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LARGE PLEISTOCENE MAMMALS OF THE MEDITERRANEAN ISLANDS

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ABSTRACT. — The large Pleistocene mammals of the Mediterranean islands show two main distinctive features: variations in body size and morphofunctional modifications of the skull, dentition and limbs, with the appearance of apomorphic characters. These variations are the result of interaction among several factors (e.g. reduction of the genetic pool, endogamy, hormonal shocks, neotenia, intra- and inter-specific relationships, food supply, free ecological niches etc.) which may have greater or lesser importance at different times. The morphofunctional modifications seem to be more dependent on the environmental change from mainland to insular biotopes. It is difficult to establish an univocal model of the insularization mechanism for the large Pleistocene mammals: each island had its faunas, each insular fauna had its history. Filtering effects of barriers, dispersal routes and modality of migration may differ based on the mammal group and may change during the time.

RÉSUMÉ. — Les Mammifères endémiques des îles méditerranéennes (Eléphants, Hippopotames, Bovidés, Cervidés, Rongeurs et Insectivores) sont caractérisés non seulement par des variations de la taille, mais aussi par des modifications morphofonctionnelles. La variation de taille est déterminée par l'interaction de nombreux facteurs (endogamie, déséquilibres hormonaux, rapports intra- et interspécifiques, niches écologiques libres etc.). En fonction des conditions du milieu et du nombre d'individus qui constituaient la population pionnière, chacun de ces facteurs peut avoir un rôle préférentiel. Les modifications fonctionnelles sont fonction de la niche écologique occupée, souvent indépendantes de la taille, et propres à chaque taxon. Les modalités du processus de spéciation, celles du peuplement et les voies de migration suivies ont été au centre de discussions assez vives. Ces modalités sont probablement diverses pour chaque taxon et pour chaque île; pour la même île elles peuvent aussi varier avec les différentes phases de peuplements.

INTRODUCTION

The associations populating geographically and/or ecologically isolated continental districts generally include a limited number of species, are less diversified, and of an unbalanced composition with respect to the cenosi of similar but unisolated biotopes.

The characteristics which allow us to identify terrestrial mammal faunas of isolated areas are basically: — more or less accentuated oligospecificity of the associations; — exclusive presence of some mammal groups and scarcity or total absence of others; — more or less accentuated endemic nature of the existent forms, which may differ so greatly from their ancestors as to make identification of the ancestral species difficult.

The decrease in the number of the species present in an isolated area is mainly due to phenomena of extinction and/or scarcity of colonizing forms, which may lead to oligotypical ecosystems with slight diversity. In the case of virgin biotopes, the oligotypy is initially primitive (Bellan, 1989), due to the low number of colonizing forms. In some cases the particular environmental, physiographical and microclimatical conditions, or more strictly speaking, the biological conditions of the isolated area, do not allow or restrict the passage to an evolutive oligotypy (Bellan, 1989), which should lead to a polispecific population.

The oligospecificity of the associations of an isolated district is the result of the interaction among various factors. Among these, particularly in the case of terrestrial mammals, the broadness and the nature of the barriers and their changing
through time are particularly important. The modality and the possibility of migration, the effects of filtering and of canalization effectuated by the barrier may greatly differ based on the mammal group, or also, in some cases, according to the species and its ecological flexibility within the realm of the same group.

DISCUSSION

In the associations to typically insular mammals (oligospecific, unbalanced, strongly endemic) of the Mediterranean islands, during the Pleistocene, for instance, the large mammals are represented by a few forms equipped with good or excellent natatorial capability (elephants, hippopotamuses, cervids)\(^1\), while the micromammals are more diversified (Soricidae, Talpidae, Gerbellidae, Arvicolidae, Muridae, Myoxidae, Ctenodactylidae, Ochotonidae). If in the case of the first, in fact, colonization comes about preferably when tectonic, climatic, and/or glacio-eustatic factors reduce the arm of the sea to be crossed, in the case of the micromammals, natural rafts may be a means for dispersal; this might come about even when the barrier is still too broad and the route too inconvenient to allow colonization by large mammals.

