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Three islands, three worlds: Paleogeography and evolution of the vertebrate fauna from the Balearic Islands

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Abstract

The Balearic Islands are an archipelago located in the Western Mediterranean Sea. Their isolation from the mainland allowed the establishment of different faunas on each island. In Mallorca, the Pliocene fauna was composed of the so-called *Myotragus*-fauna (mainly consisting of a bovid, a glirid and a soricid). In Menorca, it was constituted by the giant rabbit-fauna (mainly consisting of a giant rabbit and a tortoise), and in the Pityusics by a tortoise, a lizard and two rodents. A main faunal turnover took place during the Late Pliocene or Early Pleistocene: the *Myotragus*-fauna reached Menorca and replaced the giant rabbit fauna. In the Pityusics, all mammals and the tortoise became extinct before the Late Pleistocene for unknown reasons, leaving birds and the lizard as the only vertebrates of these islands. Almost all the endemic vertebrates of the Balearics became extinct probably due to the first human arrival to the islands.

1. Introduction

The Mediterranean is an almost completely closed sea located between Europe and Africa, with a complex geographical history. It contains archipelagos that differ in area, geology, height above sea-level, isolation, antiquity, ecology and timing of human colonization (e.g., Maldonado, 1985; Margalef, 1985; Ramis and Alcover, 2004). Almost all the Mediterranean islands have very important deposits of fossil vertebrates, some of which have been known since the end of the 19th century. Thus, the Mediterranean is an interesting scenario for the study of island vertebrate evolution. The isolation of most of the Mediterranean islands spreads over millions of years (Myr), and fossil records have documented the presence of very singular, highly modified species in these islands in the past.

The main goal of this paper is to update the knowledge of the vertebrate fossil fauna from the Balearic Islands (sensu lato) since the start of their current isolation (i.e., since the last moment they were connected to the surrounding mainland). The Balearic Islands are the most isolated islands in the Mediterranean. This archipelago is composed by two different groups of islands (''sub-archipelagos''). The Western set, or Pityusic Islands, consists of two main islands (Eivissa [''Ibiza''] and Formentera) and nearly 60 smaller surrounding islets. These two islands are separated by a narrow, shallow channel, and they shared their faunas throughout their paleogeographical history. They will be analyzed as a single unit in this paper. On the other hand the Eastern set, or Gymnesic Islands, is more isolated than the Pityusics and is constituted by two main islands (Mallorca and Menorca) and nearly 30 surrounding islets. These two islands display a different paleogeographical history at the beginning of their history as islands, and a peculiar faunal succession.

The current isolation of the Balearic Islands began at the end of the Messinian salinity crisis (MSC), 5.3 Myr ago (Gautier et al., 1994; Clauzon et al., 1996; Krijgsman et al., 1999). Although some Middle and Late Miocene insular faunas have been recorded, there is no evidence of their continuity through the Messinian. The duration of the

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current isolation of these sub-archipelagos embraces different climatic changes. On the one hand, the beginning of the Late Pliocene coincides with the change from a Subtropical climate [or warm-temperate (e.g., Fauquette et al., 1999)] to a Mediterranean one (e.g., Shackleton et al., 1984; Suc, 1984; Leroy and Dupont, 1994; Burkle, 1995; Bourillet et al., 2006). On the other hand, during the last 2.5 million years the Mediterranean area has been widely influenced by glaciations. The changing climate of this area has influenced the paleogeography and evolution of the species living there.

The Balearic Islands, due to their degree of isolation, have been colonized by humans in a very recent time (in comparison with less isolated Mediterranean islands). Although until 2001 human arrival was assumed to have occurred 8000 years ago (or even more) (e.g., Guerrero, 2000, 2001), some recent reviews document the first evidence of human presence in Mallorca in the third millennium BC (Alcover et al., 2001; Ramis et al., 2002), and the human settlement occurred probably in the last third of the millennium (Alcover, submitted).

Both the degree (distance from mainland) and duration (millions of years) of isolation have been key factors for the evolution of highly peculiar taxa in the Balearics. Thus, the Balearic Islands have been considered "oceanic-like islands" (Alcover et al., 1998). "Oceanic-like islands" were described by these authors as islands that have been previously connected to continents, but that are faunistically similar to oceanic islands (i.e., with a high level of endemism and highly unbalanced, poor faunas), because the island-continent connection occurred in a distant past, was of short duration, or did not promote a complete faunal transfer.

Although no direct evidence of the duration of the Messinian connection of the Balearic Islands with the surrounding mainlands is available, and there is no data about how the geographic filtering took place, faunal transfer has been very incomplete.

Both Balearic Islands groups contained highly distinctive faunas in the Early Pliocene. They evolved to be the most singular territories in the Mediterranean: the Pityusics were the only islands in the whole Mediterranean Sea without mammals during the Late Pleistocene and Early Holocene, while the Gymnesics were the sole Mediterranean islands inhabited by a highly modified caprine at that time (Alcover et al., 1981).

