Evolution of Island Mammals

Adaptation and Extinction of Placental Mammals on Islands

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In memory of Paul Yves Sondaar (1934–2003)

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PREFACE

This is a state of the art reference book about fossil insular mammals. It provides an extensive overview of what is known about their evolution, adaptation and extinction. Fossil insular mammals often show remarkable and sometimes even bizarre adaptations, such as dwarfism and gigantism. Understanding the processes underlying these adaptations helps us to understand the patterns of evolution, not only those on islands, but also those on the mainland and in fragmented habitats.

Many important studies describe the biogeography and ecology of extant insular mammals, but similar works on extinct insular mammals are few. Although the number of such studies is increasing, the information on individual taxa and islands is scattered over many journals, often not widely available, or information on the subject is limited to a few paragraphs in books. This long-awaited book offers a timely synthesis of available extant studies. Our overview of fossil insular faunas offers an updated approach to the subject and elaborates on published studies – excellent as some of these in many respects are. We have designed this book as a synthesis of available data somewhat less formal than research papers or systematic revisions. In this way it will be of use to the many researchers, regardless of speciality, who need a source of data and interpretations about fossil insular mammals, as well as qualified graduate students in palaeontology, zoology, evolutionary biology and biogeography.

Why is an up-to-date overview of fossil insular mammals important? Our knowledge of island biogeography, ecology and evolution is limited because it is mainly on present-day patterns of biodiversity on islands and in fragmented habitats. The main limitation of this approach is that the available sources are by definition restricted to very short and recent periods of time. To analyse similar biogeographical patterns that developed over time spans of thousands or even millions of years, fossil data need to be part of our studies.

By ignoring the fact that biodiversity on islands was much greater in the past than it is today and by only taking into account present-day biodiversity on islands, an impoverished, unbalanced view of island biogeography may come into being. For example, the megafauna of Madagascar contained large taxa, such as hippos and giant lemurs, which are all extinct now. This means that the average body mass of Malagasy taxa is lower now than during the Late Pleistocene. Furthermore, because of the effects of time, the resulting speciation differs much from what is seen today. Where present-day island taxa often are not smaller than roughly 80% of their mainland ancestor, fossil insular taxa sometimes reduced their body mass to a mere 1%, as in the case of the pygmy elephant of Sicily (*Elephas falconeri*). As a result, islands of today provide a poor example of evolution on islands.

The fossil record of the supercontinental islands Australia and South America is excluded from our synthesis. The reason is that their fossil faunas represent balanced or harmonic faunas, thus containing a representative number of elements pertaining to all orders typical for the geographical latitude and altitude, with representatives of all trophic levels. In fact, these mega-islands are more similar to continents than to islands. Their long-term isolation resulted in endemic balanced faunas with their own stamp, not comparable to the endemic faunas we describe in this book. The inclusion of Australia and South America would lead to yet another book on general vertebrate palaeontology. In order to keep the scope of the book more focused, we excluded these supercontinental islands and restricted ourselves to placental mammals.

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PART I

Beyond the Mainland

All over the world, islands were and still are inhabited by unique species, restricted to their own island and found nowhere else. Their ancestors managed to reach the island from the mainland, and once isolated from this mainland with its ecological restrictions, they often evolved spectacular adaptations. In this part, after a general introduction to island studies, a short overview of island studies is given, followed by an overview of what defines islands and island faunas as opposed to the mainland and its faunas.

CHAPTER ONE

Introduction

Isolated from the rest of the world, island species often develop adaptations to new ecological niches. In this book, the past effects of insularity on different animal species are discussed, based on about 370 fossil insular species, which were endemic to at least 30 islands all over the world.

Many groups, such as predators or close competitors, are absent from islands. This means the evolution of a new colonizer will be released from the constraining forces that were active on the mainland. As a result, species on islands evolved into new forms that were lacking particular specializations or were adapted to lifestyles or habitats formidable to their mainland relatives.

Size change is the most spectacular and certainly the best-known effect of ecological release (a shift and decline in the relative importance of interspecific interactions to an increase in the importance of intraspecific interactions). Many large mammals, such as elephants and hippopotamuses, evolved towards miniature forms and many small mammals, such as rodents, evolved towards giant forms. Size change is not the only result of this ecological release. Because island faunas are highly disharmonic, with many major groups missing, most close competitors are absent. Therefore, the colonizing species could expand or even change their niche. Other clear effects of insularity are hypsodonty in herbivores, shifts in prey species in carnivores, fusion and shortening of limb bones, and changes in body proportions. Patterns are not the same everywhere. Islands differ amongst each other, and so do their faunas: these may be balanced ('normal' ratio between carnivore and herbivore species), unbalanced (ratio between carnivores and herbivores clearly in favour of the latter), disharmonic or impoverished (poor taxonomic diversity on higher levels), endemic (restricted to the island, not found elsewhere) or mainland-like (hardly different from continental faunas of similar latitude).

