

Palaeontological aspects of island biogeography: colonization and evolution of mammals on Mediterranean islands

Richard A. Reymont

Reymont, R. A. 1983. Palaeontological aspects of island biogeography: colonization and evolution of mammals on Mediterranean islands. – *Oikos* 41: 299–306.

Island biogeography can, from palaeontological considerations, only be discussed with reasonable certainty for the last 20 million years, that is, from Miocene to the present. This is because of the increasing difficulty, as we go back in time, of recognizing ancient islands and determining their relationship to the nearest mainland. One is also limited with regard to the organisms available for study. Because of the availability of fossil remains, mammals have taken pride of place over other groups for palaeontological analyses of island speciation. In particular, the elephants, hippopotami and deer tend to become greatly reduced in size (dwarfing) whereas small mammals, such as rodents of various kinds, may become larger, even to the extent of gigantism. The present review supports the view that strong adaptive selection is the main evolutionary force concerned in the speciation of these groups. The problem of the size of the founder populations is considered from the standpoint of catastrophic events and mass migration to a marine barrier, and thereafter arrival at an island either by swimming, passive transport by oceanic currents, or a combination of both.

R. A. Reymont, Dept of Historical Geology and Palaeontology, Univ. of Uppsala, Box 558, S-751 22 Uppsala, Sweden.

Биогеография островов может обсуждаться в палеонтологическом аспекте с приемлемой определенностью лишь за последние 20 млн. лет, т.е. от миоцена до настоящего времени. Причина этого – возрастающая при анализе отдаленных геологических эрх трудность идентификации древних островов и определения их положения в отношении к ближайшему матерiku. Лимитирующим фактором оказываются также организмы, доступные для изучения. В результате доступности ископаемых остатков, млекопитающие имеют преимущество перед другими группами при палеонтологическом анализе островного видообразования. В частности, слоны, гиппопотами и олени обнаружили тенденцию к значительной редукции размеров (карликовость), а мелкие млекопитающие, например, разные виды грызунов увеличиваются в размерах, даже до степени гигантизма. Настоящий обзор поддерживает точку зрения, что строго адаптивный отбор – основная эволюционная движущая сила в процессе видообразования этих групп. Проблема размеров популяций основателей рассматривается с точки зрения катастроф, массовой миграции к морскому барьеру и последующего перехода на острова путем переплывания или пассивного переноса морскими течениями, либо с помощью комбинации обоих способов.

Introduction

Although the subject of island biogeography is important for the palaeontologist from the viewpoint of the fundamental principles involved, the possibility of direct input of biological relevance from fossil data is, for readily understandable reasons, slight. The most obvious of these reasons is that it is very difficult to identify ancient islands in the field. In fact, the only reasonably certain determinations of fossil islands date from the Neogene. Granted that some islands have been associated with rather special geological developments, it is only in very few cases that an island can be identified in sequences older than Neogene; for example, in connection with the growth of the South Atlantic ocean in Late Cretaceous and Palaeogene time. There is a natural explanation for this. The history of our Earth shows that the continents and oceans have always been in a state of flux – constantly moving in relation to each other – so that the further one proceeds backwards in time, the less certain one becomes of the large-scale relationships between land and sea. First in the Neogene, the oceans received the distributions they have today and it is therefore not so difficult to extrapolate from the present-day configurations to those of the Miocene. Nonetheless, quite important events took place on a very large scale, such as the Messinian (Late Miocene) salinity event in the Mediterranean.

We know that some islands were associated with rather special evolutionary developments in mammals and it is the occurrence of such forms that have sometimes been employed as indirect evidence of the erstwhile existence of an island. Thus, we can be reasonably certain of being able to identify correctly islands of Pleistocene age and onwards, and fairly sure of a correct identification for the Pliocene. However, there are many levels of uncertainty involved at the palaeogeographical level, as even a relatively minor fall of sealevel can bring about the union of an island with the mainland with the attendant invasion by mainland species, a happening which invariably seems to have led to the rapid extermination of endemic island forms.

