

NOTE ON THE ORIGIN OF THE PRESENT MAMMALIAN FAUNA FROM THE BALEARIC AND PITYUSIC ISLANDS

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Given the present state of palaeontological knowledge today's mammalogical fauna of the Balearic and Pityusic Islands can be considered as coming from a recent colonization resulting from the activity, voluntary or not, of man. In this paper the number of mammalian species are considered in terms of the theory of island biogeography. The human activity would have brought about a deterministic renewal of the island's mammalogical fauna, with a noticeable increase of the number of species and with the substitution of some stenocorous species, subjected to *K* selection during many years, by euricorous species, which are typical *r* strategists.

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INTRODUCTION

It is still taken for granted by various authors that the colonization of the Balearic and Pityusic Islands by the present mammalian fauna is very ancient, and happened long before the first arrival of man. Only very few classical mammalogical papers pose the question of colonization (THOMAS, 1901; CABRERA, 1914; KOLLER, 1941), and UERPMANN (1971), REY & REY (1974) and COLOM (1978) have very recently expressed the idea of an ancient origin for this fauna as common place. The former (UERPMANN, 1971) distinguishes in this work those species which were introduced into Mallorca by man from other species which, in this opinion, should be considered as autochthonous and which presumably entered in ancient times, through a "Landbrücke". REY & REY (1974) are amazed by the fact that the shrew *Crocidura suaveolens* is not found at present in Mallorca, while this island "se ha mantenido discontinuamente unida a Menorca (where *C. suaveolens* does now exist) a lo largo de diversos periodos geológicos". In his turn COLOM (1978) suggests, in the modified text of the new edition of his biogeographical book,

that some components of the present balearic mammalian fauna may have been established during Messinian. In this work I will try to demonstrate the shortcomings of these ideas, on the basis of the paleontological knowledge which we now possess about the components of the present mammalian fauna from the Balearic and Pityusic Islands.

PHYLOGENETICAL ANALYSIS OF THE MAMMALIAN BIOTA FROM THE BALEARICS

Before beginning the analysis of the phylogenetic characteristics of the species which compose this fauna, it is worth noting that none of them has ever been found in the Quaternary of the Balearics. The remains indicated by ADROVER (1966) at Muleta Cave are all Holocenic or more recent. However, from this lack of findings we cannot conclude anything about the absence of this fauna in past times, although the abundance of quaternary mammalian remains found up till now makes us think that we already have a complete record of the Quaternary fauna of terrestrial, non-flying, mammalian phyla. The fact that the

known Quaternary terrestrial mammals (*Myotragus*, *Nesiotites*, *Hypnomys*) present some traits which may be well understood and explained as adaptations to an insular environment in the absence of predators and in the absence or scarcity of competitors (LEINDERS & SONDAAR, 1974; ALCOVER & ROCA, 1975; ALCOVER, 1976; SONDAAR, 1977) is not in itself conclusive; nor can we draw any conclusion from the knowledge of the average life of Mammalian species, which, according to KURTEN (1961 b) oscillates around 540.000 years (including, for this estimation, the Chiroptera, an order which includes very conservative species, with an average life of 1.600.00 years). In the orders which we shall consider in this work, the average life of the species is situated around the following figures: 490.000 years (Insectivora, Rodentia), 600.000 years (Lagomorpha), 610.000 years (Carnivora). The morphological plasticity of the Rodents has been well studied by BERRY and his collaborators, who recorded, under insular conditions, morphological changes that took place in Muridae in only 70 years (BERRY, 1964). In any case, for our purposes we shall analyse the empirical data supplied by phylogeny and spatial and temporal paleodistribution of the different taxa involved.

