

## ORIGINAL ARTICLE

# Insular mammalian fauna dynamics and paleogeography: A lesson from the Western Mediterranean islands

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## Abstract

Since the time of Darwin (1859) and Wallace (1869), islands have been regarded by scientists as a prime target for scrutinizing the forces that may influence evolution and diversification and important elements in biogeographic studies. This research aims to scrutinize whether and to what extent the composition and structure of past mammal insular faunas and their changes through time may provide sound clues for inferring the paleogeographical evolution of a region. As a case study, I critically analyzed the dynamics shown by the Plio–Pleistocene mammalian fauna of 3 Western Mediterranean insular districts, the Balearic Islands, Sardinia and Sicily, each characterized by its own peculiar paleobiogeographical evolutionary history. The revision of faunas and the critical analysis of the dispersal ability of the ancestors of island settlers have allowed hypothesizing on the time and mode of island colonization. The results obtained confirm that the early isolation of the Balearic Islands from the mainland led to the establishment of an endemic fauna since the pre-Messinian Miocene (?Astarcian European Land Mammal Age, MN7/8), and that Sardinia has definitely been isolated since the Pliocene, although dispersal events led to some faunal turnovers during the Pleistocene. In addition, the results suggest for Sicily a complex, still imperfectly disentangled history of alternate phases of complete separation and sporadic, more or less difficult connections with southern Italy.

**Key words:** dispersal, islands, mammal, Plio–Pleistocene, Western Mediterranean

## INTRODUCTION

Since the time of Darwin (1859) and Wallace (1869), islands have been regarded by scientists as natural laboratories of evolution, and a prime target for scrutinizing

the forces that may influence evolution and diversification and disentangling how ecological driven processes may shape the structure of biological communities in isolated habitats. Islands are also a source of significant clues for a better understanding the nature and temporal/geographical extension of ecological/physical barriers that affected the genetic flow to an area from the surrounding territories: in other words, the paleographic evolution of territories inhabited by genetically isolated populations/communities (see e.g. Losos & Ricklefs 2009).

A number of causal factors contribute to shape the

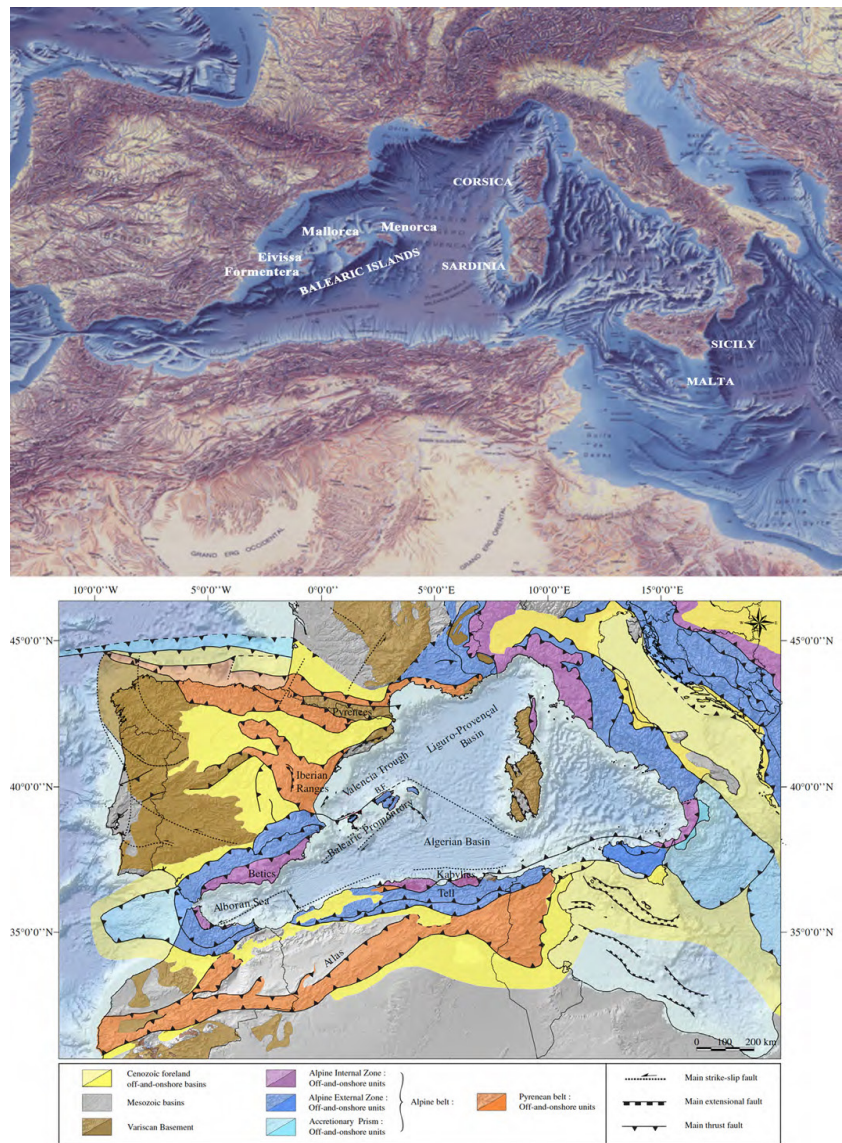
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composition and structure of isolated communities. Among others, the nature of barriers and their changes over time (depending, in turn, on geodynamics, climate and sea level changes) are of particular relevance because of the influence they exerted on the potential jump dispersal of species (i.e. quick movement of individual organisms across inhospitable terrain such as sea barriers, followed by a successful establishment of a population in the new area), and, consequently, the number and typology of the species able to reach an isolated territory, and time and degree of isolation. The composition and structure of isolated communities and their change throughout time result from the complex interplay of a

number of biotic and abiotic factors, whose relative importance and nature of influence are contextual and may vary with the characteristics of the area (e.g. climate, physiography, vegetation, productivity and resource subsidies, complexity and diversity of environments and available niches, and intensity of ecological interactions among species, such as competition, ecological displacement and release).

The composition and structure of isolated/insular mammalian fauna are basically related to the dispersal ability of the potential colonizers to cross the barrier, the release of new settlers and the potential competitive power of pre-existing endemic taxa to face the arrival



**Figure 1** (a) Morphological map of the Western Mediterranean Sea floor showing the localization of the islands mentioned in the text. (b) Structural sketch-map of the Western Mediterranean and North African regions showing the major Cenozoic structural trends (modified from Esetime *et al.* 2016). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

of new species. The mode of dispersal and the way terrestrial flightless mammals colonize islands has been a matter of debate. As Darwin wrote (1859, p. 396) “there are many and grave difficulties in understanding how several of the inhabitants of the more remote islands, whether still retaining the same specific form or modified since their arrival, could have reached their present homes.” A successful colonization varies from one species to another. It depends on the dispersal ability and habitat availability in the new territory, and on the paleogeographical context and its evolution in the course of time that may either trigger or hamper the arrival on the island of some mainland species. The turnover of insular fauna throughout time should, therefore, provide some clues regarding the nature of the connections to or disconnections from the adjacent continent, suggesting paleogeographical scenarios that have also to be explored and validated by means of geological sea-level evidence.

The research aims to critically revise the Pleistocene mammalian fauna of 3 Western Mediterranean insular districts (Balearic Islands, Sardinia and Sicily) belonging to different tectonic domains (Fig. 1), in light of the dispersal ability of the mainland ancestors of the terrestrial, flightless insular taxa, and to compare the inferences on the paleobiogeography suggested by paleobiological data with the geological and geodynamic evidence.