It is not always appreciated by ecologists that the level of the sea is far from oscillating about a stable average. Firstly, there is the question of tectono-eustasy, whereby the sealevel changes uniformly on a global scale in answer to changes in the volume of the oceans. This is an important source of instability in sealevel, as will be appreciated if the continuous lateral motion of the continents is kept in mind; clearly, it represents a long-term effect. From the particular point of view of the Neogene and Pleistocene, we have the short-term effect deriving from glacial eustasy. There is also geoidal eustasy, which is also a long-term factor and, finally, vertical movements of the crust. Some islands, particularly those of volcanic origin, have proved to be susceptible to vertical movements, which may

either lift them above the sea, or let them sink, with obvious effects on the land-life on them.

The most striking feature of some island endemics is that they may be significantly larger, or smaller, than their mainland counterparts. Examples are legion. Williamson (1981) lists small ducks and small snails on Pacific islands. The giant tortoises provide a well known example of gigantism, but island tortoises are not necessarily larger than mainland relatives. It is generally accepted that the size effects involved here are not directly comparable with those operating among mammals of the Neogene and Pleistocene islands of the Mediterranean owing to the swimming ability of tortoises (cf. Guillaume and Bons 1982, Williamson 1981, and references in these publications).

Foster (1964) summarized, in rather general terms, the effects of selective forces on living insular mammals in relation to the nearest mainland forms. In many cases, small mammals were found to have become larger under the influence of the island regime, and big mammals smaller. Thus, around 85% of island rodents are larger, a fact which has been seen as the possible effects of the absence of predators, with a resulting increase in intraspecific competition, assumedly connected with an advantage adhering to being big. At the other end of the scale, carnivores and artiodactyls become smaller in about the same number of cases. This condition has been interpreted as being the outcome of the advantage of small size in the restricted insular environment with limited food resources.

From the palaeontological aspect, most research has been devoted to dwarf hippopotami, elephants and deer and giant rodents of the Pliocene to Sub-Recent (for convenience, hereafter referred to as the HEDR-fauna).

The area considered in this review is contained in the Mediterranean (see Fig. 1). However, islands with Pleistocene unbalanced faunas occur in other parts of the world, e.g. the Japanese archipelago, Indonesia, the Canary Islands, Madagascar, and off the coast of California.

Mediterranean islands

Firstly, we need to establish an ad hoc terminology for islands. New Guinea is an island, so is Fernando Póo, likewise Madagascar and Mauritius. Island ecologists tend to talk in terms of "continental islands", which are defined as being very close to the mainland (e.g. the islands of the Bay of Bengal to which elephants swim back and forth as the whim seizes them – Sondaar (1977)). Continental islands can be easily reached by most animals with moderate swimming ability and they are usually joined to the mainland at low eustatic stands of sealevel. These islands are distinct from what are often referred to as "oceanic islands" which are per-

