxa, many of the faunal elements are indicative of an European late Miocene origin. Freudenthal (1985) observed that many of the elements quoted above, can be derived more or less directly from a 'continental' European mammal assemblage such as Crevillente 6, a late Turolian-Messinian locality in Spain. This is perhaps too drastic a view, in the sense that *Stertomys*, at least, is apparently too modified to have been a strictly coeval ancestor, as the other faunal elements, and the shrew *Lartetium* apparently have a Middle Miocene ancestor. In any case, most of the phylogenetic information agrees that this group of mammals entered the insular domain at a later time than Hoplitomericidae and *Deinogalerix*.

We must admit that the processes responsible for the occurrence of these taxa in the Gargano area cannot be satisfactorily determined. No clear evidence exists on geological grounds of a long period of direct connection to the mainland. The mammals must have reached the island by dispersal, but one could assume that some kind of filter was in operation since no large mammals occur. Such a filtering effect, that allows only the dispersal of small animals, should probably come under the category of 'floating islands' (model 3 in section 2). In any case it must be assumed that the animals dispersed from coastlines not very distant from the islands. The stronger degree of endemic modification in some taxa (e.g. *Stertomys*), or incongruent age of the potential ancestors of some taxa (e.g. Middle Miocene age for *Lartetium*), might suggest that dispersal events are not all strictly concentrated and that a certain scattering in time has occurred; a pattern to be expected if dispersals follow the 'floating islands' model.

An alternative explanation for the dispersal of small mammals, less probable but still possible, would necessitate temporary fully emerged connections ('land bridges'), since it is very hard to imagine other kinds of filter barriers that act in such an asymmetrical way with respect to body size. Moreover, on the basis of other population histories (see chapter B in this section), filter barriers on 'land bridges' would be expected to act in the opposite manner, allowing only larger faunal elements to disperse to the island (see section B of this chapter for details). In the case of a temporary land connection, however, one could expect that large mammals should also have entered the insular domain. A possible explanation of this absence could be explained by ecological considerations. If the insular system is of limited area with a rich and diversified vertebrate community, as is the case for Gargano, it could be difficult for large mammals to find suitable niches. In such a case one can speculate that large mammals, even if they entered the islands, would have become extinct in a relatively short time, thus leaving no trace in the fossil record. In the case of Gargano, the fossil record only reaches back to a time after the dispersals had taken place.

Group C - not endemic mammals

This category includes only a few taxa: *Apodemus*; *Eliomys*; *Cricetulodon*; *Cricetus* – three of which became extinct before the breakdown of the insular system in the Middle or Late Pliocene (De Giuli et al., 1990). These small mammals do not display endemic features and are fully comparable with mainland forms which occur in Europe in the Messinian and Early Pliocene (Freudenthal, 1985; De Giuli et al., 1990). Also, a strong filtering effect must

have acted in Gargano, determining the 'arrivals' in the insular realm of very few, scattered micromammals. Such a filtering effect can be again related to the process of dispersal by floating islands.

The extinction of *Eliomys* and of the hamsters has been interpreted by De Giuli et al., (1988, 1990) as the result of environmental changes related to Pliocene climatic variations and to a trend towards reduction of the area of the insular domain. We feel that these extinction events are important in highlighting a neglected aspect of island ecology. Although, as observed in the first section of this work, the dispersal of predators and competitors can have a dramatic effect on faunal composition, one must also keep in mind that in other cases the endemic insular ecology could be so integrated and co-evolved (as seems the case for Gargano, see De Giuli and Torre, 1984) that newcomers might have difficulties in adapting to it. In such conditions they could be less able to overcome environmental disturbances, and therefore the probability of them succumbing to extinction events could be higher than for the endemic taxa.

b) Quaternary mammalian population of the Sicily-Malta insular domain

Fossil documentation of Quaternary mammalian populations in Sicily is not evenly distributed in time and space. A trend is evident towards a richer fossil record from the Early to the Late Pleistocene, the latter fossils being most widespread. The geographic distribution could be related to taphonomical factors and to effective differences in paleogeography in the insular system (Bonfiglio and Burgio, 1992), while the reason why the number of sites and stratigraphic levels varies so greatly with respect to time (younger sites are much more numerous) has never been investigated. This pattern, widespread in regions in which tectonic activity is very intense, is probably due to the destruction of older deposits by intense erosion.