## THE FACT OF THE MATTER

Faunas inhabiting geographically and/or ecologically isolated districts are frequently ecologically unbalanced, dysharmonic and include a limited number of terrestrial, flightless mammals, which may display peculiar morphological traits and changes in size that make them significantly different from their ancestors. These patterns [sometimes reported as “insularity syndrome” (Blondel 1986) or island rule (Van Valen 1973) as regards to the changes in size] and the causal factors behind them have been widely debated. It is a fact that the vertebrate communities living in isolated areas (e.g. oceanic islands) are less diversified, and differ significantly in functional diversity with respect to communities inhabiting similar, but not isolated, continental biotopes. The nature of barriers that may change throughout time due, for instance, to geodynamic, tectonic, climatic or glacio-eustatic causes, is one of the causal factors most influencing the biodiversity of insular communities. The filtering and canalization action of any barrier may highly differ ac-

ording to the ecological flexibility and dispersal ability of the taxa. Therefore, the poor swimming skills and dispersal aptitude of some large and small mammals, limiting the chance to successfully cross highly selective barriers and precluding over-sea dispersals to a number of species, may account for the paucity of terrestrial flightless mammals, and the impoverished and disharmonic nature of many insular biotas.

Most terrestrial mammals can swim, generally for short stretches, as reported even for unexpected mammals such as giraffes (Henderson & Naish 2010). Swimming, however, is neither natural nor easy for the majority of terrestrial mammals. Small mammals (e.g. rodents, insectivores and lagomorphs), even the most proficient swimmers such as rats, cannot, for instance, undertake long-distance water crossings due to their poor swimming endurance (e.g. Esher *et al.* 1978). Therefore, considering their small size, a passive dispersal is reasonable in most cases. Among the most common large mammals found on islands, elephants, whose endemic species are known from a number of islands all over the world (Palombo 2007, 2016; Van der Geer *et al.*, 2010), are capable distance swimmers, with a propensity to venture out to sea and easily swim more than 50 km (Johnson 1980). Extant cervids, mostly fallow and red deer, but also moose (quite good swimmers as documented by Michaels [2015], who reported an individual swimming from Sweden to Denmark across the Øresund), potentially are more agile swimmers than elephants, although they have less swimming endurance (Held 1989), and normally prefer to swim if the opposite shore is in their sight (e.g. Vigne & Marinval-Vigne 1988; Whitehead 1993; Brown 2005). Whether hippopotamuses swim for long distances or float is a matter of debate. The extant *Hippopotamus amphibius* is not, indeed, a good swimmer because its limb structure, bone density and poor buoyancy prevent it from losing contact with the bottom for long distances (Eltringham 1999; Nowak 1999; Coughlin & Fish 2009). Endemic hippopotamuses, however, are recorded from a number of islands, even those located far from the mainland coast, such as Cyprus, and Madagascar. Their presence may imply either a remarkable swimming ability or the still unproved existence of temporary, perhaps discontinuous corridors connecting the oceanic/oceanic-like islands to the mainland. Most terrestrial animals show a low swimming ability, or are able to float but only for very short distances, as for instance some primates (Riopelle & Hubbard 1982; Zinner *et al.* 2009; Bender & Bender 2013), antelopes (Cotterill 2003), large bo-



vids (e.g. Larter *et al.* 2003; Wilson *et al.* 2009) and a few suids (Oliver *et al.* 1993) sometimes do. Horses can swim over very short distances, but swimming imposes considerable physiological demands and they have neither strong swimming skills nor the propensity to venture into water (Thomas *et al.* 1980; Tokuri *et al.* 1999).

Endemic terrestrial Carnivora, especially the large ones, are rare in insular faunas, even if a few are quite proficient swimmers. Wolves, for instance, are able to swim and to even perform hunting attacks in water (e.g. Nelson & Mech 1984; Jordan *et al.* 2010), and the notable swimming ability of tigers makes this species able to cross sea arms and colonize continental islands (Garga 1948; Meijaard 2001). *Panthera tigris* is, indeed, widely recorded in the fossil record of Java, Borneo and Bali, and on the south-west Philippine island of Palawan (Hertler & Volmer 2008; Piper *et al.* 2008). Some others large felids, such as the extant *Panthera onca*, are moderately good swimmers, while lions are less capable of swimming (Hoogsteijn 2003). The spotted hyena has poor swimming skills (Matthews 1939), while open-water swimming is critical for polar bears, and brown bears can swim over short distances (Monnett & Gleason 2006; Pagano *et al.* 2012).

“Jump” dispersal, or stochastic sweepstake dispersal by swimming, therefore, could be seen as a potential way for large mammals whose swimming ability is enough to colonize continental islands (i.e. portions of the continental shelf that in the past were part of a continent to which they were connected by an isthmus or peninsula later submerged by the sea) and maybe, in a very few cases, for proficient swimmers to reach some oceanic-like islands (territories connected to the continent in the distant past, but then separated from the mainland by persistent and wide sea barriers). Stochastic sweepstake dispersal through natural rafting is the explanation suggested by most authors for the colonization of oceanic islands (remote islands, located over oceanic plates, that have risen to the surface from the floors of the ocean basins due to tectonic ad/or volcanic activities, and have never been connected to the continental shelf).

Based on these assumptions, the structure of an insular fauna could provide important clues to infer the paleogeographical setting at the time when the mainland ancestor of endemic species entered the island, while the turnover of insular communities and changes in their composition throughout time may offer some hints about the nature of the connection with the adjacent mainland, and supply independent evidence as re-

gards to the paleogeographical evolution of the insular district. Therefore, as suggested by several authors (see among several others Simpson 1940, 1965; Carlquist 1966; Sondaar 1986; Alcover *et al.* 1981; Lomolino 1985; Palombo 1985; de Vos *et al.* 2007), it may be supposed that the terrestrial vertebrate fauna on continental islands, which results from colonization events through a broad link to the mainland (i.e. a 2-way corridor with reduced or no filter action, in which faunal interchange from one region to another is possible), has to be quite diversified, ecologically balanced and to include taxa with irrelevant or no endemic features (thus more or less similar to mainland ones). The insular faunas of continental islands that derived from the filter action of ecological barriers that prevent the dispersal of some mainland taxa are still rather balanced but impoverished, and include a few endemic taxa showing modification in size and/or ecological behavior with respect to their mainland relatives. A fairly disharmonic fauna, including endemic but also a few mainland taxa, may suggest colonization through a pendel route (a route that is easily crossed both ways between regions by some mammals, but an insurmountable barrier for others), such as a narrow sea strait, which could be easily crossed by selected taxa (e.g. large mammals with good swimming ability). Conversely, a strongly depauperate and disharmonic fauna, including few but highly modified and specialized taxa, indicates the presence of persistent, severe barriers, which are impossible to cross for most terrestrial vertebrate species; very difficult to cross for a few others, and may be actively or passively crossed by a reduced number of selected taxa through sweepstake dispersal (e.g. swimmers living in herds, or small enough and ecologically adapted to be involved in natural rafting). If a fauna has few highly modified endemic taxa (suggesting a long period of isolation), but originated by mainland relatives believed to have poor swimming ability, this may indicate that the island was in the past connected to the continent (although the connection was of short duration, or did not promote a diversified faunal transfer), and then separated by wide and severe barriers, as occurs in the so-called oceanic-like islands (Alcover *et al.* 1998). Sometimes the fauna of oceanic-like islands is dramatically depauperate and disharmonic, but this does not necessarily imply that all the ancestors of the fauna came over sea, as conversely occurs in the case of true oceanic islands, which are mainly inhabited by small terrestrial vertebrates. Mazza *et al.* (2013) consider this line of reasoning an oversimplification and suggest that unbalanced faunas may

also result from faunal relaxation (i.e. the loss of species from newly isolated islands under environmental or other pressures resulting from the island environment itself), and selective preservation (in which species exhibit different preservation potential, depending on the durability of their skeletons). On the one hand, taphonomic biases could hardly be responsible for the continuous absence of several taxa in a fossil record counting remains of species that inhabited any isolated habitat for a long geological time period (i.e. faunal complex that could be regarded as a “block of coordinated stasis fauna”); on the other hand, a faunal relaxation (i.e. a reduction in diversity following a reduction in habitat area, or a creation of a habitat island, possibly fragmented, within formerly continuous habitat) should be called upon if the fauna derive from vicariance (i.e. the geographical separation and isolation of some populations in smaller territories), but not if it originated from dispersal events, as the evolutionary radiation patterns shown by several endemic taxa demonstrate.