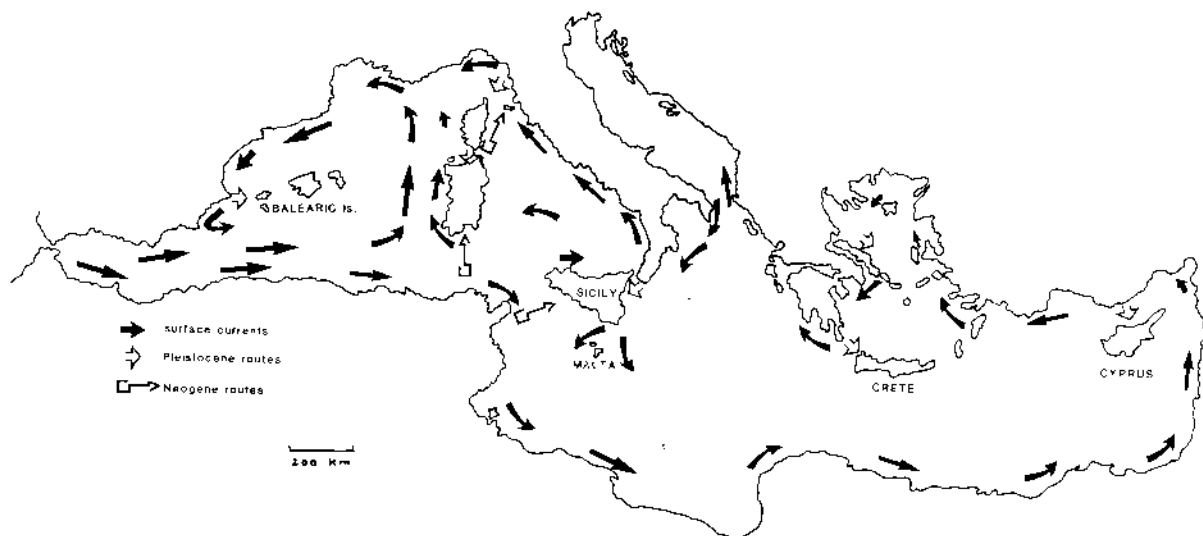


Fig. 1. The present-day system of surface currents in the Mediterranean and the presumed directions of migration across the sea, as summarized by Thaler (1973). The islands of particular interest for speciation events are Cyprus, Crete, the Aegean Archipelago, Sicily, Malta and the Balearic Islands. The migrational arrows refer to the Tertiary (mainly Neogene) and the last major glacial episode of the Pleistocene.

manently separated from the mainland (Pielou 1979: 191). Geologically, this is a very arbitrary classification and obviously far from being unchallengeable. As Sondaar (1977: 671) has pointed out, it is usually beyond the powers of the palaeoecologist to distinguish between oceanic and continental islands on field evidence alone.

For the purposes of the present discussion, we shall be mainly concerned with small islands, such as Cyprus, which can be taken as being representative of oceanic islands. The islands of the Mediterranean are here given pride of place, as their Neogene history is comparatively well known, largely owing to the work of Sondaar and his coworkers (cf. Sondaar (1977), Houtekamer and Sondaar (1979) and Thaler (1973)). All authors working in the Mediterranean agree on at least one point, to wit, that an essential property of small islands is their environmental uniformity. This observation is, however, a truth requiring not inconsiderable modification.

A few words need to be expended on the geological history of the Neogene Mediterranean.

We shall begin with the Messinian (Late Miocene) salinity episode. A little more than a decade ago, the geological world was startled by data accruing from the drilling programme of the Deep Sea Drilling Project (DSDP) in the western Mediterranean. A considerable thickness of salt was drilled in sediments of Miocene age in an area in which such deposits were quite unexpected. The prevailing theory is that the salt deposits derive from a period of marked eustatic fall in sea level with the Mediterranean subsequently becoming isolated from the world oceanic system by the Gibraltar threshold. Drying out of substantial parts of the trapped

sea led then to the formation of the salt beds. According to this model (Biju-Duval et al. 1974), there were several influxes of Atlantic water via the Strait of Gibraltar in response to minor eustatic fluctuations. Sonnenfeldt (1975: 275) has countered prevailing theory by stating that the Upper Miocene clastics and the distribution of the evaporites, do not support the concept of a deep, dry depression intermittently filled with Atlantic waters. In his opinion, a model based on inadequate water-exchange would explain the formation of the evaporites.

Whatever the case may be, the prevailing theory would not be out of tune with mammalian migrational patterns in the Late Miocene. For example, *Hypnomys* came to Mallorca during the Messinian regression (Mein 1982: 156). The Pleistocene was marked by substantial shifts in sea level due to the episodes of glaciation. During glacial maxima, many of the Mediterranean islands were joined to the mainland by "landbridges". The development of a landbridge invariably spelled doom to an unbalanced HEDR association - invasions from the mainland quickly led to the appearance of a balanced fauna.

Elephants, hippopotami and deer

The trend shown by all three of these elements on arriving on a well separated island in the Mediterranean was to display a remarkable decrease in size over a relatively short period of time. Cretan dwarf elephant remains show a wide size-range, presumably representing several phases of evolution towards the final stage. Once the process of adaptive dwarfing had reached its

zenith, the elephants were no longer fitted for long swimming tours. The flatland, lumbering ancestral form, with good swimming capabilities, had been irrevocably transformed into a clever climber of rocky slopes. This transmutation was accompanied by extensive changes in the locomotory properties of the limbs and in a marked reduction in spongy bone tissue. We note that the island form *Elephas falconeri* was only one fourth the size of the putative ancestor *E. namadicus* (Sondaar 1977). See also Houtekamer and Sondaar (1979).

