ORIGINAL ARTICLE

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

Maria Rita PALOMBO
Department of Earth Science, Sapienza University of Rome, Roma, Italy; CNR-IGAG, Monterotondo (Roma), Italy

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 palaeobiogeographical 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 (?Astartacian 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 palaeographic evolution of territories inhabited by genetically isolated populations/communities (see e.g. Losos & Ricklefs 2009).

A number of causal factors contribute to shape the
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...
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 according 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 unproven 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-
Endemic terrestrial Carnivora, even 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 (Gariga 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 exant Panthera onca, are moderately good swimmers, while lions are less capable of swimming (Hoogesteijn 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 regards 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. Mazzu 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 dynamical 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 paleographic 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, Margaritamys 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, Margaritamys 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–Serravallian 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 Pleistocene 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 *Myotragus* and *Tyrhenotragus* respectively) (Palombo et al. 2013), an insectivore, the gerbillid *Debruijinmys* 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 gerbilids 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 Pleistocene to the Holocene 5 *Myotragus* species, epitomes of homonymous mammalian faunal complexes (FCs) succeeded each other: the late Early–Late Pliocene *Myotragus pepgonellae* FC, also including *Hypnomys* sp. and *Nesiotites* sp.; the Late Pliocene *Myotragus antiquus* FC with *Hypnomys waldreni* and *Nesiotites ponsi*; the Early Pleistocene *Myotragus kopperti* 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 Minorcan 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*, *Hynomys* and *Nesiotes* 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 binigausensis*, *Hynomys elomyoides* and *Nesiotes 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 Binigaus (Menorca, older than the Middle Pleistocene) (*N. meloussae*) and Pedrera de s’Ónix (Mallorca, Early Pleistocene or maybe older) (“*Nesiotes aff. ponsi*” in Alcover et al. 1981; “*Nesiotes 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 *Nesiotes* 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 Binigaus LFA, regarded as a bona fide species (i.e. *M. binigausensis*) 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 Binigaus, together with a shrew, *N. hidalgo*, which is more advanced than the shrew from Binigaus. Therefore, the question arises as the identity of the Binigaus 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 (Tyrrenicola)* 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 *Tyrrenogliris* 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 (Tyrrenicola) FC, is difficult to ascertain. The occurrence of a primitive vole, Microtus (Tyrrenicola) sondaari, provides indirect arguments for a dating, as this vole likely derived from a Microtus (Allophaiomys) species more advanced that 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 (Tyrrenicola) FC (i.e. from Capo Figari-Orosei 1 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 Pannonicitis sp.) were present together with newcomers (M. (Tyrrenicola) 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, Xeno- cyon 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-Sardinian 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., Megalenydris 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 (Tyrrenicola) 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

© 2017 The Authors. Integrative Zoology published by International Society of Zoological Sciences, Institute of Zoology/Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd 11
for a while with the new settler accompanying Mesolithic and Neolithic humans (T. tyrhenica 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 endemicity, which suggest a decrease in 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, Pannonicitis 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 endemicity 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 golcheri, Leithia cartei and Leithia melitensis), while the ancestors of the other small vertebrates (herpetofauna and the soricids Crocidura esuae) and large mammals (the dwarf elephant and the otter Lutra trinacrius) 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 disjunctive fauna of the P. falconeri FC, which inhabited Sicily during most of the Middle Pleistocene, indicates that a quite severe barrier (crossoverable 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 pentlandii, 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. maidriensis 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 hyaena and some lions occasionally do (see above). In addition, large bovids (i.e. the forerunners of Sicilian endemic subspecies Bos primigenius sicilae and Bison priscus sicilae, 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 hipopotamus, 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. maidriensis 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. maidriensis 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. maidriensis 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. maidriensis 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 SanTeodoro 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 that 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 (?Astracanian 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
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 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 biodiversity, 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 mammals 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 (Antonioli 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.

REFERENCES

Alcover JA, Moya-Sola S, Pons-Moya J (1981). Les quimeres del passat. Els vertebrats fossils del Plio-Quaternari de les Balears i Pitiuses, Monogra-
fies Scientifiques, 1, Editorial Moll, Palma de Mallorca, pp. 1–260.

Alcover JA, Sans A, Palmer M (1998). The extent of extinctions of mammals on islands. Journal of Biogeography 25, 913–8.