2. Early insular faunas

Although the main goal of this paper is to focus on the post-Messinian fossil faunas, a short sketch of the clearly insular faunas known in the Balearic Islands predating the Messinian crisis is presented here. The earliest faunas with an unquestionable insular character known in the Balearic Islands are represented by finds in four Miocene deposits from Mallorca (Santa Margalida, Sant Llorenç, Cova de Cala Varques D, Cova des Coll) and two deposits from Menorca (Punta Nati-2 and Es Cul de Sa Ferrada).

In Mallorca, the fauna from Santa Margalida-Sant Llorenç has been attributed to the Langhian age (MN 5; Mein and Adrover, 1982), although a more recent attribution (Serravallian) cannot be rejected. The island character of this fauna is demonstrated by three facts: it is oligospecific, highly disharmonic, and endemic. The fauna includes an ochotonid lagomorph (*Gymnesicolagus gelaberti* Mein and Adrover 1982) and 3 glirid rodents (*Carbomys sacaresi* Mein and Adrover 1982, *Margaritamys llulli* Mein and Adrover 1982 and *Peridyromys ordinasi* Mein and Adrover 1982) (Mein and Adrover, 1982; Adrover et al., 1983, 1984). *G. gelaberti* is the largest of the known Ochotonidae, and *C. sacaresi* is a giant glirid with nonestablished taxonomic affinities. The recent exploration of underwater caves excavated in the East Mallorcan Miocene platform allowed the discovery of other Late Miocene pre-Messinian deposits: Cova des Coll and Cova de Cala Varques B (e.g., Gràcia et al., 2005). These deposits have yielded remains of large terrestrial tortoises (*Geochelone* sp), as well as remains of a sea turtle (*Trionyx* sp).

From Menorca, the deposit of Punta Nati 2 yielded remains of a *Gymnesicolagus*, a glirid, similar to *M. llulli* from the Mallorcan deposits of Santa Margalida and Sant Llorenç, and a large tortoise. Its precise chronology is unknown, but it predates the Messinian. A small fragment of a *Gymnesicolagus* jaw has been recovered from the second Menorcan deposit, Es Cul de Sa Ferrada. This deposit has been attributed to the Tortonian (Quintana and Agustí, in press).

All these insular faunas suggest that in the Middle and perhaps also in the Late Miocene there was a set of islands near the coast of the Spanish mainland. Another insular fauna from the Middle Miocene was found in the currently mainland area of Murchas (Granada), Spain (Martin-Suárez et al., 1993). This fauna seems to be related to the *Gymnesicolagus* faunas from Mallorca and Menorca, and it contains some insular-evolved species descendants of *Pseudodryomys* de Bruijn 1966 and *Peridyromys* Stehlin and Schaub 1951.

3. Messinian salinity crisis

A key event affecting faunal distribution and evolution in the Mediterranean during the Late Miocene was the MSC. It promoted a significant faunal exchange between Europe and Africa, and a faunal turnover in the Balearic Islands (e.g., Agustí et al., 2006; van der Made et al., 2006 and references therein), and is considered to be the time of colonization of the Balearic Islands by the fauna that evolved in this territory during the Pliocene, and, in some cases, until the Holocene (e.g., van der Made et al., 2006). The MSC was discovered in the early 1970s (Hsü et al., 1973) and there is currently a general consensus on the age that it took place, between 5.96 and 5.33 Myr (e.g., Krijgsman et al., 1999).