Cretan hippopotami developed from mainland *Hippopotamus amphibius* (Sondaar and Boekschoten 1967: 565). The small hippopotami of mainland Africa are not dwarves. *H. liberiensis* is a distinct species, quite separate from *H. amphibius*.

As regards dwarfed deer, Sondaar and Boekschoten (1967: 558), after weighing and sifting various sources of evidence and different interpretations, conceded that some island deer of the western Mediterranean might have been through the dwarfing process prior to arriving at their final destination (see also Mein 1982). The reason why this is a possibility for deer is that whereas the structural changes undergone by hippopotami and elephants were so fundamental as to quite alter their life style, and swimming ability, the dwarfing of deer did not have the same effect on this property. On the other hand, records of dwarfed mainland elephants have all proved to derive from the misidentification of juvenile individuals of *Elephas antiquus*.

The functional changes accompanying dwarfing in elephants and hippopotami are of significance when it comes to evaluating possibilities of dwarves migrating further to other islands. This would seem to be beyond the realms of normal likelihood, as has been emphasized by Sondaar (1977) and opinions to the contrary (refs. in Sondaar 1977) do not seem to be founded on a sound assessment of the pros and cons involved.

Evolutionary patterns

Some species of the Neogene-Pleistocene unbalanced faunas adopted the following evolutionary pattern, which consists of two components:

- (a) An initial phase of rapid evolution; there seems to be reasonably sound evidence for there having been a rather fast rate of development in the time immediately following on the original colonization of an island.
- (b) A phase of slow evolutionary change; this stage has been seen as a rather uneventful filling of the island niche after successful adaptation to the new conditions.

Mein (1982: 154) discusses island evolution in terms of a founder population (of unspecified size), representing a small portion of the genome, in conjunction with random effects and accelerated evolution. Although

heuristically attractive, this manner of interpreting the course of events is not without flaws. Guillaume and Bons (1982), discussing the giant turtles, stated their belief that random genetic drift in small populations of reptiles can be manifested in manifold ways.

In a relatively small number of well studied cases, the postulated phase of rapid evolution of the initial HEDR-association may be less dramatic than has been suggested. Thus, Thaler (1973: 742) noted that the Sicilian elephants probably took between 250000 and 600000 years to attain half the dimensions of the ancestral *Elephas antiquus*; it took around one million years for a reduction to quarter size to be completed.

Pielou (1979: 173) considers that the number of species involved in island speciation results from processes too rapid to be affected by evolutionary change, a statement I find both enigmatic and difficult to substantiate.

Taking the Mediterranean endemics as an example, the tendency has been for large mammals to decrease greatly in size, a phenomenon sometimes known as nanism. Sondaar and Boekschoten (1967) stated that dwarfing is a normal island adaptation. It should be understood that the dwarfing progress is by no means a "photographic reduction", as it were. Consequently, notwithstanding the fact that the ancestral *Elephas antiquus* is morphologically similar to its dwarfed descendant, this similarity is rather superficial if one examines it in detail. The skull of *Elephas falconeri*, the descendant, which stood only 0.8 to 0.9 m tall, is proportionally less reduced than the body. The brain is even less reduced than the skull, in relation to that of *E. antiquus*, which had a height of 4-5 m (Thaler 1973: 742). Mein (1982: 156) regards this example as being a "transitional case", although on grounds which are not easy to fathom.

Thaler (1973) suggested that the size increase displayed by some small mammals might be correlated with the absence of carnivores in the island habitat. An ancillary factor in this connection, he thought, might be the fact that birds of prey take small mammals in a single swoop-and-bite action. Consequently, large size in a rodent, for example, would serve to protect it from birds of prey and would not be a disadvantage in an environment in which land carnivores were absent. It is perhaps unnecessary to mention that the same birds of prey would have operated over the Mediterranean islands as above the mainland, thus implying that the small rodents of both environments would have been subjected to the same kind of predation pressure.

Colonization and initial development

The composition of unbalanced Mediterranean island faunas indicates that large mammals with good swimming capabilities have had a clear advantage over other animals - deer, elephants, hippopotami (Mein 1982:



Fig. 2. Hypothetical reconstruction of the distributions of sea and land in the Mediterranean during the last episode of glaciation (deduced from bathymetric maps of the Mediterranean). The solid arrows outline assumed major current directions. The open arrows indicate presumed optimal crossing routes for HEDR animals. The Strait of Gibraltar would have had a much reduced rate of water exchange and may have been blocked for short periods.