All in all, an attentive analysis of the composition, structure and dynamics of insular faunas could provide some indication of the type of the inhabited isolated habitat, the nature of barriers and their changes over time, and, in turn, may provide some clues about the paleobiogeographical evolution of a focal region (which, however, has to be validated and supported by geological data).

## PLEISTOCENE MAMMALIAN FAUNA DYNAMICS OF WESTERN MEDITERRANEAN ISLANDS: A CRITICAL OVERVIEW

The Western Mediterranean Basin is a hotspot for biogeographical, paleogeographical and evolutionary studies, revealing an exceptional level of biodiversity and a high rate of regional endemism both in the present and in the past. A complex geological history, characterized by orogenic processes and widespread extensional tectonics, caused repeated separations/connections of microplates and isolations/connections of insular and mainland territories, which led to a peculiar paleobiogeographical evolution. The complex and multifaceted geodynamical scenario also interacted with the important Late Cenozoic climate changes, and the consequent medium to high order sea-level fluctuations, which temporarily changed the configuration of lands and their connections, in particular during the Pleistocene. This

greatly influenced faunal dispersal and dispersion towards and across the Western Mediterranean, and, therefore, the evolution of mammalian fauna in each insular district. Most of the Mediterranean islands record fossil endemic faunal assemblages; some experienced periods of isolation that spread over millions of years, others were connected for a while with the mainland by corridors differing each other in their filtering control, and others became islands in very recent times. Therefore, the Mediterranean is an interesting setting to study the faunal dynamics on islands, to analyze the effects of isolation on the evolution of endemic taxa, and to scrutinize their significance in providing paleogeographic clues.

### The Balearic Islands

The history of the Balearic Islands, now located on the western side of the Mediterranean Sea, began in the Late Oligocene–Early Miocene, when the Gibraltar Arc migrated westwards and the Balearic archipelago completely separated from the Iberian mainland, undergoing a 25° clockwise rotation (Carminati & Doglioni 2005). The Balearic archipelago comprises 2 groups of islands (the Gymnesic islands, including Mallorca, Menorca and approximately 30 surrounding islets, and the Pityusic islands, counting Eivissa, Formentera and approximately 60 small surrounding islets), each recording a peculiar faunal history during the Neogene and Quaternary (see e.g. Bover *et al.* 2008, 2014 and references therein) (Fig. 2). The oldest endemic faunal assemblages are known in the Gymnesic islands from 4 Mallorcan (Santa Margalida, Sant Llorenç, Cova de Cala Varques D and Cova des Coll) and 2 Menorcan sites (Punta Nati-2 and Es Cul de Sa Ferrada). All these taxa have a European origin and their ancestors likely inhabited the Iberian mainland. The strongly impoverished and disharmonic Mallorcan fauna, which counts only 4 small mammals (a lagomorph, *Gymnesicolagus gelaberti*, and 3 glirids, *Carbomys sacaresi*, *Margaritامys llulli* and *Peridyromys ordinasi* from Santa Margalida and Sant Llorenç) and 2 Testudinoidea (pre-Messinian deposits of Cova des Coll and Cova de Cala Varques B), and the little more diversified Minorcan fauna (*G. aff. G. gelaberti*, *Margaritامys adroveri*, a large viperid and tortoise, a couple of small-sized reptiles and a bird), indicate, however, that the connection with the mainland was arduous, and the barriers highly severe. The hypothesis that small mammals reached the islands through a passive dispersal (natural rafting) cannot be discounted, but it is hard to conceive the same for large terrestrial tortoises. Therefore, the actual colonization process cannot be

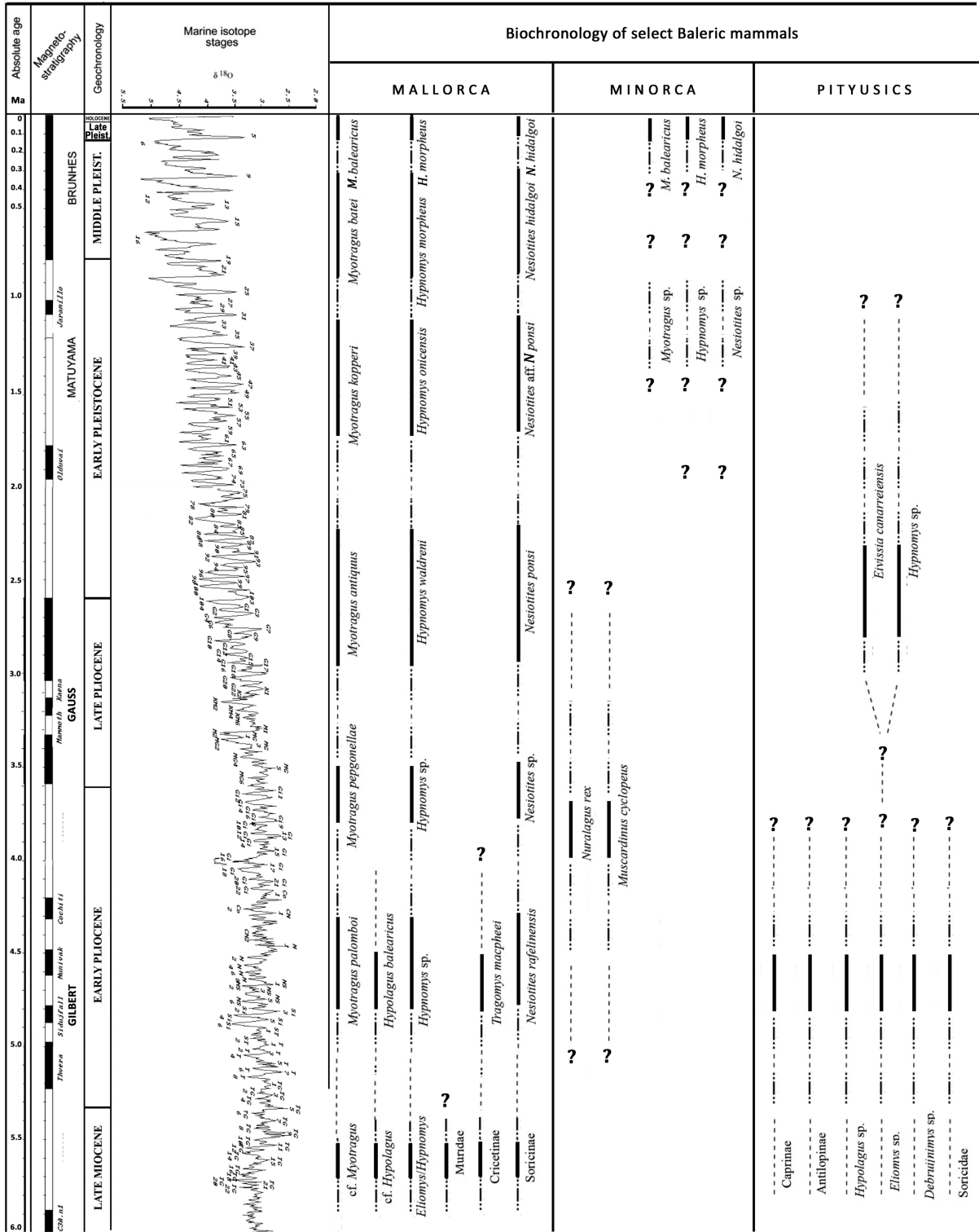


Figure 2 Tentative biochronological setting of endemic mammals recorded in the Balearic Islands from the Late Miocene to the Holocene.

firmly depicted. An impoverished endemic fauna, somehow related to those of the Gymnesic islands, was found in the Murchas area, close to Granada (Spain). The presence of endemic dormice descendants from *Pseudodyromys* and *Peridyromys*, on the one hand, may imply that during the Miocene a rather large archipelago was present close to the coast of the Betic Iberian region; on the other hand, this does not contradict the hypothesis that the ancestors of the pre-Messinian Mallorcan and Minorcan faunas entered the islands at the time of the Langhian–Serravalian regression, approximately 14 Ma. Among the Balearic pre-Messinian species none seems to have survived in the following faunas, or to have any descendants (see Bover *et al.* 2008, 2014 and references therein).