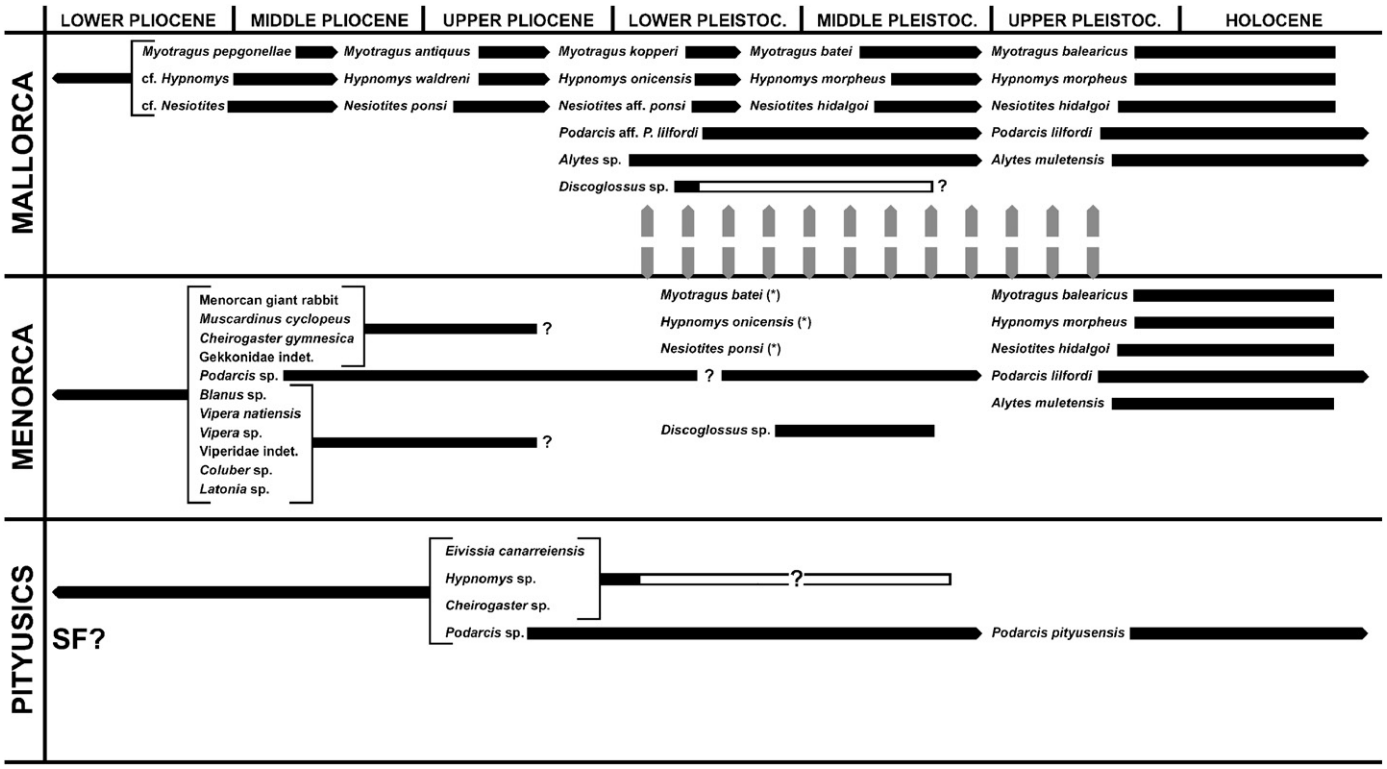

Fig. 1. Diagram of the different faunal sets (only terrestrial vertebrates are figured) that lived in the Balearic Islands during the Plio-Quaternary. (SF?) = Ses Fontanelles fauna, with unknown chronology (Late Miocene–Early Pliocene?). (*) = Considered as endemic fauna (*M. binigausensis*, *H. eliomyoides* and *N. meloussae*, respectively) by Pons-Moyà et al. (1981). The gray arrows show the contact between Menorca and Mallorca during Quaternary glaciations. See text for further explanation.

The MSC occurred when the connection between the Mediterranean Sea and the Atlantic Ocean was closed due to tectonic displacements (Krijgsman et al., 1999), promoting the partial (or perhaps total) Mediterranean dissecation and a sea level drop of nearly 1500 m between 5.6 and 5.32 Myr (Clauzon et al., 1996). Currently, three different faunal assemblages are recognized as living in the Balearics since the MSC. Mallorca, Menorca and the Pityusics display a remarkably different Pliocene vertebrate record (Fig. 1).

4. Plio-Quaternary faunas

4.1. Mallorca

Mallorca is the sole Balearic Island with a clear continuity in its terrestrial vertebrate fauna from the Messinian to the Holocene. The land mammals present at the time of human arrival are the direct descendants of those that reached Mallorca during the Messinian (e.g., Bover and Alcover, 2003). The vertebrate fauna consists of three land mammals, a lizard, two amphibians, bats and birds.

The most remarkable taxon belonging to this fauna is the bovid *Myotragus* Bate 1909. Its lineage evolved in a highly peculiar way, and it is considered the key species to understanding the palaeoecology of Mallorca, due to its potential effect on the Mallorcan vegetation (e.g., Alcover et al., 1999).

To date, five chronospecies have been described in this bovid lineage. Alcover et al. (1981) claimed that the major patterns recorded during its evolution consists of the progressive reduction of the number of incisiform teeth (incisors and canines) and premolars, the increase in the degree of hypsondonty of all teeth, the acquisition of evergrowing incisors, the shortening of the rostral part of the skull and jaw, the lengthening of frontal bones, the frontalization of eye sockets, the acquisition of short, stout limb bones (with extremely short metapodials and phalanges), the progressive fusion of tarsal bones, the change in the structure of the pelvis and the acquisition of a small size. As a consequence of this insular evolution, each of the *Myotragus balearicus* (Bate, 1909) bones is highly distinctive among caprines.