157. Sondaar and Boekschoten 1967). In cases where long distances have been involved, dispersal of such mammals must have been accomplished by a combination of active swimming and drifting (Andrewartha 1961: 44). Pielou (1979: 256) terms associations of this type "waif biotas".

Certain small mammals have been passively transported on flotsam and jetsam, i.e. by rafting (Andrewartha 1961: 44). Mein (1982: 157) speculates around the theme that such animals could also have been passively transported between islands. The generality of such a means of colonization relies on uniquely favourable patterns of surface currents. With Sondaar (1977), we relegate this model to the less likely alternatives, except for closely located islands, such as in a drowned archipelago. Freudenthal (1976) has also advanced the idea of general migration between adjacent islands, but without contributing convincing supporting evidence.

Dermitzakis and Sondaar (1979) discussed island biotas in terms of the concept of "pendulum routes". The water barrier could be easily crossed by some animals but would have been an insurmountable hurdle to others. They speak of a "corridor", a broad land-connection over which all animals could pass at will. A second category recognized by these authors is the "filter", which is a narrow landbridge, assumedly functioning as a partial hinder. The third category is the well known concept of the "sweepstake route", which involves a wide extent of sea. The idea of a pendulum route is particularly applicable to the Aegean; it covers situations in which animals are able to wander back and forth over an archipelago, with areas of skerries, but with the differentiating aspects implied by the three categories given above.

With respect to the concept of sweepstake coloniza-

tion, little attention seems to have been given to the possibility of relatively large, more or less synchronous, arrivals of HEDR animals, driven to undertake the perilous journey by some kind of catastrophic event, competition, or overpopulation. Another factor that seems to have been neglected is the routed distributional pattern that would have been the outcome of the system of surface oceanic currents. In addition to the large mammals with a skeletal structure marked by a reduced specific gravity (skull of elephants), animals with a dormant stage (dormice, some insectivores) and others of small size and endowed with great endurance so as to be able to survive for long periods on driftwood (i.e. mice and rats), would be largely distributed in accordance with the directions of surface oceanic currents. HEDR animals could be swept great distances over short periods of time by a combination of longshore drift, oceanic current systems and, where applicable, active swimming. This combination of factors would greatly extend the possible range of distribution of the HEDR group beyond what mere swimming ability could accomplish. Some of the implications of this line of reasoning can be gleaned from Fig. 1. This illustration shows the present pattern of surface oceanic currents in the Mediterranean (Sverdrup et al. 1942). The same figure also displays the migrational routes for HEDR associations as critically summarized by Thaler (1973). It will be observed that the routes for the Aegean domain are feasible. The proposed route for the Balearic Islands is, on the other hand, unlikely as the rafting animals concerned would have been transported far south by the surface currents, assuming that the Pliocene current pattern was the same as today, which seems to be a likely assumption. The suggested migrational route from Libya to Malta, thence Sicily is not supported by the current system prevailing today, at

least. A route via southern Italy is, however, acceptable. The route to Cyprus is often assumed to have gone via the shortest distance to Turkey. The current pattern suggests a longer route to have been more likely.

The information residing in the distributional patterns of surface currents would appear to indicate that the actual migrational process can have been more complicated than suggested by the conclusions of recent authors (e.g. Thaler 1973, Sondaar 1977, Mein 1982). Obviously, more analytical work is needed on this topic, combined with accurate reconstructions of the extent of islands during the glacially controlled low stands of sealevel during the Pleistocene.

A schematic attempt at reconstructing the land-sea relationships in the Mediterranean is given in Fig. 2. It was made under the following assumptions. Firstly, that there would have been a fall in sealevel of some 150 m at maximum glaciation during the Pleistocene. Secondly, that the pattern of islands was the same as that existing at the present time. These are reasonable assumptions and presumably valid at the scale concerned.

It is of course uncertain whether the Strait of Gibraltar would have been open at very low stands of sealevel and one cannot extrapolate directly from the present-day situation for geotectonic reasons. It is certain, at least, that an open strait would not have had the same water-exchange as now.