During the so-called Messinian Salinity Crisis (MSC, from 5.96 to 5.33 Ma) (e.g. Clauzon *et al.* 1996; Krijgsman *et al.* 1999), very few new mammalian settlers entered the Balearic Islands, including the ancestors of the species belonging to the well known evolutionary lineages of the bovid *Myotragus*, the glirid *Hypnomys* and the soricid *Nesiotites*, which developed from the latest Miocene to Holocene on Mallorca and are known from the Early Pleistocene to Holocene on Menorca.

To date, the oldest representatives of these lineages are reported only from Mallorca. In the latest Miocene (?) local faunal assemblage (LFA) of Na Burguesa-1, archaic bovids (cf. *Myotragus*), dormice (*Eliomys/Hypnomys*) and soricids are recorded together with a Cricetinae, a leporid (cf. *Hypolagus*), and undetermined murids. The hamster likely was the ancestor of *Tragomys macpheeii*, present in the Early Pliocene Caló den Rafelino LFA, where the other mammals (*Myotragus palomboi*, *Hypolagus balearicus*, *Hypnomys* sp. and *Nesiotites rofelinensis*) display morphological traits slightly more derived than those from Na Burguesa-1, suggesting a still incipient stage of evolution (Bover *et al.* 2004).

On Menorca, no terrestrial vertebrates have been reported to date from Late Miocene deposits, and the oldest fauna (?Early Pliocene), which includes only 2 terrestrial mammals (the endemic glirid *Muscardinus cyclopeus* and the giant lagomorph *Nuralagus rex*, a few bats, some birds and a diversified herpetofauna) (Seguí *et al.* 2002; Quintana *et al.* 2011), is quite different from that of Mallorca, as the Eivissa Messinian/Early Pliocene mammalian fauna does. The latter, depaupered, but slightly more diversified than the Gymnesic ones, includes 2 small bovids (belonging to Caprini and Antilopini tribes, perhaps close to the ancestral stocks of *Myo-*

*tragus* and *Tyrrhenotragus* respectively) (Palombo *et al.* 2013), an insectivore, the gerbillid *Debruijnimys* sp., the glirid *Eliomys* sp., and the leporid *Hypolagus* sp., together with 2 reptiles, a lizard and a tortoise. No mammals have been reported to date from Formentera (Bover *et al.* 2014).

Some descendants of the Messinian mammalian colonizers, such as bovids, logomorphs, soricids and girbellids from Eivissa and lagomorphs, murids and cricetids from Mallorca, seem to have become extinct before the Late Pliocene, as it was also possibly the case for the Early Pliocene Minorcan mammals (Fig. 2).

The Pleistocene fossil Mallorca LFAs provide a virtually continuous record of the 3 lineages stemmed from the Messinian colonizers that survived till the Holocene. The lineage of the small bovid *Myotragus* shows the noteworthy evolutionary trend (e.g. body size reduction, reduction in number of incisors and premolars, increase in hypsodonty, shift in orbits position, shortening of metapodial bones). Significant, but less marked changes characterize the evolution of the glirid *Hypnomys* (e.g. increase in size, elongation of limbs, and some cursorial ability) and soricid *Nesiotites* (Bover *et al.* 2010a,b; Rofes *et al.* 2012). From the late Early Pliocene to the Holocene 5 *Myotragus* species, epitomes of homonymous mammalian faunal complexes (FCs) succeeded each other: the late Early–Late Pliocene *Myotragus peponellae* FC, also including *Hypnomys* sp. and *Nesiotites* sp.; the Late Pliocene *Myotragus antiquus* FC with *Hypnomys waldreni* and *Nesiotites ponsi*; the Early Pleistocene *Myotragus kopperi* FC with *Hypnomys onicensis* and *Nesiotites* aff. *N. ponsi*; and the late Early–Middle Pleistocene *Myotragus batei* FC with *Hypnomys morpheus* and *Nesiotites hidalgo*. Both small mammals persisted in the successive FC, characterized by the presence of the most advanced *Myotragus* species, *M. balearicus*, which appeared by the end of the Middle Pleistocene and survived till the Holocene. The most recent radiocarbon date obtained on *M. balearicus* bones from Holocene deposits of Mallorca (4035 ± 32 BP, 2830–2470 cal. BC) is close to that obtained for the oldest human presence in the island (introduced Caprinae bone, 3884 ± 36 BP; 2470–2210 cal. BC). The evidence suggests reconsidering the hypothesis of some causal relationships between the first human arrival and the *M. balearicus* extinction (Bover *et al.* 2016).

Local faunal assemblages belonging to the *M. balearicus* FC are also recorded in the Late Pliocene–Holocene of Menorca (Fig. 2), suggesting repetitive inbreeding among Mallorcan and Menorcan mammalian



populations. The faunal interchange was likely facilitated by the late Middle–Late Pleistocene most marked glacio-eustatic sea-level lowering (MIS 6, 4 and 2) that led to the partial emersion of the Balearic shelf.

The relationships between the 2 islands during the Late Pliocene/Early Pleistocene, in particular the origin and the taxonomical identity of the Minorcan *Myotragus*, *Hypnomys* and *Nesiotites* species, are controversial. Some authors considered them as advanced representatives of mainland colonizers that arrived following a corridor dispersal route to the island during the MSC. Therefore, the Mallorcan terrestrial mammals (i.e. *Myotragus binigaussensis*, *Hypnomys eliomyoides* and *Nesiotites meloussae*) would be taxonomically different from the hypothetically contemporaneous Mallorcan species (Moyà-Solà *et al.* 2007 and references therein). Some others considered the Menorcan and Mallorcan populations rather indistinguishable and believed that the Mallorcan species arrived on Menorca during a later dispersal phase, possibly at the Plio–Pleistocene transition (Reumer 1982; Bover & Alcover 2000; Pons-Monjo *et al.* 2012). In particular, following Pons-Monjo *et al.* (2012, p. 400), the shrew populations from Binigauss (Menorca, older than the Middle Pleistocene) (*N. meloussae*) and Pedrera de s'Ònix (Mallorca, Early Pleistocene or maybe older) (“*Nesiotites aff. ponsi*” in Alcover *et al.* 1981; “*Nesiotites ex. interc. ponsi-hidalgo*” in Reumer 1982) are “morphologically undistinguishable and their dental and mandibular measurements overlap considerably. Therefore, an early post-Messinian (Pliocene) isolation of *Nesiotites* in both islands is quite unlikely.” It is worth noting, however, that interchanges between Mallorcan and Menorcan populations might have been easier for small rather than large mammals (i.e. the bovid *Myotragus*) whose dispersal was probably limited to periods of maximum sea level lowering. Therefore, the hypothesis that the Pleistocene Maiorcan fauna had a polyphasic origin cannot be discounted. Moreover, it is challenging to say to which extent (if any) the genetic pool of the oldest Maiorcan *Myotragus* populations differed from those known on Mallorca. The bovid found in Binigauss LFA, regarded as a bona fide species (i.e. *M. binigaussensis*) by Moyà-Solà *et al.* (2007), was considered as conspecific with the Mallorcan species *M. batei* by Bover and Alcover (2000), based on a reappraisal of its dental formula seen as comparable to that of the Mallorcan bovid. The latter species, however, is first reported on Mallorca in LFAs younger than Binigauss, together with a shrew, *N. hidalgo*, which is more advanced than the shrew from