The Hedgehog inhabiting the Balearic and Pityusic Islands, *Erinaceus algirus*, lives also along a narrow coastal strip of eastern and southern Spain, in southern France, as well as in vast regions of northern Africa and in the islands of Malta and Djerba. The pattern of distribution which this species present made COLOM (1978) think—following perhaps the considerations of CABRERA (1914)—that it was autochthonous, with an assigned entrance during Messinian. KOLLER (1941) also assigned it an ancient origin, and concluded that it had spread from southern Spain. UERPMANN (1971), who did not find it at S'Illot, also assumed it to be autochthonous. KAHMANN & VESMANIS (1977) say that they have not considered human interventions in presenting

the accurate range of geographical distribution of the species. STORCH (1970) and MALEC & STORCH (1972) consider that *E. algirus* has been very recently introduced by man into Malta from the neighbouring African mainland. At present, the ancestor species of *E. algirus* is not known; in fact, not even fossil or subfossil remains of this species are known. It seems that the apparition of the genus took place about the late Upper Miocene (KURTEN, 1961 a; SABAN, 1958) or about Lower Pliocene (THENIUS, 1969), so perhaps it did not yet exist during Messinian. The evolutive rate of Insectivora is, in addition, relatively high. The average life of their species oscillates around 490.000 years. Furthermore, only one species of Erinaceidae which evolved in insular conditions has ever been studied, *Deinogalerix koenigswaldi*, from the Neogene of Gargano (Italy; FREUDENTHAL, 1972) and we know that it acquired a physiognomy which makes it very different from any mainland Insectivora. Another fossil insular Erinaceidae has been found at Capo Mannu (Sardinia; PECCORINI, RAGE & THALER, 1974). As far as the genus *Erinaceus* is concerned we know that the species *E. europaeus*, phylogenetically rather close to *E. algirus*, is found occasionally in deposits of Upper Pleistocene and Holocene from Europe (ALTUNA, 1972). Their remains found in würm-II of Grotte Hortus “sont d'une taille nettement très supérieure aux plus grands individus actuels” (JULLIEN, 1972). All these facts, namely, the plasticity of this related species, the data on the average life of Insectivora species, the time of apparition of the genus, the consideration of the evolution of an Erinaceidae in insular conditions, the identical morphology of the Iberian and insular populations of *E. algirus* (belonging to the same subspecies, *vagans*), and the fact that this species may be easily transported by man (VERICAD & BALCELLS, 1965; MALEC & STORCH, 1972) make us think that *E. algirus* was brought by man to the Balearic and Pityusic Islands.

As far as the shrews, *Crocidura russula* from Eivissa and *C. suaveolens* from Menorca, are concerned, the present state of knowledge does not allow any conclusion at all. The fossil findings of both species recorded in Europe all date from Upper Pleistocene. All the findings in the Iberian Peninsula belong to Upper Pleistocene or to Holocene. Numerous remains of another species, *C. kornfeldi*, have been found in Middle Pleistocene from Cartagena (Murcia: PONS & MOYA, 1978). These data make us think that both the present species are very recent, and thus they would only have been able to colonize Eivissa and Menorca through the action (direct or indirect) of man. In addition it must be mentioned that *C. suaveolens* has not been found in subfossil state in Menorca, in spite of the numerous remains of small mammals coming from a set of deposits of the talaïotic age already analysed. It is also noticeable that *C. russula* has not appeared in the early subfossiliferous deposit which we know in Eivissa (Cova des Cuieram). It seems clear that *C. suaveolens* is a species that colonized Menorca after 500 years B. C. (date of the later subfossiliferous deposit studied in Menorca). Unfortunately the deposit of Cova des Cuieram is very poor, and of undetermined age, so it does not allow us to say anything about the chronology of colonization of Eivissa by *C. russula*.

The genera of Lagomorpha that live at the present time in the Balearic and Pityusic Islands are not very ancient. According to THENIUS (1969), "Ihr ersters Nacheweis stammt aus den älterlen Pleistozän". DESACHEAUX (1958) holds the same view, as does WALKER (1968) when he reports the genus *Lepus*. As far as species are concerned KURTEN (1961 a) states that "some records of the modern rabbit evidently back as far as the D-Holstein (e. g. Lunel-Viel in sothern France), but more definitive identifications of this species refer to the F-Eemian deposits (e. g. the Pinar Cave, Granada)"... "Fossil finds in Europe have occasionally referred to this species (*Lepus capensis*) ,....,

all of these (finds being) Late Pleistocene age...Even more uncertain are records from the Middle Pleistocene of small forms that may belong in the ancestry of its species". In the Middle Pleistocene of Cartagena, the present species of rabbit has not been found, but instead a relative, *Oryctolagus cf. lacosti* (PONS & MOYA, 1978). It appears that both taxa of Lagomorpha now living in the Balearic and Pityusic Islands are of very recent origin. UERPMANN (1971) when referring to the rabbit and hare, consider them as autochthonous, because their "hohe phylogenetische Alter" (sic). COLOM (1978) consider also an ancient origin for both Lagomorpha. The ideas expressed by these authors do not fit present-day knowledge of their phylogeny. These two species must be considered as very recent and therefore we must accept their presence in the Balearic and Pityusic Islands as due to importation by man.