The first point of interest is that Sicily is firmly bound to the Italian mainland and that the Adriatic Sea is less than half of its current size. Sicily would have extended closer to the African continent and would also have encompassed Malta. The Aegean Archipelago would have been largely a land area, although Crete and Cyprus would have been surrounded by water. Assuming that something like the present system of surface currents existed at the time, the best route to Cyprus would still not have been the closest distance to the mainland, although the areal extent of Cyprus would have been greater than it is today. The nearest migrational route to Crete would have been via the east and not from the north as might be inferred from the present-day distribution of the Greek islands.

There would still have been a serious problem for animals attempting to reach the Balearic Islands and the weight of evidence would seem to be in favour of arrival via land exposed during the Miocene regression (cf. Mein 1982). Corsica and Sardinia can be expected to have formed a single island, within easy reach of the French mainland. Azzaroli (1981) has attempted reconstructions for the Oligocene-Miocene on rather speculative grounds.

The available evidence for the Mediterranean islands suggests that in each case investigated, the colonization event was short. As far as can be ascertained from the published data, there were no arrivals of ancestral forms after the new adaptations had become established. This argument is based on the apparent lack of evidence for mixed occurrences of fossils of ancestor and descendant.

Hence, the concept of "island model migration" (cf. Wade 1982: 951) would not seem to be applicable to the history of HEDR communities.

In this connection, the question of "archaic characters" needs to be reviewed. Mallorca is thought to have been isolated from the mainland for at least 8 Myr (Mein 1982) with the result that many species conserved what have been described as archaic characters – that is, morphological characteristics long since defunct among mainland relatives. This long period of stasis in the evolution of faunal elements produced a relict fauna. Mein (1982: 155) reviews, in detail, the relict elements of the Mallorcan Neogene to Sub-Recent faunas – giant lagomorphs and glirids. The work carried out on the Mallorcan vertebrates shows that even if some of the small mammals underwent substantial size increases, many of the very small species remained untouched by bizarre innovations. Small rodents and insectivores remained similar to their continental ancestors and Mein (1982: 156) claims to have established analogous evolutionary patterns.

The giant turtles of the Indian and Pacific Oceans may not be directly analogous to the HEDR unbalanced faunas, as turtles are capable of crossing sizeable stretches of ocean, although there are numerous subspecies associated with certain islands of a group (cf. Guillaume and Bons 1982).

Some workers (e.g. Simberloff 1978) develop models of island speciation in terms of a set of species spread over a number of islands in relation to the likelihood of successful colonization for individual species. Be it noted, however, that such models are often interpreted in conjunction with forms such as birds, certain arthropods, etc. which do not have the same distributional modes as the HEDR associations; the practical studies reported in the literature seem to be directed towards studying colonization of islands in easy reach of the mainland.

Genetic drift vs. selection

Genetic drift has been frequently invoked as the prime initial evolutionary mechanism for the HEDR associations. This is a logical argument as it is assumed that the founding populations in each particular instance would have been very small, just a few individuals.

There are, however, several observations which tend to speak against such a simple evolutionary mechanism as having been the dominating force in each and every instance. Firstly, the evolution in size is not always as sudden as usually claimed (cf. Thaler 1973); in such cases a pure drift process would be difficult to fit to the data. On the other hand, Sondaar (1977: 696) made the point that there is no evidence for the occurrence of intermediates between mainland and island forms and he concluded that the main morphological change took place over a short period of time. Thereafter, there were

but small variations of the primary adaptation. Thaler's (1973: 749) interpretation was based on his work in Sicily, where there is some evidence of intermediates and which can be viewed in the light of a filter pendulum route (Dermitzakis and Sondaar 1979).

As already observed, the main changes in elephants and hippopotami were directed towards the transition from an aquatic (for *Hippopotamus amphibius*) mode of life and low-gear locomotion (for elephants and hippopotami) to an environment craving agility and climbing prowess. As regards the rate of change, Sondaar (1977) thinks that this could have been slower for elephants, owing to their low rate of reproduction. This is again a condition that may be reflected in the Sicilian associations referred to by Thaler (1973).