Most of the mammalian fossils of Sicily are found in 'morphological' traps such as caves and fissures – rather common in the carbonate mountain ranges of Northern Sicily and in the Hyblean plateau. Another important category of deposits is represented by ancient shorelines, beach deposits and marine terraces, frequently associated with a lagoon or swamp. Limnic deposits related to small freshwater basins also occur, often in relation to coastal and fully marine deposits. The Plio-Quaternary vertebrate populations can be arranged into 4 or 5 phases or Faunal Complexes (F.C.) which are characterised by the occurrence of different taxa showing, on the average, a decreasing degree of endemism, Tab. II (Bonfiglio et al., 2000)

Tab. II - Quaternary mammalian populations phases of Sicily. Assemblages are reported in stratigraphic order, i.e. younger age towards the top

Faunal Complexes	Characteristic taxa	Remarks
HOLOCENE POPULATION	<i>Canis cf. lupus</i> , <i>Vulpes vulpes</i> , <i>Felis silvestris</i> , <i>Martes sp.</i> , <i>Mustela cf. nivalis</i> , <i>Ursus sp.</i> <i>Sus scrofa</i> , <i>Cervus elaphus</i> , <i>Bos primigenius</i> <i>Erinaceus europaeus</i> , <i>Crocidura sicula</i> . <i>Glis glis</i> , <i>Apodemus sylvaticus</i> <i>Arvicola terrestris</i> , <i>Microtus (Terricola) savii nebrodensis</i>	Large mammals not endemic. Some endemic small mammals are moderately endemic. Faunal assemblage is less diversified than in the southern Italian Peninsula. Age: Early Holocene
CASTELLO F.C.	<i>Equus hydruntinus</i> , <i>Bos primigenius</i> <i>Cervus elaphus</i> , <i>Vulpes vulpes</i> <i>Microtus (Terricola) ex gr. savii</i> <i>Apodemus sp.</i> , <i>Erinaceus europaeus</i> <i>Crocidura cf. sicula</i>	Not endemic assemblage. Man spread on island. Megafauna and large predators are extinct. Age: Late Pleistocene (Late Pleniglacial-Lateglacial).
SAN TEODORO CAVE-PIANETTI F.C.	<i>Crocota crocuta spelaea</i> , <i>Canis lupus</i> , <i>Vulpes sp.</i> , <i>Ursus cf. arctos</i> , <i>Elephas mnaidriensis</i> , <i>Sus scrofa</i> , <i>Cervus elaphus siciliae</i> , <i>Bos primigenius siciliae</i> , <i>Equus hydruntinus</i> , <i>Erinaceus europaeus</i> , <i>Crocidura cf. sicula</i> , <i>Microtus (Terricola) ex gr. savii</i> , <i>Apodemus cf. sylvaticus</i>	Not endemic and moderately endemic taxa occur together. Endemic small mammals of the older phase are replaced by small mammals derived by dispersal from Southern Italy. Age: Late Pleistocene (inter-Pleniglacial ?).
ELEPHAS MNAIDRIENSIS F.C.	<i>Elephas mnaidriensis</i> , <i>Hippopotamus pentlandi</i> <i>Sus scrofa</i> , <i>Dama carburangelensis</i> <i>Cervus elaphus siciliae</i> , <i>Bos primigenius siciliae</i> <i>Bison priscus siciliae</i> , <i>Panthera leo</i> <i>Crocota crocuta cf. spelaea</i> , <i>Canis lupus</i> , <i>Ursus cf. arctos</i> , <i>Leithia cf. melitensis</i> <i>Maltamys cf. viendincitensis</i> , <i>Crocidura aff. esuae</i>	Moderately endemic ungulates, Mammalian top predators also occur. Large mammal taxa derive from dispersals from Southern Italian Peninsula. Small mammals are endemites derived directly from those of the preceding phase. Age: late Middle Pleistocene to early Late Pleistocene
ELEPHAS FALCONERI F.C.	<i>Nesolutra trinacriae</i> , <i>Elephas falconeri</i> <i>Crocidura esuae</i> , <i>Leithia melitensis</i> , <i>Leithia cartei</i> , <i>Maltamys gollcheri</i>	Strongly endemic assemblage, low biodiversity. Age: early Middle Pleistocene
MONTE PELLEGRINO F.C.	<i>Pannonictis arzilla</i> , <i>Asoriculus burgioi</i> <i>Pellegrinia panormensis</i> , <i>Hypolagus sp.</i> <i>Apodemus maximus</i> , <i>Leithia sp.</i> <i>Maltamys cf. gollcheri</i>	Strongly endemic taxa are associated to moderately endemic ones. Some taxa have an African affinity. Age: Early Pleistocene.