The Rodentia fauna from the Balearic and Pityusic Islands contains 6 species: *Eliomys quercinus* (F. Gliridae), *Apodemus sylvaticus*, *Mus musculus*, *M. spretus*, *Rattus rattus* and *R. norvegicus* (F. Muridae). Among these species, *M. musculus*, *R. rattus* and *R. norvegicus* are typical commensals of man. All the authors consider them as allochthonous. *M. musculus* may have been imported before talaïotic age (UERPMANN, 1971), while the *Rattus* species may have colonized the islands more recently, *R. rattus* probably during the Middle Ages, and *R. norvegicus* provably around the first half of the 19 th century (ALCOVER, 1979).

About *M. spretus* we can say very little. This species has very recently identified and typified as an independent taxon (BRITTON, PASTEUR & THALER, 1976), and now it will be necessary to revise all the fossil material considered up till now as *M. musculus*. In any case the fossils gathered under this name in Europe are only known from Middle and Upper Pleistocene (KURTEN, 1961a) and not from early times. For this reason, we must assume that this species, is of recent importation.

Remains of *Apodemus sylvaticus* are furnished by all the subfossiliferous deposits from the Balearic and Pityusic Islands, and UERPMANN (1971) considers it as autochthonous, because it is a very early taxon. The presence of the genus *Apodemus* in the European fauna goes back to the end of Turolian (MICHAUX & PASQUIER, 1974; CHALINE & MEIN, 1979). Nevertheless, it must be taken into account that during Pliocene this genus was represented by two extinct species, *A. primaevus* and *A. dominans*. The oldest remains of *A. sylvaticus* come from the early Middle Pleistocene. In different deposits of Lower Pleistocene from the Iberian Peninsula and southern France an *Apodemus* sp. has been found that may perhaps belong to the evolutive line of *A. sylvaticus* (MICHAUX & PASQUIER, 1974). In addition, it is known that *A. sylvaticus* is morphologically very plastic, with more than 30 subspecies described in Europe (NIETHAMMER, 1978) and at least 3 in northern Africa (SAINT-GIRONS, 1972). Besides, we know that during the Quaternary giant species of *Apodemus* lived in Sardinia (*A. mannu*; PECCORINI, RACE & THALER, 1974) and in Sicily (*A. major*; THALER, 1972). A very close genus, *Rhagapodemus*, colonized Sardinia and originated the endemic line of *Rhagamys* (*R. minor* and *R. orthodon*; BRANDY, 1978). This morphological plasticity of *Apodemus* and related genera facilitates rapid morphological changes when it is put under insular conditions. Thus we would expect that if an ancestor of *A. sylvaticus* had colonized the Balearic and Pityusic Islands during Messinian, some endemic species, or even a genus, would have originated. This has not been the case, and therefore we must consider it as a very recent colonization due, beyond any doubt, to importation by man.

Among Rodents, only *E. quercinus* remains to be dealt with. This species, found in all the subfossiliferous deposits of Mallorca, Menorca and Eivissa, has been considered as autochthonous by various authors. On the basis of this consideration UERP-