The acquisition process of these features can be traced through the different species of the lineage, from *M. pepgonellae* Moyà-Solà and Pons-Moyà 1982 (attributed to the Early Pliocene), through *M. antiquus* (Pons-Moyà, 1977) (Middle Pliocene), *M. kopperi* Moyà-Solà and Pons-Moyà 1981 (Plio-Pleistocene boundary), *Myotragus batei* Crusafont and Angel 1966 (Early-Middle Pleistocene), to *M. balearicus* (uppermost part of the Middle Pleistocene to the Holocene). The last three species are characterized by the reduction of the number of incisors at

adult age, with a remarkably increased lengthening of their enameled part.

M. balearicus presents a high number of anatomical derived characters. Such apomorphies have been traditionally interpreted as morphological adaptations to a Mediterranean xerophytic isolated environment free of mammalian carnivores (e.g., Sondaar, 1977; Alcover et al., 1981). Some of the peculiarities of *M. balearicus* are related to an increase in the efficiency of herbivorous feeding and, thus, to a higher potential impact on the vegetation.

Caprines are considered some of the most efficient consumers of vegetation, and the impact of goats on islands is well known [see Campbell et al., 2004; Campbell and Donlan, 2005, for a review of the known impacts of goat introductions on islands]. Such a putative effect would have been increased in the case of Mallorca and Menorca where *M. balearicus*, the terminal species of the lineage (Fig. 2), was not only the sole middle-sized herbivore, but was also living in an isolated environment without carnivore predators, and developed a highly powerful feeding apparatus. Increased hypsodonty, reduction of distal jaw length (Alcover et al., 1981), proportional increase of insertion ridges for mastication muscles in skull and jaw, and concentration effort mainly on M3 and distal part of M2 (Bover, 2004) might be related to this high efficiency of feeding on vegetation with a xerophytic character.

The phylogenetic relationships of *Myotragus* are still not clearly understood. Initially (Andrews, 1915; Gliozzi and Malatesta, 1980; Palombo et al., 2006) it was related to *Nemorhaedus* Smith 1827 and *Capricornis* Ogilby 1837. These genera were traditionally related to *Rupicapra* de Blainville 1816 and *Oreamnos* Rafinesque 1817 and included with the former in Rupicaprini (see Simpson, 1945). Further approaches (e.g., Gentry, 1978; Gatesy et al., 1997; Hassanin and Douzery, 1999, 2003) questioned the monophily and recognition of the Rupicaprini and Caprini by Simpson (1945). Recent biomolecular research (Lalueza-Fox et al., 2005) supports a relationship between *Myotragus* and *Ovis* Linnaeus 1857, excluding the assumed relationship with the "Rupicaprini". A formerly proposed relationship of *Myotragus* to the clade *Ovis+Budorcas* is rejected as an artifact derived from a wrong adscription of *Budorcas* Hodgson 1850 data in the GenBank (see Lalueza-Fox et al., 2005).

Fig. 2. *M. balearicus* skull (MNIB 81723) from Cova des Tancats (Menorca) in lateral view. The presence of a single evergrowing incisor, reduction of number of premolars and frontalization of eye orbits are some of the most important derived features in the skull of the species. Scale bar 2 cm.

Recently, Bover and Alcover (2005) proposed to include the earlier Mallorcan *Myotragus* species in a new genus, *Insulotragus* Bover and Alcover 2005. This proposal emphasizes the existence of an evolutionary change between the two earlier recognized species in the lineage and the last three ones, although the new name could be used as a subgenus of *Myotragus* to emphasize that they belong to a single insular lineage. One of the most distinctive characteristics of this bovid lineage is the progressive reduction in the number of incisiform teeth. This reduction has been interpreted as related to the acquisition of monophiodoncy in these teeth (Bover and Alcover, 1999).

The clearest sequence of the evolutionary patterns explained above can be observed in the series extending from *M. kopperi* (Plio-Pleistocene boundary), through *M. batei* (Early-Middle Pleistocene) and *M. balearicus* (latest Middle Pleistocene to Holocene). In the later species, an extreme effect of insular evolution can be observed, mainly on the feeding apparatus, locomotion, sense organs and body size.

The fusion of some tarsal bones (naviculocuboid fused to small and great cuneiforms and to the canon bone) was first functionally described by Leinders and Sondaar (1974), in which the zig-zag movements allowed by the movement of these bones when unfused were not possible in *M. balearicus*. Later, more features related to joint stabilization and "low-gear" locomotion in the species were described. Some of the most significant are the presence of reduced joint angles in several bones (Spoor, 1988), the peculiar calcaneum shape (Moyà-Solà, 1979), the reduced metapodial joint surface (Spoor, 1988; Köhler, 1993), some metacarpal bone fusions (Bover et al., 2005) and the femur, humerus–radius joint and pelvis characteristics (Bover, 2004, 2006).