Binigauss. Therefore, the question arises as the identity of the Binigauss bovid ancestor (? *M. kopperi*) and the time of its dispersal from Mallorca. Although the Early Pliocene turnover of Maiorcan fauna (i.e. the replacement of *Hypolagus* fauna by the *Myotragus* fauna) was likely related to some dispersals of small and large mammals from Mallorca, based on available data, it is challenging to assert whether the Maiorcan mammalian species (in particular *Myotragus*) actually belong to the same genetic stock as the Mallorcan mammalian species or whether they resulted from a local, independent evolution, and whether or not the morphological similarities between the early Pleistocene bovid populations of the 2 islands depend on convergence. Due to these uncertainties, I prefer to provisionally leave open the nomenclature of the Early Pleistocene Mallorcan mammals (Fig. 2).

### The Pleistocene endemic fauna from Sardinia

Since the separation from Iberia approximately 30 Ma ago, Sardinia has experienced a long history of alternating phases of complete isolation and mainland connections. It was part of an archipelago of the Tusco–Sardinian paleobioprovince during the Late Miocene, and then became a complete isolate insular district by the end of the Messinian. From the Pliocene to the Late Pleistocene–Holocene, several episodes of colonization from the European bioprovince affected Sardinia, giving rise to successive endemic faunas.

The evolutionary succession of Plio–Pleistocene Sardinian mammalian fauna shows a decrease in biodiversity from the impoverished but balanced Pliocene/Earliest Pleistocene fauna to the Latest Pleistocene fauna, which is disharmonic, strongly impoverished and highly unbalanced with respect to those inhabiting similar continental ecosystems. Two main FCs succeeded each other, the *Nesogoral* FC and the *Microtus (Tyrrhenicola)* FC, each including 2 lower-rank Faunal sub Complexes (FsC): the Mandriola and Capo Figari I/Orosei 1 FsC, and the Orosei 2 and Dragonara FsC, respectively (Palombo 2006, 2009) (Fig. 3).

The oldest fauna of the Mandriola FsC had a polyphasic origin given that it includes a representative of the long-lasting Miocene *Tyrrhenoglis* lineage, some descendants of taxa that colonized the island by the end of the Messinian throughout temporary emerged filter routes (i.e. *Sus* aff. *S. sondaari* and *Nesogoral* sp., but not the running hyena *Chasmaporthetes*), as well small mammals that passively dispersed during the Pliocene at the Zanclean/Piacentian transition. The fauna represents



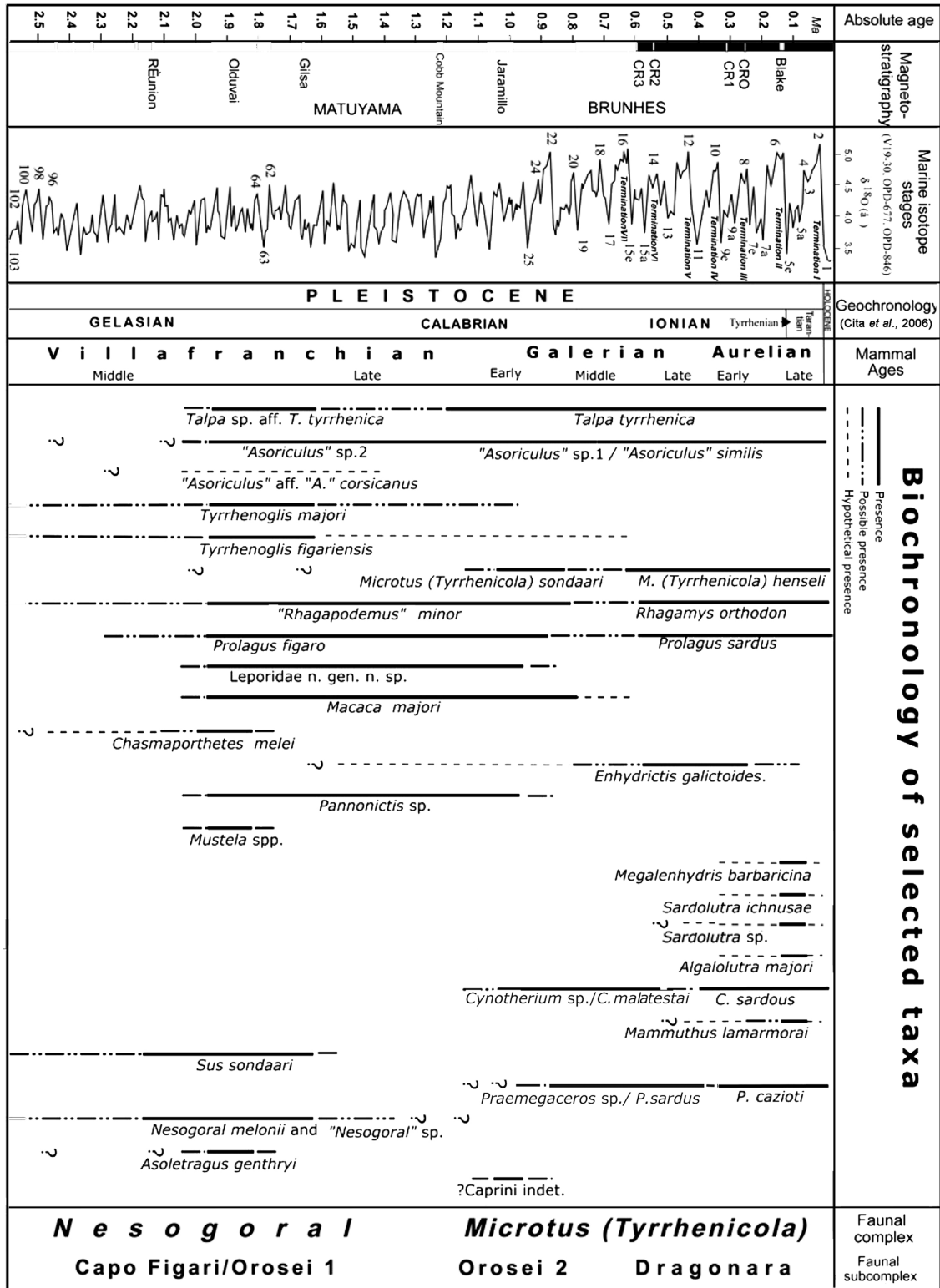


Figure 3 Chronological range chart of mammalian taxa recorded in the Pleistocene to Early Holocene Sardinian local faunal assemblages (updated and modified from Palombo [2009]).

the nucleus of the successive Capo Figari I/Orosei 1 FsC that was enriched by new species (mustelids and maybe a macaque) that reached Sardinia through an over-sea dispersal, possibly facilitated by the earliest Pleistocene low sea-level standings that reduced the distance from the continent (Haq *et al.* 1987; Miller *et al.* 1996; van der Made 1999; Palombo 2009; Palombo *et al.* 2013). The onset of this FsC was already completed at approximately 1.8 Ma (Palombo 2006, 2009), while the time of the transition to the successive Orosei 2 FsC, the oldest of the *Microtus* (*Tyrrhenicola*) FC, is difficult to ascertain. The occurrence of a primitive vole, *Microtus* (*Tyrrhenicola*) *sondaari*, provides indirect arguments for a dating, as this vole likely derived from a *Microtus* (*Allophaiomys*) species more advanced than the specimens recorded in Italy at Pietrafitta, Pirro Nord and Soave Cava Sud (Sala & Masini 2007; Marcolini *et al.* 2013). This suggests that the arrival of the ancestor of the Sardinian vole occurred not earlier than 1.3–1.2 Ma.