1) Monte Pellegrino Faunal Complex. This is the older Quaternary fossil record so far known and is documented only in the very restrict geographic area of Monte Pellegrino, close to the town of Palermo (Thaler, 1972; Burgio and Fiore, 1988). The faunal assemblage has been recovered from soil deposits infilling karst fissures. The poorly diversified fauna includes taxa with different degrees of endemism and of different geographical affinity, indicating a polyphasic origin. After the first report by Thaler (1972) some of the taxa have been revised more recently but knowledge of this very peculiar and intriguing faunal assemblage is still not exhaustive.

Moderately endemic: *Hypolagus* and *Pannonictis*. These two taxa (*Pannonictis* in particular) are characterised by moderately endemic features with respect to both size and morphology (Burgio and Fiore, 1994). On the basis of available knowledge, the potential ancestors appear to be typical European forms, not found so far in Northern Africa.

Endemic *Asoriculus burgioi*. This shrew is about twice as large as *Asoriculus* representatives from the mainland, but not particularly modified in comparison with them (Masini and Sarà, 1998). Its occurrence in Sicily parallels the occurrence of *Nesiotites* in the Balearics and in Corsica/ Sardinia, suggesting a separate origin for the two taxa within a clade of common ancestors. *Asoriculus* is well documented in Europe from the Early Pliocene, and it has been found recently also in Northern Africa, in late Pliocene early Pleistocene deposits (Geraads, 1995; Rzebik-Kowalska, 1988). This find complicates the paleobiogeographical picture, making any hypothesis of its geographic provenance more uncertain.

Endemic dormice *Leithia* and *Maltamys*. *Leithia* n. sp. was briefly described by Thaler (1972), but these taxa have not been studied in detail. There is, however a certain consensus in the literature regarding them as the direct forerunners of the better known and better described *Leithia* and *Maltamys* from the Middle to Late Pleistocene of Sicily and Malta (Zammit Maempel and De Bruijn, 1982). They have been assigned to the tribe Eliomyini and, according to some authors, they are the direct offspring of a taxon, no better identified than *Eliomys* sp. (Daams and De Bruijn, 1995). These authors considered *Leithia* and *Maltamys* as relics of a poorly-known older (Messinian) population phase and these elements have remained isolated in the Sicilian Malta archipelago for the entire Pliocene and most of the Quaternary.

The presence of *Pellegrinia panormensis* in the Monte Pellegrino assemblage is enigmatic. This rodent has been described by Thaler (1972) as a strongly endemic form belonging to Ctenodactilids, a rodent family which nowadays has an exclusive African distribution. Ctenodactilids probably originated in Asia in the Oligocene; the oldest African representative of the family dates to the Middle Miocene (Locality Beni Mellal). Ctenodactilids are known also from Sardinia in deposits of Early Miocene age. According to Thaler *Pellegrinia* has derived characters of the African stock of Ctenodactilids, thus indicating a dispersal from that region. Again, a Late Miocene (Messinian) age have been invoked for this dispersal.