Köhler and Moyà-Solà (2001) suggest that the presence of notches in some *M. balearicus* phalange joints could be related to the presence of intracapsular ligaments as a special joint stabilization mechanism. Nevertheless, these same notches are present on the phalange joints of some recent bovids deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. (NMNH). They correspond to very old specimens from zoological parks. This suggests that the notches could be more related to the acquisition of a very old age than to

the presence of a special joint stabilization mechanism (Bover, 2004).

The proportional size of the brain is reduced in *M. balearicus* (Köhler and Moyà-Solà, 2004), and some sense organs could have been less sensitive. It has been suggested that the reduction of the eye sockets could have affected the vision (Köhler and Moyà-Solà, 2004) and the presence of a less developed criba nasalis would have affected the sense of smell (Bover and Tolosa, 2005).

Together with the ancestors of *Myotragus*, two other terrestrial mammals evolved in Mallorca after the Messinian, a glirid rodent, probably derived from *Eliomys truci* Mein and Michaux 1970 or a close species, and a soricid insectivore. Both genera evolved together with *Myotragus* but they did not reach the extreme differentiation observed in the bovid lineage. Two endemic genera were proposed for them, *Hypnomys* Bate 1918 and *Nesiotites* Bate 1944, sometimes included as subgenera of other genera (*Eliomys* for the glirid and *Episoriculus* Horsfield 1851, *Soriculus* Blyth 1854 or *Asoriculus* Kretzoi 1959 for the soricid). These species are larger than their mainland relatives, which is in agreement with the general patterns recorded for island mammals (e.g., Thaler, 1973; Case, 1978; Heaney, 1978).

Three species of *Hypnomys* (Rodentia: Gliridae) have been described. *Hypnomys waldreni* Reumer 1979, which coexisted with *Myotragus antiquus* (Middle Pliocene), *Hypnomys eliomyoides* Agustí 1980 [= *H. onicensis* (Reumer 1994), sensu Reumer (1994)], contemporary with *Myotragus kopperi* and probably *M. batei* (Plio-Quaternary boundary to Middle Pleistocene) and *Hypnomys morpheus* Bate 1918 which coexisted with *M. balearicus* (uppermost part of the Middle Pleistocene to the Holocene) (Alcover et al., 1981). Although a few glirid bones have been found in the type deposit of *Myotragus pepgonellae* (Cala Morlanda, Early Pliocene) (Bauzá, 1961), they have not been ascribed to any particular species (Alcover et al., 1981).

The main evolutionary pattern observed in the *Hypnomys* lineage consists of the progressive acquisition of a large size, the increase of tooth crown height and the acquisition of a flat occlusal surface in the molars (related to the presence of xerophytic vegetation). According to Mills (1976), *H. morpheus* was probably more adapted to a rat life-style than to a dormouse life-style, probably displaying a less scansorial behavior than recent dormice.

Only two species of *Nesiotites* (Soricomorpha: Soricidae) have been described in Mallorca. *Nesiotites hidalgoi* Bate 1944 was described by Bate (1944) to include the fossil shrew of Late Pleistocene deposits from Mallorca and Menorca, coetaneous with *M. balearicus* and *H. morpheus*. Reumer (1979) described its ancestor, *N. ponsi* Reumer (1979), coming from deposits containing *M. antiquus*. This species displays a small size and a characteristic dental pattern, with secondary cusps on the M_1 and M_2. Some Soricidae remains described as cf. *Nesiotites* have been obtained in the deposits where *M. pepgonellae* was present. Furthermore, an intermediate form has been found in the Pedrera de s'Òmix deposit (from where *M. kopperi* was recovered, Plio-Quaternary boundary) but it has been described as *Nesiotites* aff. *ponsi* (Alcover et al., 1981).

Remains of a lizard have also been found in deposits from the Early Pleistocene to the Holocene. Although the Early Pleistocene remains were described as *Podarcis* sp, and are characterized by a very small size, the Middle Pleistocene to Holocene remains were ascribed to the same species as is nowadays living in the isles surrounding Mallorca and Menorca, *Podarcis lilfordi* (Günther 1874).

Two amphibians are known from the Pleistocene deposits of Mallorca. *Discoglossus* sp, a large-sized discoglossid frog, is only known from Pedrera de s'Òmix, the type deposit of *M. kopperi.* It is absent in all the known deposits of the Middle and Late Pleistocene. *Alytes muletensis* Sanchíz and Adrover 1977, the Mallorcan Midwife Toad, has been identified from deposits ranging from the Early Pleistocene to the Holocene. After its description as a fossil frog (Sanchíz and Adrover, 1977), *A. muletensis* was found living in very inaccessible torrents from the Serra de Tramuntana of Mallorca 25 years ago (Mayol et al., 1981) and is now one of the main species concerned in the wildlife preservation programs in the Balearic Islands.