The question of initial population sizes remains unresolved. However, the belief that dispersal was completely random, as implied by the sweepstake hypothesis, must be modified in the light of the rôle of surface oceanic currents. Obviously, most migrating animals perished, but those lucky enough to ride with a favourable current would have had an enhanced success of a successful passage to an oceanic island. If this be coupled with some kind of special event (catastrophic or not), there is a reasonable possibility that founder populations can have been larger than is generally conceded.

Presumably, all cases of Mediterranean HEDR evolution represent relatively small founder populations in which random effects can be expected to have been important. What seems to have taken pride of place, however, is that the new island environment (Mediterranean islands are usually mountainous) placed such an adaptational stress on the new arrivals that adaptive selection has overridden random effects. We note that the direction of changes are always the same irrespective of the island involved. The large mammals become radically smaller and the small mammals larger. I know of no documented case of a lagomorph or glirid becoming dramatically smaller than its ancestor. A useful overview is given by Mayr (1982).

Sondaar (1977: 694) concluded that the changes undergone by island HEDR faunas were independent products of evolution occurring in similar environments and parallelly manifested in each of these. Mein (1982: 156) also remarked on the parallel evolutionary patterns on different islands which he also observed to occur in the dentition of various groups. He interpreted these developments as deriving from the adaptation from an omnivorous to a herbivorous diet which would have entrained a change in the chewing process.

Wade (1982), writing on the subject of the differentiation of small populations, reiterated the axiom that in the absence of selection, the subdivision of a large population will result in the genetic differentiation of the sub-units owing to random genetic drift. In the case of the Mediterranean unbalanced faunas, selection has been so strong that unfavourable evolutionary direc-

tions deriving from random genetic drift have been eliminated as they appeared. The need to be able to extend the search for nourishment beyond the immediate coastal lowlands has had a profound effect on the survivability of the larger mammals. Sondaar and Boekschoten (1967) referred frequently to the evidence for mass mortality following on episodes of overpopulation.

In most natural populations, some migration between demes is likely to occur. The arguments presented by Sondaar (1977) seem to rule this out for the larger elements of the HEDR associations, except in cases where islands were close and probably connected to each other at periods of heavy glaciation. As noted earlier, the osteological properties making hippopotami and elephants good swimmer-drifters were largely lacking in the dwarfed descendants.

Concluding remarks

The present analysis is mainly based on published work and my personal field experience of Mediterranean islands and their unbalanced fossil HEDR associations is confined to a collecting trip to Cyprus in 1972 when I discovered a new cave (the Aphrodision locality of Boekschoten and Sondaar (1972) containing numerous osteoporos remains (collection in the Palaeontological Museum, Uppsala).

The rather remarkable development of dwarfed forms during the Neogene and Pleistocene seems to me to echo the very special suite of gross ecological conditions colouring that period of time, to wit, the Late Miocene salinity episode in the Mediterranean, which provided avenues of colonization to some animals, followed by the severe environmental effects of the ice ages; these conditions would have forced animals such as hippopotami and elephants to seek new pastures. Overcrowding along the eastern Mediterranean shores could have sparked off "follow-the-leader" migratory waves towards and into the sea. It seems necessary to postulate some kind of extreme situation in order to justify a migrational event of this kind on the scale that must have taken place in the Mediterranean realm.

Elephants and hippopotami as well as deer have been reported now and then well out to sea (cf. Sondaar 1977), but this cannot be claimed to be common behaviour for these animals. Hippopotami reached Madagascar during the Holocene, but I know of no reports of *H. amphibius* having gone ashore on that island in our time. Even in this case, the sub-recent hippopotami of Madagascar seem to have changed their mode of life to a degree almost corresponding to what as the case in the Mediterranean.

Predators are important agents for selection and it is widely accepted that they can provoke remarkable adaptations in prey animals. Vermeij (1982) has given a review of the literature for some predator-prey

co-adaptational relationships. The occurrence of gigantism in some small animals – lagomorphs, dormice, etc. is quite on the cards as a possible selectional development in the absence of land-predators. The evolutionary developments in these small mammals are less easy to understand than those of the large mammals and there are clearly many exceptions to the change towards gigantism. If the relaxation of predation pressure and an adaptation towards larger size to thwart birds of prey is to be accepted as a valid mechanism, it is necessary to explain why only some of the small mammals were touched by this type of development (cf. Thaler 1973, Mein 1982).