The information derived by the poorly studied *Apodemus maximus* is limited to the observation that this mouse is more than twice as large as living *Apodemus sylvaticus*. The size increase, comparable to that observed in *Asoriculus*, indicates that this taxon underwent a certain amount of differentiation in isolated conditions.

To summarise, the composition of the Monte Pellegrino fauna – unique for the Mediterranean islands – suggests it may have been derived in part from an

older, not locally known, phase of population (Messinian age?; Azzaroli, 1974; Azzaroli and Guazzone, 1979), and partially from younger dispersals from Europe. It should be pointed out that, at present, geological observations are unable to provide more detail in identifying the route and the age of dispersal.

2) The *E. falconeri* Faunal Complex is even poorer in biodiversity in terms of mammals. The dormice from Monte Pellegrino are still present in the insular system, while all the other small mammals are apparently extinct.

The shrew *Crocidura esuae* is an endemic, of uncertain biogeographic affinity (Kotasakis, 1986). The genus *Crocidura* is recorded in Italy from the Late Pliocene (Locality Montagnola Senese; Fondi, 1972; Maul et al., 1998) and occurs widely in the Quaternary, probably correlating with a degree of climatic aridity in Europe (Rzebik-Kowalska, 1995; Reumer 1984). Approximately coeval occurrences are the oldest evidence of this genus in eastern Africa (Late Pliocene at Omo Valley and Laetolil), while its oldest record in Northern Africa is more recent, dating back to the Middle Pleistocene (Butler, 1998). At present no more detailed information is available in the literature on the origin of this endemic. It deserves a more thorough investigation.

'Large' mammals include the pigmy elephant *Elephas falconeri*, strongly reduced in size, and a member of the *Lutrinae* (genus *Lutra*). The occurrence of a small bear and of 'Vulpes' is considered uncertain and deserves further investigation. Neither the ancestor nor the geographic provenance of *E. falconeri* has been determined unequivocally. Even though its derivation from a Paleoloxodontine elephant is accepted by several authors, its possible origin from European *Elephas antiquus* stock, or from a north African species is still a matter for discussion.

Overall, this F.C. denotes the occurrence of an insular system made up of strongly geographically isolated small islands, with very difficult and sporadic connections with the mainland. Moreover, the composition of this faunal complex reveals a polyphasic origin; some taxa are relics from the preceding phase and others are 'newcomers' that probably entered the island through a strongly filtering barrier (dispersal model).

3) The large-mammal assemblage of the *Elephas mnaidriensis* Faunal Complex is almost completely new with respect to the preceding F.C. The pigmy *E. falconeri* is extinct, while the faunal composition is more balanced and includes top predators as the lion and the spotted 'cave' hyena. The only significant absence is of perissodactyls (rhinos and horses). The herbivore taxa (bison, aurochs, fallow deer, red deer, hippo) are moderately modified with respect to the co-generic or conspecific taxa from the mainland; the endemic nature of the fauna is apparent mainly from the modest reduction in size. The continental forerunner of most

of these taxa has been identified fairly accurately. For instance, *E. mnaidriensis* can be easily seen as a smaller, but not extremely modified, descendant of *Elephas antiquus*, a rather common taxon throughout Europe. The red deer *Cervus elaphus* is slightly reduced in size (about 20%). *Dama carburangelensis* is probably derived from fallow deer populations (*Dama dama tiberina*) widespread in central and southern Italy during the late Middle Pleistocene (Abbazzi et al., 2001).

The faunal composition is quite similar to that found in the southern Italian peninsula and indicates a large island, with abundant resources and a well developed trophic chain.

The only peculiarity of this fauna is in the very low biodiversity of small mammals, which are represented only by survivors from the *E. falconeri* F.C. (*Leithia*, *Maltamys* and *Crocidura esuae*); *Maltamys*, however is represented by different species.