4.2. Menorca

Two successive post-Messinian insular faunas have been reported from Menorca. The earliest faunal assemblage is situated inside the Pliocene, and probably spread during the Early and Middle Pliocene (Quintana, 1998; Alcover et al., 1999). Its most characteristic elements are a giant tortoise (Bate, 1914) and a yet unnamed giant rabbit (Fig. 3). Additional taxa include the remains of a dormouse (*Muscardinus cyclopeus* Agustí, Moyà-Sola and Pons-Moyà 1982), a bat (*Rhinolophus* cf. *grivensis* Depéret 1892) (Pons-Moyà et al., 1981) and several genera and species of birds: a petrel (*Pterodromoides minoricensis* Seguí, Quintana, Fornós and Alcover 2001), a woodcock (*Scolopax carmesinae* Seguí 1999), a crane (*Camusia quintanai* Seguí 2002), two owls [*Tyto balearica* Mourer-Chauviré, Alcover, Moyà-Solà and Pons-Moyà 1980 and *Athene* sp (Seguí, 1998)], a crow (*Corvus* sp) and an unidentified passeriform (Seguí, 1998).

Among the reptiles, fossils include a lizard (*Podarcis* sp) (Bailón, 2004), which could be the *P. lilfordi* ancestor), a geckonid (Gekkonidae indet.), an amphisbaenid (*Blanus* sp) (Garcia-Porta et al., 2002; Bailón et al., 2005), a colubrid (*Coluber* sp) (Bailón et al., 2005), and two viperids (*Vipera natiensis* Bailón, Garcia-Porta and Quintana 2002 and *Vipera* sp) (Bailón et al., 2002). Included in the giant rabbit fauna there is just one species of amphibian: *Latonia* sp (Quintana et al., 2005).

The low number of species, the lack of representatives of Carnivora and Perissodactyla, the gigantism of the dormouse and the rabbit, and the change in the morphol-

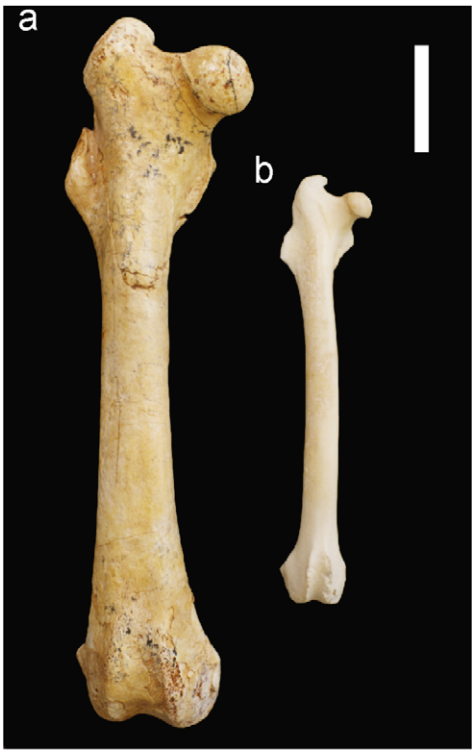

Fig. 3. Comparison between a right femur of the giant rabbit from Menorca (a) and a right femur of a recent *Oryctolagus cuniculus* (b). The difference in size, together with the different orientation and joint surface of the femur head, are among the major distinctive features of the bone of the Menorcan giant rabbit. Scale bar 2 cm.

ogy of the skeleton of the latter, allow us to state that this faunistic group evolved in island conditions. The giant rabbit from Menorca clearly displays some of these insular characteristics. It has been estimated to have had a body weight of 14 kg, very small eye sockets and tympanic bulla, a relatively small head in relation to the body, and limbs and vertebral column shorter than those of the recent cursorial rabbits (Quintana, 2005; Quintana et al., 2005).

A faunal turnover occurred in Menorca during the Late Pliocene or Early Pleistocene. To date, the Menorca giant rabbit fauna have not been recorded in Pleistocene deposits, suggesting that this fauna disappeared from this island before then. In Menorcan Pleistocene and Holocene deposits only the *Myotragus* fauna is recorded. The arrival of this fauna to Menorca could be related to the beginning of the glaciations and the related melting of Mallorca and Menorca (e.g., Cuerda, 1975).