Antonioli F, Lo Presti VL, Morticelli MG et al. (2016). Timing of the emergence of the Europe–Sicily bridge (40–17 cal ka BP) and its implications for the spread of modern humans. Geological Society, London, Special Publications 411, 111–44.

Belluomini G, Bada JL (1985). Isoleucine epimerization ages of the dwarf elephants of Sicily. Geology 13, 451–2.

Bender R, Bender N (2013). Brief communication: Swimming and diving behavior in apes (Pan troglodytes and Pongo pygmaeus): First documented report. American Journal of Physical Anthropology 152, 156–62.

Blondel J (1986). Biogéographie Evolutive. Masson, Paris, France

Bonfiglio L, Di Maggio C, Marra AC, Masini F, Petruso D (2003). Bio-chronology of Pleistocene vertebrate faunas of Sicily and correlation of vertebrate bearing deposits with marine deposits. Il Quaternario 16, 107–14.

Bonfiglio L, Mangano G, Masini F, Pavia M, Petruso D, Spigo U (2004). S. Teodoro cave Stop 2.3. In: Quaternary Eustatic Fluctuations and Biochronology of Vertebrate-bearing Deposits Correlated with Marine Terraces in Sicily. 32nd International Geological Congress, Field Trip Guidebook Pre-congress, Messina, pp. 17–21.

Bonfiglio L, Esu D, Mangano G et al. (2008). The Late Pleistocene vertebrate bearing deposits at San Teodoro Cave (North-Eastern Sicily): Preliminary data on faunal diversification and chronology. Quaternary International 190, 26–37.

Bover P, Alcover JA (2000). La identitat taxonòmica de Myotragus binigausensis Moyà-Solà i Pons-Moyà 1980. Endins 23, 83–8.

Bover P, Quintana J, Alcover JA (2008). Three islands, three worlds: Paleogeography and evolution of the vertebrate fauna from the Balearic Islands. Quaternary International 182, 135–44.

Bover P, Quintana J, Alcover JA (2010a). A new species of Myotragus Bate, 1909 (Artiodactyla, Caprinae) from the Early Pliocene of Mallorca (Balearic Islands, western Mediterranean). Geological Magazine 147, 871–85.

Bover P, Alcover JA, Michaux JJ, Hautier L, Hutterer R (2010b). Body shape and life style of the extinct Balearic dormouse Hypnomys (Rodentia, Gliridae): New evidence from the study of associated skeletons. PLoS ONE 5, e15817.

Bover P, Rofes J, Bailon S et al. (2014). Late Miocene/Early Pliocene vertebrate fauna from Mallorca (Balearic Islands, Western Mediterranean): An update. Integrative Zoology 9, 183–96.

Bover P, Valenzuela A, Torres E, Cooper A, Pons J, Alcover JA (2016). Closing the gap: New data on the last documented Myotragus and the first human evidence on Mallorca (Balearic Islands, Western Mediterranean Sea). The Holocene 26, 1887–91.

Brown D (2005). Secretary Island Deer Eradication. Southland Conservancy, New Zealand Department of Conservation.

Brown JH (1971). Mammals on mountaintops: Non-equilibrium insular biogeography. American Naturalist 105, 467–78.

Burgio E, Fiore M (1997). Mustelertica arzillla (De Gregorio, 1886). Elemento villafranchiano nella fauna di Monte Pellegrino (Palermo, Sicilia). Il Quaternario 10, 65–74.

Carlquist S (2004). The biota of long-distance dispersal. I. Principles of dispersal and evolution. Foundations of Biogeography: Classic Papers with Commentaries 41, 247–70.

Carminati E, Doglioni C (2005). Mediterranean tectonics. Encyclopedia of Geology 2, 135–46.

Catalano R, Di Stefano P, Sulli A, Vitale FP (1996). Paleogeography and structure of the central Mediterranean: Sicily and its offshore area. Tectonophysics 260, 291–23.

Clauzón G, Suc J-P, Gautier F, Berger A, Loutre M-F (1996). Alternate interpretation of the Messinian salinity crisis: controversy resolved? Geology 24, 363–6.

Cotterill FPD (2003). Geomorphological influences on vicariant evolution in some African mammals in the Zambezi Basin: Some lessons for conservation. In: Proceedings of the Ecology and Conservation of Mini-antelope: An International Symposium on Duiker and Dwarf Antelope in Africa. Filander Verlag, Fürth, pp. 11–58.