MANN (1971) and PALACIOS, CASTROVIEJO & GARZON (in RODRIGUEZ DE LA FUENTE, 1975) developed rather imaginative theories in order to explain the origin of the present day distribution of subspecies groups *quercinus* (with the underpart of the tail completely white) and *lusitanicus* (with a black ring on the under part of the tail). In Central Europe, remains of *E. quercinus* from Lower and Middle Pleistocene have been found. Previously, other species of the genus are found, which are probably its ancestors, *E. intermedius* from Upper Pliocene and *E. truci* from Middle and Lower Pliocene (STORCH, 1978). It is clear then, that the present species could not have reached the Balearic and Pityusic Islands during the Messinian, because it did not yet exist. Furthermore, it must be pointed out that the morphological plasticity of Gliridae is very high. Some endemic genera are known from the Plio-Pleistocene of certain Mediterranean Islands, *Hypnomys* (Mallorca and Menorca), *Leithia* (Sicily and Malta) and *Thyrrhenoglis* (Sardinia). It seems reasonable to assume that if any species of *Eliomys* had colonized the Balearics or Pityusics during the Messinian, it would have evolved in a quite different way from those on the mainland, without becoming *E. quercinus*. Thus, we must agree with THALER (in MAS-COMA, 1978) that its present occurrence in the Balearic and Pityusic Islands is only explainable if we accept that it has been imported by man.

Regarding the wild Carnivora from the Balearic and Pityusic Islands, it must be indicated that the Genet, *Genetta genetta*, is probably an African element which probably invaded Europe after Würm (KURTEN, 1961a), but of which no fossil remains are known. The *Genetta* sp. material mentioned by ADROVER (1966) from Muleta Cave was wrongly identified, and is surely very recent. The Weasel, *Mustela nivalis*, is a species of recent apparition, which arose from another, *M. praeivalis*, which existed up to the earlier Middle Pleistocene (KURTEN, 1961a; THENIUS, 1969). Both species

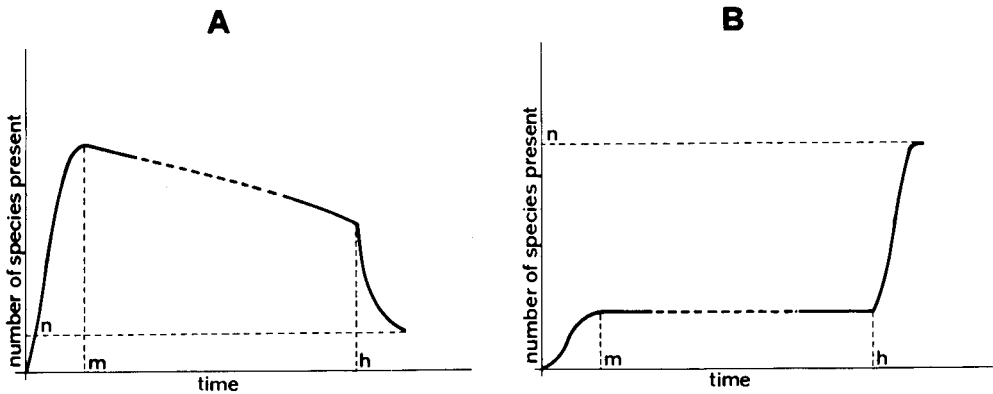


Fig. 1. Colonization curves of mammalian fauna from Balearic and Pityusic Islands. A. After Colom (1978); B. Model proposed in this paper. m. Messinian; h. arrival of man; n. present-day species number.

of Marten which occur now in the Balearic and Pityusic Islands are likewise of relatively recent origin. They arose from *Martes vetus* (ANDERSON, 1970), a species found in Lower Pleistocene from Europe. The oldest remains of *M. martes* come from Middle Pleistocene, while those of *M. foina* come from Upper Pleistocene. All these data can only be related to a colonization of the Balearic and Pityusic Islands due to importation by man.

Considering all we have said, we can conclude that the present terrestrial (non-flying) mammalian fauna from the Balearic and Pityusic Islands has all been imported by man. The source areas have varied, and further data is needed in order to determine them accurately; for this reason, they will be subject to future researchs. It must also be considered that the colonization process has been complex, and some islands have probably acted as stepping stones in the colonization of others.