The faunal turnover from the *Nesogoral* to *Microtus* (*Tyrrhenicola*) FC (i.e. from Capo Figari-Orosei1 to Orosei 2 FsC) is mainly characterized by the appearance due to anagenetic evolution of new species in some endemic small mammal lineages, the dyachronous disappearance of the large mammals recorded in the previous FsC, and the discrete appearances of new incomer species since the time of Jaramillo paleomagnetic subchron. The Orosei 2 FsC may be regarded as a transitional phase to the following Dragonara FsC given that a few pre-existing taxa (*Rhagapodemus minor*, *Prolagus figaro*, Leporidae, *Macaca* cf. *M. majori* and *Pannonictis* sp.) were present together with newcomers (*M. (Tyrrhenicola) sondaari*, *Cynotherium* sp., and *Praemegaceros* sp. aff. *P. sardus*) whose ancestors likely entered Sardinia through a sweepstake over-sea dispersal. The possible long transitional phase, marked by discrete dispersal events, suggests the presence of a strong barrier that highly reduced the successful chance of colonizing Sardinia for animals adventuring in the sea. In particular, it has been hypothesized that the ancestors of *Cynotherium* (a descendent of a lycaon-like dog, *Xenocyon lycaonoides*, believed to have had some swimming abilities as the modern lycaons have) and *Praemegaceros* might have reached the island by the end of the Early Pleistocene when the glacial cycles of the so-called Mid-Pleistocene Revolution (Maslin & Ridgwell 2005) were particularly pronounced and the increased amplitude of sea-level fluctuations led to the temporary emergence of limited areas of the continental shelf, reducing the width of the sea-arms that separated the Corso-Sar-

dinian Massif from the mainland (Palombo 1985). The assumption is consistent with the hypothesis that the Sardinian wild canid and giant deer (whatever their putative ancestor should be) stemmed from late Early Pleistocene continental stocks (Croitor *et al.* 2006; van der Made & Palombo 2006; Madurell-Malapeira *et al.* 2015; Melis *et al.* 2016). It is interesting to note, however, that in the Orosei 2 FsC, good swimmers like elephants are missing, though it has been hypothesized that the ancestor of *Mammuthus* ex gr. *M. lamarmorai* would have entered Sardinia at that time, if originated by *M. meridionalis* (Palombo & Rozzi 2014) or later, if stemmed from *M. trogontherii* (Palombo *et al.* 2017b). Assuming that mammoths colonized Sardinia just one time by the end of the Early Pleistocene, the only mammals that successively entered the islands were the ancestors of endemic otters *Algarolutra majori*, *Sardolutra ichnusae*, *Sardolutra* sp., *Megalenhydris barbaricina*, recorded in the Dragonara FsC (Palombo & Zedda, 2016). Because otters have an aquatic attitude, they could have reached the island at some time, possibly in the Late Pleistocene, even if the paleogeographical setting may have prevented any other terrestrial mammals to enter into Sardinia through sweepstake over-sea dispersal.

In the Dragonara FsC, excluding otters, the biodiversity is lower than in the previous Orosei 2 FsC because a few advanced species anagenetically originated in the long-lasting phyletic lineages, but some others (e.g. glirids, leporids and *Macaca*) disappeared. Climatic and environmental changes possibly contributed to the faunal change, negatively affecting the most specialized endemic species. During the time of Dragonara FsC (approximately from the late Middle Pleistocene to the beginning of the Holocene) successive evolutionary stages can be detected in some taxa: for instance, *Prolagus sardus* was characterized by a progressive increase in the size of teeth and postcranial bones (Angelone *et al.* 2008), the size of *Cynotherium* and *Praemegaceros* slightly decreased, and in *Microtus* (*Tyrrhenicola*) *henseli* populations the frequency of advanced morphotypes became more and more important. The nucleus of the fauna of Dragonara FsC persisted nearly unchanged up to the Holocene; no new mammalian settlers arrived in Sardinia during the Last Glacial Maximum (LGM) (cf. Palombo *et al.* 2017a as regards to anatomically modern humans). *C. sardous* and *P. cazioti* are last recorded at approximately 11 350 and 7000 years ago, respectively, while most of the Sardinian endemic small mammals progressively disappeared in the Holocene, coexisting

for a while with the new settler accompanying Mesolithic and Neolithic humans (*T. tyrrhenica* and ‘*A.*’ *similis* disappeared at the beginning of the Holocene, *Rhagamys orthodon* was still present during the Neolithic, *M. henseli* is recorded in the late Bronze Age, and *P. sardus* survived until historical times) (see Palombo & Rozzi 2014 and references therein).

### The Pleistocene fauna from Sicily

Sicily was part of an African paleobioprovince for most of the Miocene, was an archipelago close to the southernmost point of the Italian Peninsula during most of the Pliocene and reached nearly the same configuration as today’s during the Middle Pleistocene, though in the early Middle Pleistocene a quite large embayment was still present in the territory where the Etna Volcano and the plain of Catania extend nowadays (Bonfiglio & Piperno 1996; Bonfiglio *et al.* 2008). A detailed paleogeographic reconstruction of the island in the Pleistocene and the extent of its connection (if any) with the mainland during this period are only approximately depicted (e.g. Catalano *et al.* 1996; Schmincke *et al.* 1997; Di Grande *et al.* 2002; Guarnieri *et al.* 2002; Pepe *et al.* 2003; Rosenbaum & Lister 2004; Rook *et al.* 2006; Macchiavelli 2014).

Some hints may come from the analysis of the structure of the diverse faunal complexes: Monte Pellegrino, ‘*Elephas*’ *falconeri* (= *Palaeoloxodon falconeri*) FC, ‘*Elephas*’ *mnaidriensis* (= *Palaeoloxodon mnaidriensis*) FC, San Teodoro-Cave Pianetti FC and Castello FC, which succeeded each other during the Pleistocene-early Holocene, showing an increase in biodiversity and a reduction in endemism, which suggest a decrease in the filtering power of barriers that separated the island from southern Italy (Bonfiglio *et al.* 2003, 2008; Masini *et al.* 2008; Antonioli *et al.* 2016) (Fig. 4).

The poorly diversified LFA of Monte Pellegrino includes some small mammals, relics of an older, unknown endemic fauna (*Asoriculus burgioi*, ‘*Apodemus*’ *maximus*, *Maltamys* sp.), a ctenodactilid (*Pellegrinia panormensis*) strongly modified with respect to the putative African ancestor, and moderately endemic taxa of European origin (*Hypolagus peregrinus*, *Pannonictis arzilla*). Age and duration of Monte Pellegrino FC are uncertain, although an age of approximately 1.6–1.5 Ma has been proposed for the LFA, based on the morphology of *P. arzilla* (Burgio & Fiore 1997; Fladerer & Fiore 2002). The different degree of endemism shown by the taxa and their different geographical origin indicate that the fauna had a polyphasic origin (Masini *et al.* 2008).

The last colonizers, of European origin, may have entered Sicily shortly after the Olduvai–Matuyama paleomagnetic inversion through an over-sea dispersal event.