The above description suggests that the elements of the mega and large fauna, have dispersed through a some kind of filter barrier which has prevented small mammals entering the island. Such kind of barrier could be a partially emerged sea floor or a swampy lagoonal system.

The dispersal route must have been the Straits of Messina, which were probably partially exposed during an eustatic low-stand phase of the late Middle Pleistocene (according to the most recent interpretation probably OIS 6; Bonfiglio et al., 2000).

4) The two younger Faunal Complexes (Pianetti-San Teodoro and Castello FC'ses), date to the last glacial cycle and to the Lateglacial respectively, and demonstrate that faunal exchanges become more frequent, so that the mammalian population of Sicily becomes very similar to that of the southern Italian peninsula, even though less diversified (Bonfiglio et al., 1997; Bonfiglio et al., in press).

The faunal history of this period is dominated by extinction events (large predators, elephant, fallow deer, endemic dormice and shrew), and by the dispersal of 'continental' small mammals (*Microtus (Terricola)*, *Crocidura cf. sicula*, *Apodemus cf. sylvaticus*, *Erinaceus europaeus*) and Equids (*Equus hydruntinus*, *Equus caballus*), red deer, auroch, etc. Also humans entered the island likely during Lateglacial. The only taxon which shows a certain degree of endemism is *Crocidura sicula*. Even though the affinities of this shrew are still not well established, its morphological features are sufficient to rule out the possibility of a derivation from the older Sicilian endemic *Crocidura esuae*.

The dispersal to Sicily of the ground vole, which has a fossorial habit, and of horses, that prefer open landscapes, might imply that a fully exposed connection (a temporary land bridge related to eustatic lowstand) had formed, perhaps more than once during the last glaciation (the mixed dispersal-vicariant model in section 2).

5. CONCLUSIONS

We feel it is more helpful to highlight starting points and make suggestions, rather than to present definite conclusions and proposals. Our ideas have developed reflecting on a comparison between models with a marked speculative component, and on historical cases.

A first consideration, perhaps trivial at first glance, is that the complexity of real cases cannot be reduced to classical models (dispersive and vicariant) without unacceptable simplifications.

Secondly, the concept of 'polyphasic' populations appears to have great value when applied to unravelling the history of island populations.

Thirdly, there is an apparent difference in behaviour between large sized and small sized mammals with respect to island colonisation. For small mammals the 'floating islands' model may be important. However, since this conclusion is somewhat speculative, we feel that this argument should be investigated in more depth.

From the discussion in section 4, it is clearly necessary to further investigate the role of ecological conditions in controlling biodiversity and extinction in insular environments. One can speculate whether the 'unbalanced' faunal composition, that is typical of most insular faunas, results primarily from the differential behaviour of some taxa with respect to dispersal, or is controlled by island system ecology (see Zunino and Zullini, 1995). This interpretation can be sustained by several lines of argument. It is plausible that, bearing in mind that resources are the main limiting factor on islands, at least for large animals (including megafauna), the restricted diversity could be the result of differential extinctions that preferentially strike some of the taxa that occupy 'high' positions in the trophic net.

Another possibility is that, particularly for islands that have been isolated for long periods, the ecological system is highly integrated and co-evolved, which creates problems for any newly-arrived taxon and enhancing the likelihood of its extinction. All these arguments should be more extensively and deeply developed as system models. If true one should take a fresh view of island assemblages, since several 'crypto' extinctions may have occurred during the history of populating islands.

Another consideration concerns the intrinsic value of the fossil record in reconstructing the history of the faunal populations of islands. Again we are reminded that much work has still to be done to enhance the quantity and the quality of paleontological information

With regard to model development, model testing and interpretation of case histories, it is evident that a "cross checking" strategy is the most effective: acquiring as much information as possible from as many sources as possible, and

using multidisciplinary information to constrain models and results. This methodology is often difficult to follow owing to difficulties in communication between specialists in different disciplines. We hope, however, that this contribution will stimulate further criticisms and discussions.

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