DISCUSSION

The conclusion to which this work comes modifies noticeably some of the current concepts on which the present-day biogeographical conception of the biotas from the

Balearic and Pityusic Islands depends. Fig. 1A shows the classical conception of the colonization process of these islands by mammalian fauna. It has been drawn on the commentaries of COLOM (1978), who states that “desde el punto de vista de sus mamíferos las tres islas se caracterizan por poseer un reducido conjunto de especies, conjunto que a través de los tiempos cuaternarios y en la fase antigua de los actuales ha ido empobreciéndose cada vez más debido a la misma acción del medio insular”, and farther on, delating also with Mammals, he speaks of the “...empobrecimiento paulatino de las biotas isleñas por la acción directa del hombre”. Fig. 1B supports the ideas that have been presented in this paper. Both graphs are schematic, as they simply try to summarize each theory, without making an accurate analysis of the colonization process.

According to our view, the presence of man would certainly not have implied the gradual impoverishment of the insular mammalian fauna, at least as far as the number of species is concerned. On the contrary, it may be seen that there has been an increase of about four times in the number of species in the Balearic Islands and probably a higher increase in the Pityusic Islands.

It seems that the approach of COLOM (1978), according to which “las plantas y los animales que ahora se desenvuelven en las

islas son los descendientes directos de los que estuvieron en posesión de facilidades innatas para una supervivencia en las peculiares condiciones restrictivas de los monótonos biotopos insulares”, is not entirely suitable to explain the present-day mammalian fauna. It seems more proper to consider the present fauna not merely as a residue of an ancient fauna, but as the result of a balance between the immigration and extinction of species, as the theory of island biogeography postulates (MAC ARTHUR & WILSON, 1967). In this sense, it must be considered that before the arrival of man, either the mammalian saturation is not reached, or an equilibrium is reached with a very low number of species ($\hat{S} = 3$ species of terrestrial mammals in Mallorca and Menorca), due to the fact that the immigration rate (it must not be forgotten that the Balearic Islands are the most isolated islands in the whole of the Mediterranean, and that the dispersal capacity of non-flying mammals is very limited) and the extinction rate (once they succeeded in their colonization, the few surviving species would be unlikely to become extinct, thanks to the great availability of empty habitats and to the lack of predators and competitors), both being functions of the number of species present in the insular area at any moment, were both very low (see fig. 2A). The fact that at another moment of the biogeographic history of the Balearic Islands an insular mammalian fauna of apparently only four species is found (ADROVER, 1977) leads us to think that the pleistocenic mammalian fauna was probably saturated or nearly so.

Therefore, the arrival of man implied not only a rise in the curve of extinctions, as inferred from the work of COLOM (1978), but also, and to a greater extent, a rise in the curve of immigration of new species; thus, given that a perfect balance can never be reached between immigration and extinction, because it would be approached exponentially, the situation tends towards a new number of species “in equilibrium”, \hat{S}_h (in equilibrium so long as the human presence in

these islands continues), higher than the former, \hat{S} . From the similarity of the mammalian faunas presently inhabiting the Balearic and Pityusic Islands together with the relatively large size of the species pool in source mainland areas, it may be inferred that the new immigration curve must be very concave (see MAC ARTHUR & WILSON, 1967). So we may consider that the action of man on the Balearic and Pityusic mammalian fauna has had the effect of bringing the islands nearer, as it were, to mainland source areas, rather than that of reducing the island areas. If this action has been similar for all the Mediterranean islands, it must be expected that, except for special complications (as for instance the establishment of unions between the islands during the glaciations), its effect, measured as $d \log \hat{S}_h / d A$, will be slower in larger islands, because “the logarithm of the number of species decreases with the distance more rapidly in the archipelago with small islands, although the absolute number does not”. This is a prediction drawn directly from the theory of island biogeography, which may readily be tested.

The new number of mammalian species in equilibrium, \hat{S}_h , is determined by a new balance between the immigration and extinction curves. We must emphasize that both processes are not stochastic, but deterministic. In fact, the extinguished taxa are, among others, those which lived during Quaternary, while those imported by man are a selective sample from the species pool in the mainland source areas, including basically “good colonists”. In this sense, we must speak about competitive replacement of the ancient fauna of stenochorial mammals by the present-day fauna of eurychorial mammals. Probably the same process is found in all the Mediterranean Islands, with the arrival of man and also in at least some islands during previous periods of faunistic turnover (see MAYHEW, 1977).