Once on the island, the interaction among several biotic and abiotic factors (physiological, ecological, and ethological characteristics of colonizing forms, of those possibly pre-existing on the island and their inter- and intra-specific relationships; the physiographical and microclimatical characteristics of the island, the entity of the available ecological niches, the size and stability of the barrier, the possibility of new migrations), whose relative importance may vary from one island to another or on the same island at different times, leads to the appearance of new forms. The evolutionary process may be relatively quick, and it is likely to come about in the phases immediately following colonization. It may be that initially the modifications concerned in the phenotype and only afterwards in the genotype. The type and modality of speciation, even originated by common ancestors, are typical of each species on each island and may vary in the case that the same form colonize the same island at different times. Two main distinctive features can be recognized: – variation of body size (rarely isometrical, most generally allometrical, also depending on phenomena of heterochronical growth in ontogenesis) – morphological and functional variations with the appearance of apomorphic characters in the skull, dentition, and limbs.

Variation in size

The variation in size of insular mammals is one of the most widely known and discussed phenomena in literature (see inter alia Thaler, 1973; Sondaar, 1977; Alcover et alii, 1981; Azzaro, 1981, 1982; Malatesta, 1986 and references included in those papers) and is usually manifested by a decrease in body size of the large mammals (the only exceptions being "Pseudodama" (Leptocervus) major of Crete – withers height of about 165 cm, Dermitzakis & de Vos, 1987 – and Megalolutra barbaricina of Sardinia, Willemansen & Malatesta, 1987) and by the increase in body size of micromammals, birds and reptiles. In the past, in order to explain the variations in size, great importance was attributed to the absence, in insular environments, of large carnivores. It is undoubtedly relevant, but the variations in body size are actually the result of interaction among numerous factors, essentially connected with the acquired characteristics of pioneer populations once they reached the island (the number of species and individuals for each species, the reduction of the genetic pool, reproduction and mortality rates, endogamy, hormonal shocks, heterochrony in ontogenesis, neotenia, phenomena of progenesis and hypermorphosis, etc.), with those of the environment (type and extension of free niches, quantitative and qualitative decrease in food supply) and with the intercurring relations among various forms (absence of large carnivores, competition, predation, overpopulation, etc.). Each factor may have greater or lesser importance at different times. In the case of the large herbivores, the decrease in body size favours the preservation of relatively numerous populations and reduces the risk of a high rate of extinction. The reproduction rate could furthermore be higher, if phenomena of neotenia were associated to small size. The presence of herbivores with an increased size could be due to the presence of peculiar ecological niches in situations of strong competition or to the casual fixing of apomorphic character or to the phenomenon of hypermorphosis. For a long time, it was hypothesized that the phenomenon of the decrease in body size was progressive, and in the case of the presence on an island of more than one similar form of different size, when biostratigraphical data was lacking, the smaller forms were considered more recent. In some cases, however, as in the Crete cervids, where there was a congeneric form of different size, no biostratigraphical evidence confirms that the larger forms were actually older. In other cases, as in species of Myotragus genus of Majorca, the size appears to have already decreased in the older species, while the morphological modifications of the limbs and especially of the skull and dentition come about over a longer period of time (cf. Caloi & Palombo, 1994 with references). The decrease in size and morphofunctional modifications therefore are not strictly interdependent.
Morphofunctional modifications

The large endemic mammals of the Mediterranean islands generally inhabit environments with peculiar features if compared with the typical habitats of their ancestors. This environmental change seems to have played a very important role in the insularization process. Morphology and function are interdependent elements closely related to biotope characters and to the animals' ways of life. Some morphological variations are already dependent on a decrease in size (especially in the graviportal animals), but most of the apomorphic characters are selected and established by the occupation of new niches. The most significant variations concern the type of deambulation, diet and feeding patterns. Proportions of the limbs and individual bones vary, and the conformation of the joints and muscular insertions undergo greater or lesser changes; the skull, jaw, and teeth, generally larger in proportion, may modify to the extent that their morphology makes it difficult to identify the direct ancestor (i.e. in the case of the Cyprus hippo, *Phanourious minor*, and the Balearian bovids of *Myotragus* genus).

Primates

The only Pleistocene monkey known from the Mediterranean islands is the Cercopithecidae *Macaca majori* of Sardinia. This monkey, possibly originated from *Macaca sylvana florentina*, shows reduction in body size and proportional increase in molar dimensions (Caloi et al. 1988 with references).