Coughlin BL, Fish FE (2009). Hippopotamus underwater locomotion: Reduced gravity movements for a massive mammal. Journal of Mammalogy 90, 675–9.
Croitor R, Bonifay MF, Bonifay E (2006). Origin and evolution of the Late Pleistocene island deer Praemegaceros (Nesoleipoceros) cazioti (Dépétret) from Corsica and Sardinia. Bulletin du Musée d’Anthropologie Préhistorique de Monaco 46, 35–68.

Darwin C (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, Abemarle Street, London, UK.

De Vos J, van den Hoek Ostende LW, van den Berg GD (2007). Patterns in insular evolution of mammals: A key to island palaeogeography. In: Renema W, ed. Biogeography, Time, and Place: Distributions, Barriers, and Islands. Springer Science & Business Media, Dordrecht, the Netherlands, pp. 315–45.

Di Grande A, Mazzoleni P, Lo Giudice A, Beccaluva L, Macciotta G, Siena F (2002). Subaerial Plio-Pleistocene volcanism in the geo-petrographic and structural context of the north/central Iblean region (Sicily). Periodico di Mineralogia 71, 159–89.

Di Maggio C, Incandela A, Masini F et al. (1999). Oscillazioni eustatiche, biocronologia dei depositi continentali quaternari e neotettonica nella Sicilia Nord Occidentale (Penisola di San Vito Lo Capo - Trapani). Il Quaternario 12, 25–50.

Eltringham SK (1999). The Hippos: Natural History and Conservation. Princeton University Press, Princeton, New Jersey, USA.

Esestime P, Kearns H, Hargreaves P (2015). The Balaeric Basin in the West-Mediterranean: A back-arc basin or a foreland-foredeep basin? Proceedings of 77th EAGE Conference and Exhibition 2015, 1-4 June 2015, Madrid, Spain. http://www.spectrumgeo.com/wp-content/uploads/Esestime-Balearic-Basin-West-Med-WEB.pdf

Esher RJ, Wolfe JL, Layne JN (1978). Swimming behavior of rice rats (Oryzomys palustris) and cotton rats (Sigmodon hispidus). American Society of Mammalogists 59, 551–8.

Fladerer FA, Fiore M (2002). The Early Pleistocene insular hare Hypolagus peregrinus sp. nov. from Northern Sicily. Palaeontographia Italica 89, 37–63.

Garga DP (1948). How far can a tiger swim? Journal of the Bombay Natural History Society 47, 545.

Guarnieri P, Carbone S, Di Stefano A (2002). The Sicilian orogenic belt: A critical tapered wedge? Bollettino della Società Geologica Italiana 121, 221–30.

Haq BU, Hardenbol J, Vail PR (1987). Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–67.

Held SO (1989). Early prehistoric islands archaeology in Cyprus: Configurations of formative culture growth from the Pleistocene–Holocene boundary to the Mid-3rd Millennium B.C. (PhD dissertation). University College, London, UK.

Henderson DM, Naish D (2010). Predicting the buoyancy, equilibrium and potential swimming ability of giraffes by computational analysis. Journal of Theoretical Biology 265, 151–9.

Hertler C, Volmer R (2008). Assessing prey competition in fossil carnivore communities – A scenario for prey competition and its evolutionary consequences for tigers in Pleistocene Java. Palaeogeography, Palaeoclimatology, Palaeoecology 257, 67–80.

Herridge VL (2010). Dwarf elephants on Mediterranean islands: A natural experiment in parallel evolution (doctoral dissertation). UCL, University College London.

Herridge V, Nita D, Schwenninger J et al. (2014). A new chronology for Spingallo Cave (Sicily): Implications for the evolution of the insular dwarf elephant Palaeoloxodon falconeri. Abstract Book of the VIth International Conference on Mammoths and their Relatives. S.A.S.G., Special Volume 102, p. 70.

Johnson DL (1980). Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. Journal of Biogeography 7, 383–98.

Jordan PA, Peterson RO, LeDoux KA (2010). Swimming wolves, Canis lupus, attack a swimming moose, Alces alces. Canadian Field-Naturalist 124, 54–6.

Krijgsman W, Hilgen FJ, Raffi I, Sierro FJ, Wilson DS (1999). Chronology, causes and progression of the Messinian salinity crisis. Nature 400, 652–5.