The mammalian fauna of the Balearic and Pityusic Islands, with the action of man, probably passed from a total lack of har-

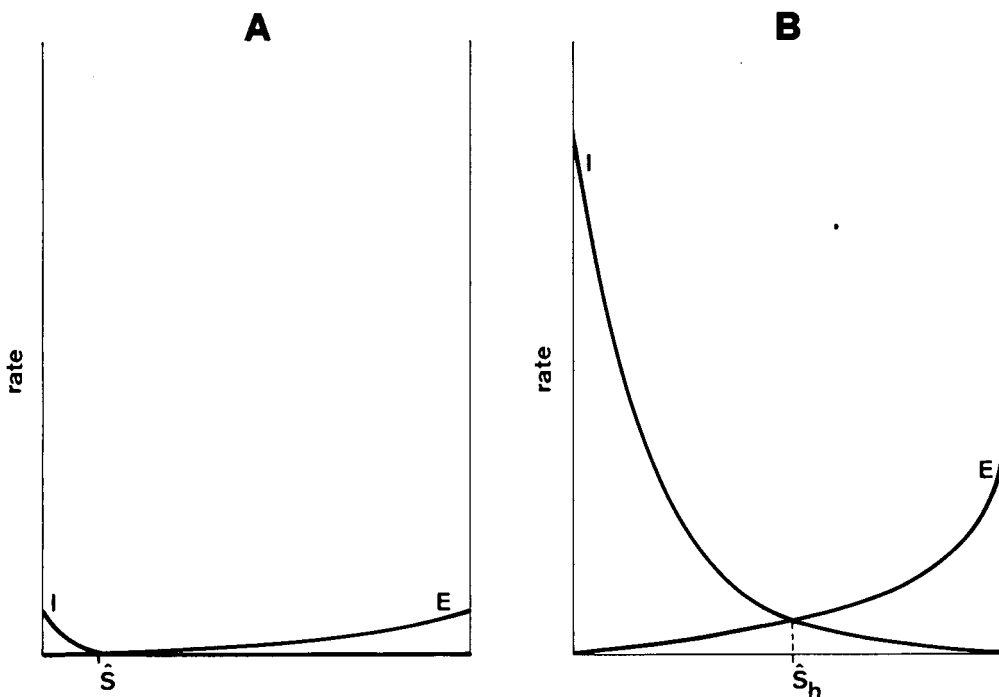


Fig. 2. Equilibrium model of the mammalian biota of the Balearic Islands proposed in this paper. A. Equilibrium model before arrival of man; B. New equilibrium reached in presence of man. It can be seen that a greater change takes place in the immigration curve than in the extinction curve; E. curve of rate of extinction ("extinction curve"); I. curve of rate of immigration ("immigration curve").

mony⁽¹⁾ to a certain degree of harmony and from a very low number of species in equilibrium to another higher. Regarding the discrete taxa affected by this process, we may say that the action of man results in the replacement of a set of taxa that are, without doubt, very adapted for a high biological efficiency in an insular environment by other opportunistic ones; of some species subject during many years to a K-selection, so-called K-strategists (for their characteristics see MARGALEF, 1974) by others subject in varying degrees to an r-selection.

The conclusions of this paper, although they refer strictly to terrestrial –non-flying– mammals from the Balearic and Pityusic Islands, may have a wider application. It

seems that in different degrees a similar phenomenon has taken place in the herpetological, batracological and terrestrial malacological faunas in the Balearic and Pityusic Islands and also in other, if not all, islands. Future research is required in order to obtain an accurate knowledge of the way these phenomena occur.

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RESUM

D'acord amb els coneixements paleontològics que es tenen, cal considerar la mastofauna actual de les

(1) An insular biota is considered harmonic if it contains all of the basic adaptive types found in other ecologically comparable regions.

Balears i Pitiüses com a provinent d'una colonització recent, deguda a l'acció, voluntària o involuntària, de l'home. Es considera el número d'espècies de mamífers a la llum de la teoria de la biogeografia insular. L'acció humana hauria comportat una renovació determinística de la mastofauna illenca, amb un increment notable en el número d'espècies i amb la substitució d'unes espècies estenocores sotmeses durant molts d'anys a selecció *K* per unes altres euricores, típiques estrateques de la *r*.

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