Carnivora

One of the characteristics of endemic insular mammal faunas is the absence of large carnivores, which, among other things, favours the great variability usually found in insular herbivores. Actually, hyenas and lions are pointed out only in Sicily, in associations that are not balanced but relatively diversified, in which, along with elements with a more or less pronounced degree of endemism, forms exist that are not substantially different from those to be found on the continent. Instead, in the case of insular fauna, we find (though generally with very few remains) endemic carnivores of average or small size (mustelids, canids), and ursids. The most widely spread forms are the otters (also considering the greater possibility of colonization by swimming); while the canid of the Sardinian-Corsican massif is the most richly represented species (Caloi et al., 1988, with references). Little indeed is known of the foxes and bears pointed out in Sicily; while the adaptations of *Enhydrictis galictoides* of Sardinia are not yet clear, they may have had greater aquatic aptitudes than the probable ancestor *E. ardea* (Ficarelli & Torre, 1967). The fossil Crete mustelins possibly represent different intermediate stages between the mainland species and the recent endemic form of Crete (Steensman & Reese, in press for discussion).

Lutrinae. Otter remains are rather rare, but lutrines are found in many unbalanced faunas of Mediterranean islands. Six species have been described: *Lutrogale cretensis* from Crete, *Lutra euxena* from Malta, *Lutra trinacriae* from Sicily, and the more endemic species from Sardinia: *Sardolutra ichnusae*, *Algalolutra majori* and *Megalolutra barbaricina* (Willemsen, 1992).

The endemic island otters do not show a common trend in their morphological adaptation, and the variation in size, if present, may lead either to an increase or to a decrease in size. The morphological variations and different types of adaptation seem to emphasize the differential characters already present in the ancestral forms. *Lutra euxena*, *L. trinacriae* and *Sardolutra ichnusae*, for example, exhibit a definitely aquatic life, to a greater extent than that characterising the probable ancestral form *Lutra simplicidentis*. On the contrary, *Lutrogale cretensis* accentuates the terrestrial adaptation already present in *Lutrogale*. In the case of Sardinia, where three species are present, competition promoted the adaptation to different ecological niches and perhaps more endemic character of Sardinia otters: *Megalolutra barbaricina* (probably coming from the Aonychina group) was extremely large and actively preyed on large fish and even shellfish; *Sardolutra ichnusae* was smaller, very aquatic and preyed on fish; *Algalolutra majori*, not very large, had a mixed diet (Willemsen, 1992).

Caninae. *Cynotherium sardous*, known from Sardinia and Corsica in the middle and late Pleistocene deposits, is a small canid, more closely related to *Canis* than to *Cuon*, with peculiar character of dentition, depressed elongated skull and short limb bones; it was not a good runner and probably preyed on micromammals, such as *Prolagus sardus* (the conformation of the acropodium might also suggest fossorial capability), and perhaps birds (Malatesta, 1972; Eisenmann & Geer, in press). The latter authors examined the *C. sardous* skull in comparison with several samples of (sub) - recent island canids; those authors do not find evidence for parallel evolution of the groups of island canids on the whole; in their opinion, for a canid, the island is comparable to the mainland and each form became adapted to different environments of the islands on which they were found.
Elephantidae (Fig. 1)

Endemic elephants were the most common settlers on the western (Sardinia, Sicily, Malta and the Egads Islands) and eastern (Crete, Cyclades, Dodecanese, Cyprus) Mediterranean islands (Caloi et alii, 1988; Theodorou, 1986, 1988; Burgio & Cani, 1989; Capasso, Barbato et alii, 1989 with references included in those papers). The insular elephants are generally considered as paleoloxodontine, originated by the Middle and late Pleistocene species Elephas antiquus. The only exception should be the small Sardinian mammoth Mammuthus lamarmorae, descendant of an averagely evolved mammothine species of Late Villafranchian or Early Galerian (M. (Archidiskodon) meridionalis or M. (Mammutus) trogontherii).