Larter NC, Nishi JS, Ellsworth T, Johnson D, More G, Allaire DG (2003). Observations of wood bison swimming across the Liard River, Northwest Territories, Canada. Arctic 56, 408–12.

Locatelli E (2011). Insular small mammals from Quaternary deposits of Sicily and Flores (doctoral dissertation). Università degli Studi di Ferrara, Ferrara.

Lomolino MV (1985). Body size of mammals on islands: the island rule reexamined. The American Naturalist 125, 310–6.

© 2017 The Authors. Integrative Zoology published by International Society of Zoological Sciences, Institute of Zoology/Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd
Los SJ, Ricklefs RE, eds (2009). *The Theory of Island Biogeography Revisited*. Princeton University Press, Woodstock, Oxfordshire, UK.

Macchiavelli C (2014). Tectonic reconstruction of Sicily in the framework of the Central Mediterranean geological evolution (PhD thesis). School of Advanced Studies, Doctoral Course in Earth Sciences (XXVI cycle). Camerino University, Italy.

Madurell-Malapeira J, Palombo MR, Sotnikova M (2015). *Cynotherium malatestai* sp. nov. (Carnivora, Canidae) from the early middle Pleistocene deposits of Grotta dei Fiori (Sardinia, Western Mediterranean). *Journal of Vertebrate Paleontology* 35, p. e943400.

Mangano G (2011). An exclusively hyena-collected bone assemblage in the Late Pleistocene of Sicily: Ta-phonomy and stratigraphic context of the large mammal remains from San Teodoro Cave (North-Eastern Sicily, Italy). *Journal of Archaeological Science* 38, 3584–95.

Marcolini F, Masini F, Argenti P (2013). The rodents of the Pirro Nord fauna (Foggia, Southern Italy). *Palaeontographica Abteilung A Palaeozoologie Stratigra- phie* 298, 73–85.

Masini F, Petrusio D, Bonfiglio L, Mangano G (2008). Origination and extinction patterns of mammals in three central Western Mediterranean islands from the Late Miocene to Quaternary. *Quaternary International* 182, 63–79.

Maslin MA, Ridgwell AJ (2005). Mid-Pleistocene rev-olution and the ‘eccentricity myth’. *Geological Society, London, Special Publications* 247, 19–34.

Matthews LH (1939). The biomics of the Spotted Hyena, *Crocuta crocuta* Erx. *Proceedings of the Zoological Society of London* 39, 43–56.

Mazza PP, Lovari S, Masini F, Masseti M, Rustioni M (2013). A multidisciplinary approach to the analysis of multifactorial land mammal colonization of is-lands. *BioScience* 63, 939–51.

Meijaard E (2001). Successful sea-crossings by land mammals: A matter of luck and a big body. In: Sudijono J, Aziz F, eds. *Towards Ahead: Geological Mu-seum in a Changing World*. Papers Presented in the International Symposium on Geological Museum. 22–24 August 2000, Bandung, Indonesia. Geological Research and Development Centre, Special Publications 27, 87–92.

Melis RT, Palombo MR, Ghaleb B, Meloni S. (2016) A key site for inferring the timing of dispersal of giant deer in Sardinia, the Su Fossu de Cannas cave, Sada-li, Italy. *Quaternary Research* 86, 335–47.

Moyá-Solà S, Köhler M, Alba D, Pons-Moyá J (2007). El significado de *Myotragus batel* y *M. binigau-sensis* en la evolución del género *Myotragus* (Bovidae, Mammalia) en las Islas Baleares. *Monografies de la Societat d’Historia Natural de les Balears* 14, 155–80.

Michaels C (2015). Weird news – Animals fleeing Swe-den and swimming to Denmark. [Cited 30 March 2017.] Available from URL: http://www.justtheweird-news.com/2015/02/18/weird-news-animals-fleeing-sweden-and-swimming-to-denmark/.

Monnet C, Gleason JS (2006). Observations of mortal-ity associated with extended open-water swimming by polar bears in the Alaskan Beaufort Sea. *Polar Biology* 29, 681–7.

Nelson ME, Mech LD (1984). Observation of a swim-ming wolf killing a swimming deer. *Journal of Mammalogy* 65, 143–4.

Nowak RM (1999). *Walker’s Mammals of the World*. Cambridge University Press, Cambridge.