A chronological gap separates the Monte Pellegrino FC from the following *P. falconeri* FC. Although the *P. falconeri* FC was assumed to be configured at approximately 0.9–0.8 Ma (e.g. Di Maggio *et al.* 1999; Bonfiglio *et al.* 2003), the actual age may be younger considering that *Palaeoloxodon antiquus*, the ancestor of the Sicilian endemic elephants, is first recorded shortly before the end of the Early Pleistocene in North Italy and in the early Middle Pleistocene in the South of the peninsula (Palombo 2014, 2017). A noticeable turnover marks the transition from the Monte Pellegrino to *P. falconeri* FC. In the latter, 3 taxa are related to the Monte Pellegrino dormouse (*Maltamys gollcheri*, *Leithia cartei* and *Leithia melitensis*), while the ancestors of the other small vertebrates (herpetofauna and the soricids *Crociodura esuae*) and large mammals (the dwarf elephant and the otter *Lutra trinacriae*) entered the island through over-sea dispersal, crossing a strongly filtering barrier. The amino acid racemisation (AAR) age of 455 ± 90 ka obtained by Belluomini and Bada (1985) for some *P. falconeri* bones from Spinagallo cave is roughly consistent with the age of approximately 350 ka proposed by Herridge *et al.* (2014). In the AAR analysis specimens, indeed, the standard was represented by specimens from Isernia la Pineta (central Italy), considered at that time older than 700 ka, but whose age is actually younger than 600 ka (583–561 ka) (Peretto *et al.*, 2015). The structure of the highly depauperated and disharmonic fauna of the *P. falconeri* FC, which inhabited Sicily during most of the Middle Pleistocene, indicates that a quite severe barrier (crossable only by large mammals with exceptional swimming ability, but precluding a successful potential passive dispersal of small vertebrates) extended between Sicily and the southernmost Italy during most of the Middle Pleistocene.

Faunal evidence from the successive *P. mnaidriensis* FC suggests a reduction of the barrier before the end of the Middle Pleistocene, although the time and mode of such paleogeographical change and the time of the transition from the 2 FCs are difficult to ascertain. The presence of *Hippopotamus pentlandi*, a species commonly found in LFAs of *P. mnaidriensis* FC, *Maltamys* and *Leithia* in the lower levels of the Site K22 (San Vito Lo Capo, Trapani), laying at the top of a marine deposit tentatively correlated with MIS 11, suggests that species of the *P. mnaidriensis* FC were already present in Sicily before MIS 8 (Locatelli 2011). The FC was al-



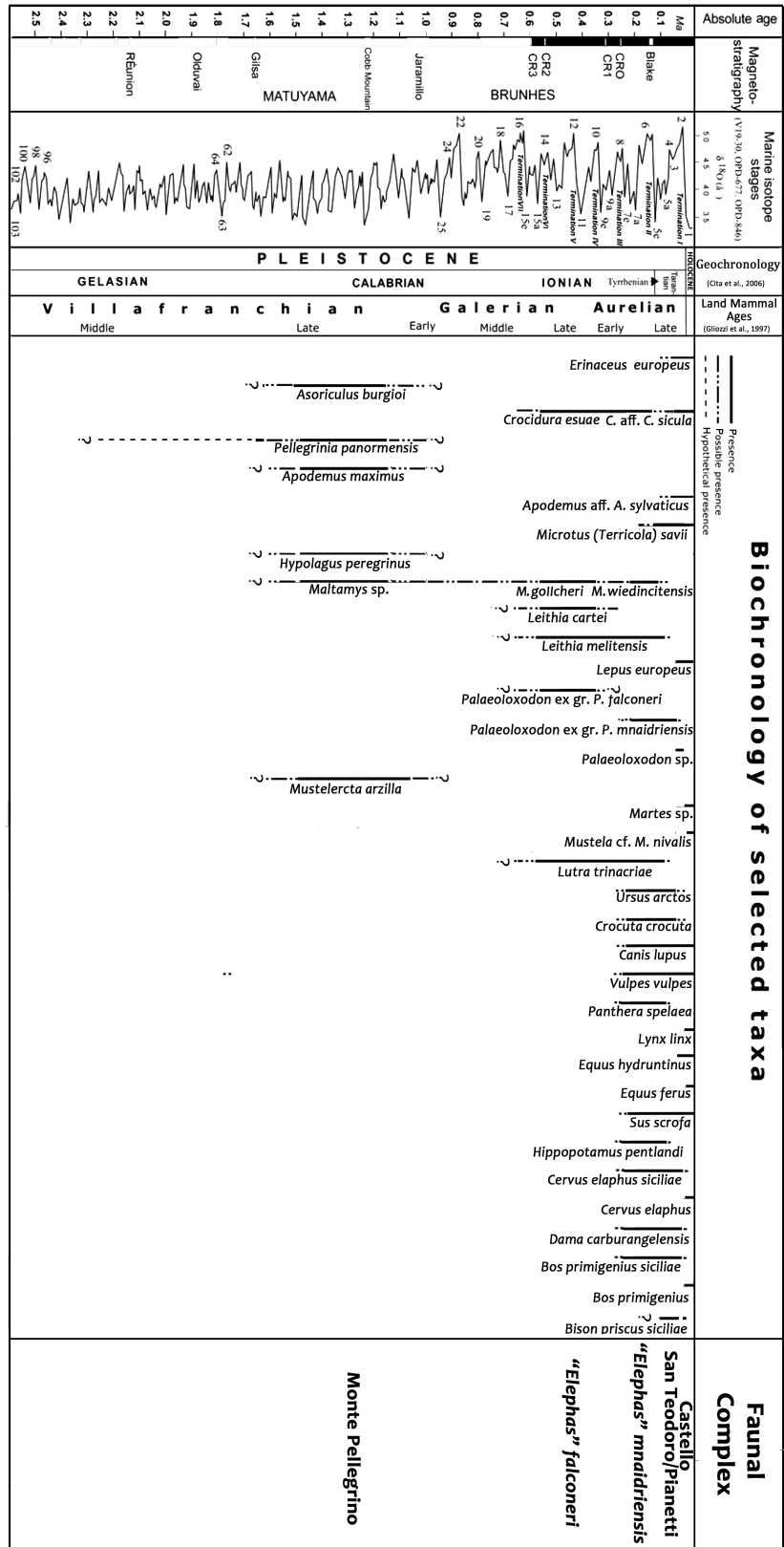


Figure 4 Chronological range chart of mammalian taxa recorded in the Pleistocene to early Holocene Sicilian local faunal assemblages.

ready established on the island before the beginning of the Late Pleistocene, as confirmed by the stratigraphic relations of deposits bearing fossils of this complex with marine deposits and marine terraces. At Contrada Fusco, for instance, fossiliferous layers belonging to the *P. mairiensis* FC are locally overlaid by marine deposits dated to MIS 5e (Di Maggio *et al.* 1999; Bonfiglio *et al.* 2003, 2004). Among the new large mammals characterizing the FC (elephant, spotted hyena, brown bear, wolf, fox, hippo, wild boar, red deer, fallow deer, bison and auroch) (Fig. 4), most have poor swimming ability. Among carnivores, for instance, brown bears generally swim over short distances, as spotted hyena and some lions occasionally do (see above). In addition, large bovids (i.e. the forerunners of Sicilian endemic subspecies *Bos primigenius siciliae* and *Bison priscus siciliae*, if actually present in Sicily at that time, cf. Petruso *et al.* 2011b) and wild boars are generally regarded as poor or short-distance swimmers. Moreover, it seems reasonable to presume that the forerunner of the Sicilian hippo, sharing the same body plan of extant hippopotamus, had similar aquatic behavior, and was more used to walking underwater, rarely losing contact with the bottom, than swimming to cross sea arms. All in all, at the time of the onset of *P. mairiensis* FC, stochastic sweepstakes dispersal by swimming was possible only for elephants, which show the best buoyancy and equilibrium, swimming speed and endurance among all land mammals, and deer, which are good island colonizers too, although with generally less endurance than elephants. The only new small mammal recorded in the *P. mairiensis* FCs, the vole *Microtus (Terricola)*, is first reported in a geological context suggesting a pre-MIS 5e age, and possibly entered Sicily during the cold stage MIS 6 through a connection made possible by a sea level drop (cf. Petruso *et al.* 2011a).