The islands of the Neogene and Pleistocene of the Mediterranean provided a set of experiments in evolution, the lessons of which we need to keep in mind in today's discussions of evolutionary mechanisms. The island HEDR populations formed "peripheral isolates", of this there can be no doubt. On being reunited with the mainstream of mammalian events in the Mediterranean region, they failed to thrive and were rapidly wiped out by the combined forces of unsuccessful competition with related species and a total lack of defense against predators.

References

- Andrewartha, H. G. 1961. – Introduction to the study of animal populations. – Univ. of Chicago Press, Chicago, IL.
- Azzaroli, A. 1981. Cainozoic mammals and the biogeography of the island of Sardinia, western Mediterranean. – *Palaeogeogr., Palaeoclim., Palaeoecol.* 36: 107–111.
- Biju-Duval, B., Letouzey, J., Montadert, L., Courrier, P., Mugniot, J. F. and Sancho, J., 1974. Geology of the Mediterranean Sea basins. – In: Burk, C. A. and Drake, C. L. (eds.), *The geology of continental margins*. Springer, Berlin, pp. 695–721.
- Boekschoten, G. J. and Sondaar, P. Y. 1972. On the fossil mammals of Cyprus. – *Proc. Koninkl. Nederl. Akad. Wetensch. B.* 75: 306–330.
- Dermitzakis, M. D. and Sondaar, P. Y. 1979. The importance of fossil mammals in reconstructing paleogeography with special reference to the Pleistocene Aegean Archipelago. – *Ann. Géol. Pays Hellén.* 29: 808–840.
- Foster, J. B. 1964. Evolution of mammals on islands. – *Nature, Lond.* 202: 234–235.
- Freudenthal, M. 1976. Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy). – *Scripta Geologica* 37: 1–23.
- Guillaume, C. P. and Bons, J. 1982. Les reptiles insulaires: mise en place et évolution. – *Modalités de l'Evolution: Mécanismes de Spéciation. Coll. Int. CNRS (Dijon 1982):* 287–295.
- Houtekamer, J. L. and Sondaar, P. Y. 1979. Osteology of the forelimb of the Pleistocene dwarf hippopotamus from Cyprus with special reference to phylogeny and function. – *Proc. Nederl. Akademie Wetensch. B* 82: 411–448.
- Mayr, E. 1982. Speciation and macroevolution. – *Evolution* 36: 1119–1132.
- Mein, P. 1982. Particularités de l'évolution insulaire chez les petits mammifères. – *Modalités de l'Evolution: Mécanismes de Spéciation. Coll. Int. CNRS (Dijon, 1982):* 153–159.
- Pielou, E. C. 1979. *Biogeography*. – Wiley, New York.
- Simberloff, D. 1978. Using island biogeographic distributions to determine if colonization is stochastic. – *Am. Nat.* 112: 713–726.
- Sondaar, P. Y. 1977. Insularity and its effect on mammal evolution. – In: Hecht, M. K., Goody, P. C. and Hecht, B. M. (eds.), *Major patterns in vertebrate evolution*, pp. 671–707.
- and Boekschoten, G. Y. 1967. Quaternary mammals in the south Aegean Island Arc with notes on other fossil mammals from the coastal regions of the Mediterranean. – *Koninkl. Nederl. Akad. Wetensch.* 70: 556–576.
- Sonnenfeldt, P. 1975. The significance of Upper Miocene (Messinian) evaporites in the Mediterranean Sea. – *J. Geol.* 83: 287–311.
- Sverdrup, H. U., Fleming, P. and Johnson, M. W. 1942. *The oceans*. – Prentice-Hall, Englewood Cliffs, NJ.
- Thaler, L. 1973. Nanisme et gigantisme insulaires. – *La Recherche* 37: 741–750.
- Vermelij, G. J. 1982. Unsuccessful predation and evolution. – *Am. Nat.* 120: 701–720.
- Wade, M. J. 1982. Group selection: migration and the differentiation of small populations. – *Evolution* 36: 949–961.
- Williamson, M. 1981. *Island populations*. – Oxford Univ. Press, London.