The geological time covered in this book ranges from the late Early–Middle Eocene to the terminal Pleistocene or Early Holocene. The earliest faunas, however, have a poor fossil record, and many uncertainties prevail about the level of endemism of the individual taxa. The late Early or Middle Eocene fauna of Sardinia, for example, is known only by two endemic tapiroids and an opossum. The fauna of Jamaica of the same period contains a rhinocerotid and a walking sirenian, but no endemic features have been described. The Early Oligocene sloth of Puerto Rico may even belong to an ancestral mainland fauna. The Miocene insular faunas on the other hand are well documented, such as the Early Miocene faunas of Sardinia and Japan and the Late Miocene faunas of the Balearics, Gargano and Tuscany). However, the vast majority of fossil insular faunas belong to the Pleistocene Period. Especially the Late

Pleistocene is known for its wealth of fossil insular mammals in, for example, the West Indies, Madagascar and Cyprus, to name but a few. When relevant to the discussion, recently extinct and still living but endangered insular mammals are also included in our synthesis.

Not included in this book is the Eocene of Europe. Most of these faunas (e.g. Messel, Quercy) bear a mainland stamp and have been extensively covered by studies on mainland mammals. In some textbooks these Eocene sites are ascribed to an archipelago. Findings of fossil crocodilians indicate the existence of islands (e.g. Monte Boca) during the Eocene and Oligocene, but at present, this has not been confirmed. Excluded as well are the Middle Miocene mammal remains from New Zealand. They seem to belong to a very primitive mammal, which may have arrived during the Mesozoic (a vicariant event) but its phylogenetic and endemic status is unresolved.

Throughout this book not all islands in the biogeographical sense (a habitat surrounded by inhospitable areas) are included. Our selection has been restricted to islands in the geographical sense: a piece of land surrounded by water. In the geological sense, roughly two main types of islands are further recognized: (a) continental shelf islands, which are islands sitting on a continental shelf and may have been connected to the mainland; and (b) oceanic islands, which sit on an oceanic crust and were never connected to the mainland and arose from the sea bottom.

The first type of islands are characterized by an impoverished fauna, consisting of a limited but often representative subset of the continental fauna, with a low degree of endemism. The second type is characterized by a disharmonic fauna (fewer higher taxa when compared with equivalent patches of nearby mainland) with a high degree of endemism. In the biogeographical sense, some continental shelf islands are like oceanic islands and have a similar fauna. Many gradations do exist within the continental shelf islands, with faunas ranging from balanced and harmonic to balanced but impoverished and unbalanced and endemic, depending on the degree of isolation.

Part I of this book forms an introduction to island studies, starting with a general introduction, followed by a short overview of the history of island studies and ending with a chapter on the various factors that typify insular faunas, such as distance to the mainland, type of island and area, and the various ways of dispersal to islands.

Part II gives an overview of the faunas of separate islands, starting with the Mediterranean Islands, followed by Madagascar, the Indonesian and Japanese islands, the Californian Channel Islands and ending with the West Indies. In these chapters an overview is offered of the biozones or faunal units. For the purpose of this book, we define a biozone as a stratigraphic layer characterized by one or two taxa, sometimes divided into subzones when an evolution within the taxon can be discerned. A faunal unit (at times also referred to as a faunal complex) on the other hand, is a subset of the fauna with the most characteristic elements, sometimes applied when the complete fauna is unknown. For some islands, biozones are defined, for other islands faunal units. Part II thus defines the context of the various insular taxa, their time span, arrival and extinction, insofar known. Non-mammalian taxa are included where relevant.

Part III starts with an overview of insular mammals in a taxonomical arrangement, including proboscideans, artiodactyls, carnivores, rodents, insectivores, bats and lagomorphs. Insular faunas are by definition endemic and thus unique to the island, but the area-by-area treatment of Part II obscures the existence of parallelisms. Dwarf and pygmy proboscideans are, for example, found all over the world. Discussing them in relation to each other allows us to highlight similarities and dissimilarities. The reader should note that although the terms dwarf and pygmy are both in use for plants or animals of unusually small stature, we reserve the term pygmy for extremely small forms (half the ancestral size or even less), and the term dwarf for the other small forms (some 80–60% of the ancestral body size) for convenience and to stress the different outcomes of size increase. We apply the term ‘small’ to slightly smaller forms (some 90% size reduction only).