Although a *Myotragus* species was described from the Early Pleistocene of Menorca, *Myotragus binigausensis* Moyà-Solà and Pons-Moyà 1980, it has recently been synonymized to *M. batei* (the same species as in Mallorca) by Bover and Alcover (2000). *M. binigausensis* was initially considered to be a representative of a different lineage of the genus on the island of Menorca, whose ancestor reached this island during the Messinian (Moyà-Solà and Pons-Moyà, 1980; Alcover et al., 1981). Other endemic mammalian species from Menorca that were described from a Menorcan site, including the glirid *H. eliomyoides* Agustí 1980 and the soricid *Nesiotites meloussae* Pons-Moyà and Moyà-Solà 1980, are also currently considered to be conspecific with the representative of those genera for that period in Mallorca. Thus, the available evidence argues in favor of the dispersal of these three land mammals (*Myotragus*, *Hypnomys* and *Nesiotites*) to Menorca from Mallorca during a glaciation period, at an unknown moment in the Late Pliocene or Early Pleistocene (Bover, 2004). No evidence of specific differentiation of any mammal has been obtained in Menorca once the *Myotragus* fauna reached the island, probably because of the recurrent coalescence of both islands during the glaciations, which allowed repetitive inbreeding between both populations (Bover, 2004).

The lizard of genus *Podarcis* Wagler 1830 was also present in Menorca, at least since the Pliocene (Bailón, 2004). Its evolutionary lineage can be traced until the arrival of the Romans (Reumer and Sanders, 1984). Currently, as happens in Mallorca, the species survives only on some small islets.

A species of Midwife toad, *Alytes talaioticus* Sanchíz and Alcover 1982, was described in Menorca from Holocene deposits (Sanchíz and Alcover, 1982). It is currently considered to be the same species as the Mallorcan *Alytes muletensis* (e.g., Barbadillo, 1987). A still undescribed species of *Discoglossus* Otth 1837 is known from the Plio-Pleistocene boundary deposit of Barranc de Binigaus, Sa Segonya and Punta Esquitxador (Alcover et al., 1981; Quintana, 1998).

4.3. Eivissa

An early insular fauna from Eivissa comes from Ses Fontanelles. Its stratigraphic position is unknown. The Ses Fontanelles fauna contains two bovids, two rodents (one gerbilid, *Protatera* sp, and one glirid, *Eliomys* sp), an insectivore, and a leporid (*Alilepus* sp) as well as some reptiles (a lizard and a tortoise) (Moyà-Solà et al., 1984, 1999). The presence of the two rodents and the leporid suggest that this deposit could be attributed to the Messinian (Agustí and Moyà-Solà, 1990), given that these taxa have also been recorded in deposits of the Late Miocene and Early Pliocene from the Iberian Peninsula. One of the bovids present in this deposit was identified as *Tyrrhenotragus* sp by Agustí and Moyà-Solà (1990). Current knowledge, however, suggests that *Tyrrhenotragus* Hürzeler and Engesser 1976 lived between 6 and 9 Myr ago, and that the fauna of Ses Fontanelles has a more recent age (Moyà-Solà et al., 1999). Due to the paucity of more material from the two bovids, it seems prudent to attribute this fauna to the Late Miocene–Early Pliocene, namely in the same compatible context as the giant rabbit fauna and *Myotragus* fauna.

Only one Eivissian site is attributed here to the Late Pliocene, Cova de Ca Na Reia. It is a karst deposit with a

fauna containing the remains of two glirids (*Eivissia canarreiensis* Alcover and Agustí 1985 and *Hypnomys* sp) (Alcover and Agustí, 1985), a middle-sized tortoise (*Cheirogaster* sp) (Bour, 1985) and a lizard (*Podarcis* sp) (Kotsakis, 1981). Bats and birds are also present. This is the type locality for *Puffinus nestori* Alcover 1989, the presumed ancestor of *Puffinus mauretanicus* Lowe 1921/*yelkouan* Acerbi 1827.

Giant tortoises are known from three other sites: Es Pouàs (lower levels), Pedrera de Can Bessora (Sant Antoni de Portmany) and La Mola cliffs (Formentera). None of these deposits has been isotopically dated and they should be tentatively attributed to some time inside the Late Pliocene–Middle Pleistocene. It is not known whether the absence of glirid remains in these deposits represents only a sampling problem or whether it reflects true absence.

Eight Late Pleistocene deposits are known from Eivissa and Formentera. These deposits have yielded tens of thousands of vertebrate bones (only one deposit, Es Pouàs, yielded over 120,000 bones). The vertebrate fauna consists only of fossil birds, bats and a lizard species (*Podarcis pityusensis* Boscá 1883). The bird fauna is highly peculiar, and has been ecologically paralleled to the Hawaiian fossil bird fauna (Seguí and Alcover, 1999). One of the species of this fauna is *Rallus eivissensis* McMinn, Palmer and Alcover 2005, the sole endemic rail described so far from a Mediterranean island (McMinn et al., 2005).

5. Faunal extinction

5.1. Last occurrence data

Key data for the establishment of the extinction chronology of a species is the date of its last occurrence. The last record of a species is an important datum because it provides a terminus post quem for the extinction event. It is also important to establish the earliest documentation of the species absence (i.e., a datum representing a terminus ante quem for the extinction event). The earliest age for the absence of the endemic mammals was estimated through the recurrent lack of evidence of their presence over all the archaeological deposits containing bones dated previous to 2040 cal BC in Mallorca.