At the time of the onset of the “San Teodoro Cave–Pianetti” FC, a turnover occurred in the small mammal community where new insectivores and rodents appeared (*Erinaceus europaeus*, *Crocidura* cf. *C. sicula*, *Apodemus* cf. *A. sylvaticus*), while endemic glirids disappeared. The composition of the large mammal fauna is, conversely, similar to that of the previous FC, with the exception of hippos and lions, which are not recorded in the San Teodoro Cave–Pianetti FC. It is, however, difficult to ascertain whether the large mammals of San Teodoro Cave–Pianetti FC were the descendants of those recorded in the *P. mairiensis* FC or originated from successive dispersal events. This may be especially true as elephants, whose size sometimes exceeds that of the specimens typically recorded in the *P. mair-*

*riensis* FC (see e.g. Chilardi 2001; Palombo 2001, 2007; Herridge 2010). From a paleogeographical point of view, the most significant new entry is that of the slender horse *E. hydruntinus*, a species with extremely reduced swimming ability, which arrived in Sicily thanks to a stable land bridge that temporarily emerged between 21.5 and 20 cal ka BP, as supported by the age of the oldest fossil record of the species thus far known in Sicily (cf. Antonioli *et al.* 2016). Although *E. hydruntinus* entered Sicily at a later date than the other species, it has to be regarded as a member of the San Teodoro Cave–Pianetti FC due to its presence in the level BII of San Teodoro cave recording species typical of this FC (Bonfiglio *et al.* 2008; Mangano 2011). This evidence, in turn, implies that the onset of the successive Castello FC, counting LFAs without endemic species still unbalanced but with typically continental features, was slightly more recent than previously supposed.

## REMARKS

The Western Mediterranean islands belong to a different tectonic domain, and each has its own peculiar paleobiogeographic evolutionary history. The results obtained by analyzing the composition of insular faunal complexes in light of the dispersal ability of the ancestors of the taxa present in each fauna enable us to hypothesize whether the time and mode of island colonization is consistent with the paleogeographic reconstruction and to provide fresh data useful to address still unanswered questions. The results obtained confirm, on the one hand, that the early isolation of Balearic Islands from the mainland led to the establishment of an endemic fauna since the pre-Messinian Miocene (?Astaracian European Land Mammal Age, MN7/8), and that Sardinia has definitely been isolated since the Pliocene, although dispersal events led to some faunal turnovers during the Pleistocene. On the other hand, the results suggest for Sicily a complex, still imperfectly disentangled history of alternate phases of complete separation and sporadic, more or less difficult connections with southern Italy.

More in particular, the recent discovery of an anuran assemblage in the Early Pliocene of Mallorca (Torres-Roig *et al.* 2017), especially the presence of a ranid and *Discoglossus*, supports the hypothesis of a Messinian dispersal to Mallorca by some vertebrates through a riparian corridor connecting the Iberian mainland to the subaerial exposed Balearic Promontory. The presence on the 3 main Balearic Islands (Mallorca, Menorca and Eivissa) of different taxa in the local Early Pliocene

LFA's poses, however, the question as to whether these faunas originated from independent colonization events by different mainland taxa following different dispersal routes, or ecological factors, taphonomical biases and incomplete knowledge of the fossil record may account for such differences. The morphological characteristics displayed by some taxa suggest that these faunas would be at the beginning of the evolutionary process that developed under conditions of a complete isolation hampering any successive colonization events by terrestrial mainland species. The faunal turnover on Menorca at the Plio–Pleistocene was likely caused by the arrival of Mallorcan species. The new Minorcan settlers may have independently evolved up to the latest Middle Pleistocene when marked sea-level lowering triggered faunal interchanges between Menorca and Mallorca. The more than 5 Myr of anagenetic evolution shown by the endemic Mallorcan lineage accounts for the structural stability of isolated faunas in the absence of the arrival of alien species. The arrival of anatomically modern humans (AMH) and their accompanying fauna seems to have had a key role in the extinction of preexistent endemic mammals, which was possibly more significant than the effect of climatic changes. Conversely, faunal dynamics and ecological factors likely triggered the progressive disappearance of endemic mammals on Eivissa, where only birds and lizards survived.

Evidence from Sardinia indicates that during the Quaternary the island was mainly populated by long-lasting phyletic lineages. Dispersal events rarely occurred and new appearances were mostly related to local anagenetic evolution. The main fauna turnover, rather gradual and including the extinction of some pre-existing lineages and the arrival of few new settlers, likely developed during the late Early Pleistocene at the time of the marked climate upsetting known as the Mid-Pleistocene revolution. The biodiversity dropped and since that time the composition of the fauna at genus level remained the same until the transition to the Holocene, except for the appearances of 3 endemic otters whose actual time of dispersal on the island is uncertain. The peculiarity of Sardinian faunal dynamics, characterized by the predominance of phyletic evolution, few dispersals and long-lasting turnover phases, on one hand fits well with the expectations for an insular system that remained completely isolated by quite severe barriers for long time intervals; on the other hand, it makes unfeasible any hypothesis of a human colonization of the island during the Middle Pleistocene (see Palombo *et al.* 2017a).

During the Pleistocene, Sicily experienced a faunal renewal that led to a progressive increase in biodiversi-

ty, in turn suggesting marked changes in the extension and filter powering of the barrier that separated the island from southern Europe. Evidence from fauna structure and composition indicates that a period of strong geographic isolation occurred at the time of *P. falconeri* FC. A marked faunal turnover took place by the end of the Middle Pleistocene, when several large mammalian taxa with high to low swimming ability entered the island, while among small mammals no substitution of the pre-existing faunal elements occurred. As a result, it is rational to suppose that some time during the late Middle and early Late Pleistocene, Sicily was connected to southern Calabria by temporarily emerged and discontinuous strips of land (whose existence has still to be proved) that allowed mammals with poor swimming abilities to enter the island. Conversely, it seems that environmental conditions were not suitable for a passive dispersal of small mammals, possibly due to hazardous sea currents in the Strait of Messina.

The pattern of the transitions from the *P. mnaidriensis* to SanTeodoro Cave–Pianetti FC and then to the Castello FC would suggest a stepwise extinction of the endemic taxa and a repeated dispersal of mammals from southern Italy to Sicily that rendered the composition of the Sicilian fauna rather similar to that of the southern Italian peninsula, although slightly impoverished.

On the whole, available data suggest that Sicily as an insular system is a relatively young geographical entity (Early–Middle Pleistocene) and its faunal history testifies for a nearly complete isolation during the Early and most of the Middle Pleistocene. Temporary connections with southern Calabria occurred during the latest Middle Pleistocene through filtering strips of land, while during the Late Pleistocene the island was connected with the mainland by temporary land bridges, as partially supported by the paleogeographic evolution of the Strait of Messina during the latest Pleistocene (Antonoli *et al.* 2016).

## ACKNOWLEDGEMENTS

I want to thank Drs. Jacob Wickham and Wenhua Xiong (Editorial Office, Integrative Zoology) for inviting me to contribute to this special issue to celebrate 10 years anniversary of INZ Journal, and the two anonymous reviewers for critically reading the manuscript.

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**Cite this article as:**

Palombo MR (2018). Insular mammalian fauna dynamics and paleogeography: A lesson from the Western Mediterranean islands. *Integrative Zoology* **13**, 2–20.