The single populations of the different islands (in some cases represented by a little number of remains) are polymorphous, but the different forms all present more or less significant decreases in size, ranging from the minimal decrease in the case of Elephas antiquus leonardi of Sicily, to that of the dwarf elephant of Malta (E. falconeri) and Sicily, not over 90 cm at the withers. The greater morphological variability within the insular populations seems to have been associated, at least in part, with an increase of sexual dimorphism and of morphological gap between the two sexes.

More common characters of endemic elephants were a decrease in the number of molar laminae (with a parallel increase of enamel thickness) and decrease in graviportal morphofunctional characters of the bones of the limbs, which became more marked as size decreased. The morphobiometrical variations of molars were partially allometric and partially due to the fact that the molars had to maintain their chewing function though they were smaller (on the other hand, when the size of the animal is reduced also the food requirements also decreases) and were obliged to grind highly abrasive food, due to the more xerophilous vegetation of the Mediterranean island environment.

In the smallest elephants, the smaller size and the reduced weight favour the development of joints which bring the limbs closer to the sagittal plane and facilitate anterior-posterior oscillation.
with respect to the ancestral forms. Furthermore, the foot becomes more digitigrade. The endemic elephants tend to acquire a more agile gait and in some cases, a certain increase in cursorial aptitudes (Caloi & Palombo, 1994). It is however possible that the fixing of apomorphical characters in the limbs be due not only to static elements connected with the lighter body weight, but also to the need for more secure movements on relatively uneven ground and in climbing rather steep slopes. Those modifications were, in fact, also present in populations where decreasing in size was smaller.

One of the most showy variations is that of the different proportions between the encephalon and the cranium, studied in the Sicilian specimens from Spinagallo (Accordi & Palombo, 1971) but also present, though to a lesser degree, in the medium size population of Puntali (unpublished data). The proportional increase in size of the cerebral mass observed in the elephants of Spinagallo is due primarily to the functional impossibility of going below certain limits while maintaining the basic encephalic structure, and second, to neotenic factors which allow the adult to maintain an enough globose cranium with very reduced pneumatization.

Hence, the most thoroughly studied populations of endemic elephants show, on the various islands, rather similar basic modifications, connected with the decrease in size and the adaptation to environments with little even ground where shrubbery-like vegetation should prevail.

**Hippopotamidae** (Fig. 2)

Endemic hippos are known to be present in Sicily (**Hippopotamus pentlandi**, represented by various populations, perhaps taxonomically distinguishable, originating from *H. ex gr. H. amphibius*), Malta (**H. pentlandi** and the smaller *H. melitensis*), Crete (**H. creutzburgi**, originated by *H. ex gr. H. antiquus*) and Cyprus (**Phanourios minor**, the smallest insular hippo of doubtful origin). Each population generally shows great variability both in size and morphology, in some cases leading to the supposition of the presence, on the same island, of more than one form with different degrees of endemism (Spaan, in press).

The most specialized was the Cyprus hippo, which shows marked biometrical and morphological modification of the skull, dentition (molars were e.g. lophodont) and limb bones (Boeckschoten &
The lateral skiddings were reduced, the anterior-posterior movements were wider, the structure and shortness of the phalanges imparted greater stability to the autopodium.

Similar limb modifications are observed, to a different extent, in various hippos from different Mediterranean islands, also in the slightly reduced hippo from Puntali (Sicily) (Caloi & Palombo, 1985). They must thus be interpreted as responsive to new environments and consequent to adaptation to different ecological conditions, on land where marshes and running water were scarce and the ground could be rough and rarely level. However, these modifications are not wholly independent from the decrease in size and body weight, and seem to be more evident where reduction increased (Caloi & Palombo, 1985 with references).

In conclusion the insular speciations of hippos should be due more to environmental changes than to size reductions.