Oliver WLR, Cox CR, Groves CP (1993). The Philip-pine warty pigs (*Sus philippensis* and *S. cebifrons*). In: Oliver WLR, ed. *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan*. International Union for Conservation of Nature, IUCN, Washington, US, pp. 145–54.

Pagano AM, Durner GM, Amstrup SC, Simac KS (2012). Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water. *Canadian Journal of Zoology* 90, 663–76.

Palombo MR (1985). I grandi mammiferi pleistocenici delle isole del Mediterraneo: tempi e vie di migrazi-one. *Bollettino Della Societa Paleontologica Itali-an*a. 24, 201–4.

Palombo MR (2006). Biochronology of the Plio-Pleisto-cene terrestrial mammals of Sardinia: The state of the art. *Hellenic Journal of Geosciences* 41, 47–66.

Palombo MR (2007). How can endemic elephant help us understanding ‘island rule’? *Quaternary Interna-tional* 169–70, 105–24.

Palombo MR (2009). Biochronology, palaeobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integrative Zoology* 4, 367–86.

Palombo MR (2014). Deconstructing mammal disper-sals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews* 96, 50–71.
Palombo MR (2016). Lights and shadows in the evolutionary patterns of insular Elephantini. In: Holwerda F, Madern A, Voeten D et al. eds. Programme and abstract book. XIV Annual Meeting EAVP - European Association of Vertebrate Palaeontologists, 6-10 July 2016, Haarlem, The Netherlands, p. 106

Palombo MR (2017). Discrete dispersal bioevents of large mammals in Southern Europe in the post-Olduvai Early Pleistocene: A critical overview. Quaternary International 431, 3–19.

Palombo MR, Ferretti MP, Pillola GL, Chiappini L (2012). A reappraisal of the dwarfed mammoth Mammutthus lamarmorai from Gonnese (south-western Sardinia, Italy). Quaternary International 255, 158–70.

Palombo MR, Rozzi R, Bover P (2013). The endemic boids from Sardinia and the Balearic Islands: State of the art. Geobios 46, 127–42.

Palombo MR, Antonioli F, Presti VL et al. (2017). The late Pleistocene to Holocene palaeogeographic evolution of the Porto Conte area: Clues for a better understanding of human colonization of Sardinia and faunal dynamics during the last 30 ka. Quaternary International 439, 117–40.

Palombo MR, Zedda M (2016). The intriguing question of the Pleistocene Sardinian otters. In: Holwerda F, Madern A, Voeten D et al. eds. Programme and abstract book. XIV Annual Meeting EAVP - European Association of Vertebrate Palaeontologists, 6-10 July 2016, Haarlem, The Netherlands, p. 144.

Palombo MR, Zedda M, Melis RT (2017). A new elephant fossil from the Late Pleistocene of Alghero: The puzzling question of Sardinian dwarf elephants. Comptes Rendus Palevol, doi:10.1016/
j.crpv.2017.05.007

Pepe F, Sulli A, Agate M et al. (2003). Plio-Pleistocene geological evolution of the northern Sicily continental margin (southern Tyrrhenian Sea): New insights from high-resolution, multi-electrode sparker profiles. Geo-Marine Letters 23, 53–63.

Peretto C, Arnaud J, Moggi-Cecchi J et al. (2015). A human deciduous tooth and new 40Ar/39Ar dating results from the middle pleistocene archaeological site of isernia la pineta, southern italy. PLoS ONE 10, p.e0140091.

Petruso D, Locatelli E, Surdi G, Dalla Valle C, Masini F, Sala B (2011a). Phylogeny and biogeography of fossil and extant Microtus (Terricola) (Mammalia, Rodentia) of Sicily and the southern Italian peninsula based on current dentalmorphological data. Quaternary International 243, 192–203.

Petruso D, Sarà M, Surdi G, Masini F (2011b). Le faune a mammiferi della Sicilia tra il tardo-glaciale e l’Olocene. Biogeographia 30, 27–39.

Piper PJ, Ochoa J, Lewis H, Paz V, Ronquillo WP (2008). The first evidence for the past presence of the tiger Panthera tigris (L.) on the island of Palawan, Philippines: Extinction in an island population. Palaeogeography, Palaeoclimatology, Palaeoecology 264, 123–7.

Pons-Monjo G, Moyà-Solà S, Furió M (2012). New data on the origin of Nesiotites (Soricidae, Mammalia) in Menorca (Balearic Islands, Spain). Comptes Rendus Palevol 11, 393–401.