Currently, new chronological data directly obtained from collagen samples of endemic mammal bones from the Gymnesics is available (Bover and Alcover, 2003, and Bover and Alcover, submitted). The available datings show that *Myotragus* was present in Mallorca after 3700 cal BC (although there is some discussion on this date: see van Strydonck et al., 2005), later than 3970 cal BC in Menorca (Quintana et al., 2003) and later than 3650 cal BC in Cabrera (Bover and Alcover, 2003). Data available for Mallorca document the presence of *Hypnomys* later than 4840 cal BC and *Nesiotites* later than 3030 cal BC (Bover and Alcover, submitted). These are the datings of the last occurrence records.

5.2. First human presence data

Currently, no direct evidence of the contact between the first human settlers and the autochthonous fauna from the Gymnesics has been recorded. The first archaeological record showing unquestionable human presence in Mallorca can be dated in the last century of the III millennium BC (e.g., Alcover et al., 2001; Ramis et al., 2002). A more recent analysis of the chronology suggests that the first human arrival in Mallorca could have occurred at an unknown moment between 2350 and 2150 BC, a date highly compatible with the evidence available.

Although there is no direct evidence of contact between humans and the autochthonous mammals from the Gymnesics, the only explanation for the *Myotragus* extinction appears to be related with human arrival. Even in the absence of such evidence, the extinction of the Quaternary mammal fauna is also probably related to human presence.

Bover and Alcover (1999) situated the extinction of *Myotragus* inside the range 3600–2030 BC. A new approach on the accurate timing of the human colonization (Alcover, submitted) suggests (but does not prove) that the extinction occurred after 2350 cal BC. It represents the last event of the extinction of an insular "megafauna" in the Mediterranean. It probably occurred just after human arrival, as well as occurred for the extinction of small mammals (Bover and Alcover, submitted).

Extinction also affected the Pityusic endemic *Rallus eivissensis*. The last evidence of its presence post-dates 5300 cal BC. Its extinction is presumably related to the arrival of the first human settlers (McMinn et al., 2005).

The improvement of the palaeontological and archaeological record of the III millennium cal BC. in Mallorca will be decisive to obtain more precise information of the chronology and causes of the extinction of the endemic fauna of the Balearic Islands.

6. Conclusion

The vertebrate fossil record in the Pliocene and Quaternary of the Balearic Islands reveals that different faunal successions took place on different islands, following different paleogeographic events. In the Messinian all the islands were connected in some way with the surrounding mainland. Three different faunas inhabited the islands at that time. The *Myotragus* fauna lived in Mallorca, Menorca was inhabited by the giant rabbit fauna and Eivissa and Formentera would have been inhabited by a fauna that originated the Pliocene assembly of Cova de Ca Na Reia, including two glirids and a giant tortoise. Currently, it remains unknown whether three different faunas colonized each island or whether the same faunal assemblage reached all islands and became different after local extinctions of several species. New studies of recently discovered and known deposits would shed light on this subject.

After the end of the MSC, these three faunas started to evolve separately, in complete isolation from one another and the mainland. Among the Messinian faunas only the Mallorcan fauna survived in insular conditions until human arrival. Although this fauna was initially exclusive to Mallorca, it later spread to Menorca. It represents the longest isolated evolutionary experiment in the Balearics and one of its elements, *Myotragus*, represents an extreme case of evolution under conditions of insularity.

Both in Menorca and Eivissa, some faunal succession has been recorded. In Menorca, the faunal succession was represented by a land mammal turnover. The giant rabbit fauna was substituted by the *Myotragus* fauna. Although the precise timing of this substitution is still not well established, it should have occurred between the Middle Pliocene and the Early Pleistocene, according to the faunal record. The start of the glaciations 2.6–2.7 Myr ago (e.g., Shackleton et al., 1984, but see Mudelsee and Raymo, 2005), with the merging of Mallorca and Menorca, emerges as a reasonable possibility. After the turnover, roughly the same fauna lived in Mallorca and Menorca until human arrival.

Faunal succession has also been recorded in Eivissa. A part of the original fauna disappeared at an indeterminate time between the Pliocene and the Late Pleistocene. This faunal change took place without mammalian turnover.

Definitively, the three main Balearic Islands acted as separate worlds after the MSC. Each island had its own fauna, which evolved in isolation. The start of the glaciations was probably the origin of the homogenization of the Mallorcan and Menorcan faunas, through the melting of the islands. In Eivissa, an unknown event was the cause of a faunal change producing the complete extinction of all terrestrial mammals. As a consequence of all these changes, the Pityusics and the Gymnesics were ecologically different at the time of the first human arrival.

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