**Cervidae** (Fig. 3)

Endemic cervids were among the most common species in the unbalanced faunas of the Mediterranean islands. They belong to the megacerine or cervine groups and several forms with varying levels of endemism originated. No form with an
entirely comparable way of life existed on different islands and it is difficult to single out a dominant factor in their evolution (Caloi & Palombo, 1995). For example, in the processes of speciation of the cervids of the three main islands (Sardinia, Sicily, and Crete), the presence of free niches and the competitive inter- and intra-specific relationships seem to be more important than the basic morphological characteristics of the ancestral forms. The Sardinia megacerines (Mega-ceroides "cazioti", withers height of about 75-100 cm) were grazers, moving with agility both on hard and on uneven ground, while those in Sicily (Megaceroides (Notomegaceros) carburgaense, with a 50% decrease in size) were browsers, living on soft ground in a wooly environment. A cervid (Cervus elaphus siciliae, with body size reduced by about 20%) was also present in Sicily, and its way of life was similar enough to the Sardinia megacerines. The Crete cervids exemplified the possibility of colonizing very different niches (possible example of radiative adaptation and speciation) and are the only large endemic mammals that show both a decrease and an increase in size. The two megacerines (Megaceroides ex gr. M. (Candiacervus) "ropalophorus" (2), withers height of about 40-50 cm, and Megaceroides (Candiacervus) cretensis, withers height of about 65 cm; Demitzakis & De Vos, 1987) moved with reduced agility on hard, uneven ground; the three larger species (of uncertain origin, perhaps originated from a cervine close to Pseudodama) (?Pseudodama (Leptocervus) re-thymensis, withers height of about 90 cm, ?Pseudodama (Leptocervus) dorothenis, withers height of about 120 cm and ?Pseudodama (Leptocervus) major, withers height of about 165 cm; Demitzakis & de Vos, 1987) moved with a slow and rigid gait (cf. Caloi & Palombo, 1995, and references included).

In the cervids, size reduction does not imply a significant decrease in weight and morphofunctional modifications may lead either to a shortening or to a relative lengthening of the limbs. For example, the megacerines of Crete (present in unbalanced faunas where large carnivores are absent) have shortened legs, the Sicilian deer (present both in unbalanced faunas and in more diversified ones with lions and hyenas) and Sardinian megacerines (present in unbalanced faunas where Cynotherium sardous was not a potential predator for them) were the most slender reduced forms having some degree of cursorial aptitude.

**Bovidae** (Fig. 4)

Pleistocene endemic bovids were not frequent in insular Mediterranean faunas, but they include one among the most interesting endemic species: *Myotragus balearicus*. This strange bovid was the only large mammal on the Balearian Islands and shows very peculiar features in the skull, dentition and body proportions (the incisors had continuous growth; the face was shortened; the number of teeth was reduced, eyesight was stereoscopic, the tarsus bones were fused, the metapodials were shortened, etc.) and was perfectly adapted to slow and powerful locomotion on steep ground (Alcover et al., 1981; Spoor, 1988 a, b with references). The ancestors of the *Myotragus* genus colonised the Balearian Islands in the Pliocene. Three lineages were present: the earliest was represented on Majorca by the terminals species *M. pepgonellae*, the second includes *M. antiquus, M. kopperi, M. batei* of Majorca and finally *M. balearicus*, also reported on Minorca. On this island, the third lineage of *M. binigausensis* evolved. It is difficult to identify the continental ancestor of *Myotragus* and, in the case of Majorca, a polyphyletic origin of the two lineages cannot be ruled out (cf. Caloi & Palombo, 1994, with references). On Majorca, no radiation process seems to be

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Fig. 4. – 1, Hypothetical reconstruction of *Myotragus balearicus* (1). 2, Stereoscopical vision in *M. balearicus*, after Sondaar & Braber (1988). 3, Metacarpal and phalanx and metatarsal and phalanx of modern *Capra ibex* (3a, c) and *M. balearicus* (3b, 3d). 4, Skull of *M. balearicus* from Maiorca, in frontal (4a) and lateral (4b), after Alcover et al. (1981).
present, perhaps due to the scarce environmental differentiation.

Contrary to findings in Myotragus, in the goat of Sardinia (Nesogoral melinii, known from very few remains) the metapodial proportion did not differ greatly from that of continental caprine species (Gliozzi & Malatesta, 1980).

Bovids of relatively reduced size were reported from Sicily (Bos primigenius siciliae and Bison priscus siciliae) and from Pianosa (Bos pr. bubaloides) but the degree of endemism was not marked. The disproportion between limb bones and skull of the Sicilian bison might be consequent to phenomena comparable with achondroplastic dwarfism (Caloi & Palombo, 1994, with references).