Reumer JWF (1982). Some remarks on the fossil vertebrates from Menorca, Spain. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen: Series C: Biological and Medical Sciences 85, 77–87.

Riopelle AJ, Hubbard DG (1982). Vestibular function and development of swimming behavior in rhesus monkeys. Journal of Human Evolution 11, 377–82.

Rofes J, Bover P, Cuenca-Bescós G, Alcover JA (2012). Nesiotites rafelinensis sp. nov., the earliest shrew (Mammalia, Soricidae) from the Balearic Islands, Spain. Palaeontologia Electrónica 15, p. 8A.

Rook L, Gallai G, Torres D (2006). Lands and endemic mammals in the Late Miocene of Italy: Constrains for paleogeographic outlines of Tyrrenhian area. Palaeogeography, Palaeoclimatology, Palaeoecology. 29, 263–9.

Rosenbaum G, Lister GS (2004). Neogene and Quaternary rollback evolution of the Tyrrenhian Sea, the Apennines, and the Sicilian Maghrebides. Tectonics 23, TC1013, 1–17.

Sala B, Masini F (2007). Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. Quaternary International 160, 4–16.

Schmincke HU, Behncke B, Grasso M, Raffi S (1997). Evolution of the northwestern Iblean Mountains, Sicily: Uplift, Pliocene/Pleistocene seal-level changes, paleoenvironment, and volcanism. Geologische Rundschau 86, 637–69.

Simpson GG (1940). Mammals and land bridges. Journal of the Washington Academy of Science 30, 137–63.

Simpson GG (1965). The Geography of Evolution. Chilton Books, Philadelphia, New York.
Sondaar PY (1986). The island sweepstakes: why did pygmy elephants, dwarf deer, and large mice once populate the Mediterranean? *Natural History* **95**(9), 50–57. [http://www.naturalhistorymag.com/htmlsite/master.html?http://www.naturalhistorymag.com/htmlsite/editors_pick/1986_09_pick.html]

Summerhayes CP (2015). *Earth’s Climate Evolution*. John Wiley & Sons, Chichester, West Sussex, UK.

Thomas DP, Fregin GF, Gerber NH, Ailes NB (1980). Cardiorespiratory adjustments to tethered-swimming in the horse. *Pflugers Archiv* **385**, 65–70.

Tokuri M, Ohtsuki R, Kalt M et al. (1999). EMG activity of the muscles of the neck and forelimbs during different forms of locomotion. *Equine Veterinary Journal* **30** (Suppl), 231–4.

Torres-Roig E, Bailon S, Bover P, Alcover JA (2017). An early Plioene anuran assemblage from Mallorca (Balearic Islands, Western Mediterranean): Palaeobiogeographic and palaeo-environmental implications. *Palaeobiodiversity and Palaeoenvironments*, 1–13.

Van Valen L (1973). A new evolutionary law. *Evolutionary Theory* **1**, 1–33.

Van der Geer A, Lyras G, de Vos J, Dermitzakis MD (2010). *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands*. Wiley-Blackwell, Oxford.

Van der Made J (1999). Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. *Deinsea* **7**, 377–60.

Van der Made J, Palombo MR (2006). *Megaloceros sardus* n. sp., a large deer from the Pleistocene of Sardinia. *Hellenic Journal of Geosciences* **41**, pp. 163–76.

Vigne JD, Marinval-Vigne MC (1988). Contribution à la connaissance du Cerf de Corse (Cervus elaphus, Artiodactyla, Mammalia) et de son histoire. *Bulletin Ecologie* **19**, 177–87.

Wallace AR (1869). *The Malay Archipelago—The Land of the Orang-utan and the Bird of Paradise: A Narrative of Travel with Studies of Man and Nature*. Macmillan, London, UK.

Whitehead GK (1993). *The Whitehead Encyclopedia of Deer*. Swan Hill Press, London.

Wilson M, Kenady S, Schalk R (2009). Late Pleistocene *Bison antiquus* from Orcas Island, Washington, and the biogeographic importance of an early postglacial land mammal dispersal corridor from the mainland to Vancouver Island. *Quaternary Research* **71**, 49–61.

Zinner D, Arnold ML, Roos C (2009). Is the new primate genus *Rungwecebus* a baboon? *PLoS ONE* **4**, e4859.

**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.