CONCLUSIVE REMARKS

It is difficult to establish univocal models for the large Pleistocene mammals of the larger Mediterranean islands that explain the mechanisms that lead to insularization.

There is undoubtedly an "insularity syndrome" and this is borne out by the fact that we can identify "insular" forms in areas which are currently part of the continent (e.g. southern Calabria, Caloi et alii, 1988, with references); palaeogeographical reconstructions are carried out, among other grounds, also on that of the degree of oligospecificity of faunas and of the endemism of the species; and the nature of the barriers, timing, routes, and modalities of migrations are hypothesized. However, each island has its faunas: each insular fauna has its history. The relative weight of the different parameters which intervene in the insularization process may differ not only according to the animal group being considered but also according to the same group on the different islands and/or in different environmental contexts, and may lead to phenomena of adaptational convergence in some cases.

All the same, the relationship is undeniable between certain parameters and the kind of fauna present on an island, such as barriers, the dispersal route and degree of oligospecificity, environmental diversification and radiative speciation, the presence or absence of carnivores and the degree of intraspecific variability. The relations are, however, highly complex as in the case of morpho-functional and size modifications, which depend both on the interactions of several biotic and abiotic factors and their change in function of the dynamic equilibrium which sets in in the insular populations.

Considering only the larger Mediterranean islands (for whose populations the factor of "insula area" seems to have slight importance) we can observe that:
— the more oligotypical faunas with endemical characteristics and with more marked specialisation are those of the Balearic Islands and Cyprus, islands which are divided from the continent by broad, durable barriers, which have allowed only a few pioneers to reach these islands, at only during one or, perhaps, two migration phases. Cyprus may be reached only by swimming very long distance. In the case of the Balearic Islands, it is difficult to establish which route was followed and the length thereof. The pioneer should have found some dry ground along the way; in this case, the distance to be covered by swimming would be shorter than in the Cyprus case. In theory, colonisation of virgin environments by only a few forms should lead to radiation phenomena. This does not seem to have taken place on Cyprus nor on the Balearic Islands, and if, on Majorca, the lack of radiation may be due to a slight environmental differentiation; for Cyprus, the question requires further investigations;
— inconvenient dispersal routes with important filtering effects were followed by the colonisers of Sardinia and Crete. Dispersal routes were represented by arms of sea and undurable dry ground with sparse or no vegetation; pioneers were required to swim across not particularly broad distances. In Crete the paleographical position of the area, its distance from the coast, tectonical and glacio-eustatical factors seem to have combined in such a way as to allow large mammals to have more phases of colonization than Sardinia (also the hippo, which is absent from Sardinia, became on Crete) (Palombo, 1986; de Vos, in press). In the case of the cervids, the migrations were followed by two radiation phases. These probably allowed the endemic species of the oldest colonisation to survive side by side with new settlers;
— in the case of Sicily, the barrier and dispersal route must have changed in time, progressing from inconvenient (the pioneers were required to swim across not very large arms of sea) to transitable (unstable land bridges interrupted by little areas of sea) for a variety of groups, with reiterated migration phases which might also have determined phenomena of generic introgression in the unstabilised insular populations.

In conclusion, in the all groups of the large endemic mammals of the Mediterranean islands the reduced number of pioniers and the environment change seem to have played a very important role in the insularization process. Most of the apomorphic characters are selected following the occupation of new niches. The tendency towards a relative shortening of the legs, and development of low gear locomotion (due to the lack of predators), if common, is not the rule; on the other side some morphological variations which lead to more slender limbs depend on the decrease of the
graviportal position. Likewise, the size reduction is not a set rule; it does not necessarily lead to the appearance of forms of a gradually decreasing size, and various forms of different size can co-exist, occupying different niches. In rare cases, it is, however difficult, especially in the case in which insufficient documentation is available, to establish the boundaries between intraspecific variability and taxonomic diversity.

1) In insular faunas, bovids were present or with subspecies little differentiated in associations relatively diversified, or with highly specialised forms (for which it is difficult to identify ancestors, times and migrations routes) in oligotypical faunas.

2) There is controversy regarding the systematics of Crete cervids; see Caloi & Palombo (in press) and de Vos (in press) for the discussion.

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