Information about shared ancestry, similar morphological changes and taxonomic confusions is also found in this part of the book. Finally, a number of islands are known only for a single species and this is also noted in this part of the book. The second part of Part III discusses overall patterns and trends, observed in more than one order, and the drive behind the processes of speciation on islands. The conceptual context for viewing biogeographical patterns is based on Whittaker and Fernández-Palacios (2007). In this part of the book, non-mammalian taxa are included where relevant. Part III ends with a chapter on the possible reasons for the extinction of insular mammals.

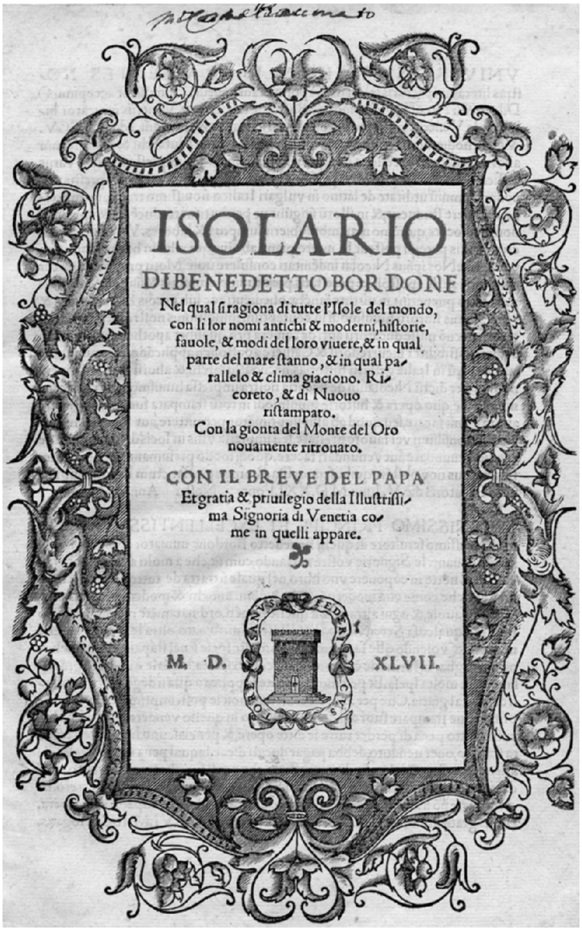
CHAPTER TWO

History of Island Studies

Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands, 1st edition. © 2010 by A. van der Geer, G. Lyras, J. de Vos and M. Dermitzakis. Published 2010 by Blackwell Publishing Ltd.

Since Charles Darwin's earliest report on his voyage around the world (1839), his seminal book on natural selection and evolutionary theory (1859), and the many writings of Alfred Russel Wallace on evolution and island life (e.g. 1855, 1858, 1869, 1876, 1880), generations of naturalists and biogeographers have maintained a keen interest in the nature and evolution of insular biotas. The first book on islands worldwide, however, predated Darwin by roughly three centuries. In 1528, Benedetto Bordone, an astronomer and cartographer from Padua, Italy, had his *Libro* published in Venice, renamed to *Isolario* in the edition of 1534 (figure 2.1). The book was an illustrated guide about the then known islands for seafarers. It is divided into three parts, describing respectively the islands and peninsulas of the western ocean (now the Atlantic Ocean), the Mediterranean Sea, and the Indian Ocean plus the waters of the Far East. The New World was presented as an island, because at that time the entire contours were unknown. Apart from many valuable maps it contains the earliest known European map of Japan, known to Bordone as the island Ciampagu. For our purpose, his descriptions of the insular biota are interesting, especially those that refer to fossil faunas. For example, in the part on Cyprus ('Cipro'), Bordone described a hill at Kyrenia ('Zyrenes'), entirely made of bones of animals and humans. This would lead naturalists in the 19th century to investigate these and similar fossiliferous deposits, eventually resulting in the discovery of pygmy hippopotamuses and dwarf elephants. Indeed, the lessons were not lost on Darwin and Wallace, who both remarked on the bizarre life forms reported in the fossil record.

Although many early naturalists and travellers deliberately went to the various islands to search for fossils, as given in detail in the relevant chapters of this book, Charles Forsyth Major was one of the first naturalists to seriously make an attempt to compare the fossil faunas from various islands in order to understand the underlying evolutionary principles. His search for fossil island faunas started in 1877 when he was funded by the Italian government to collect fossils on Corsica, Sardinia and Sicily. In 1886 he began to study fossils from Cyprus, Crete and Samos, which were partly sent to the British Museum of Natural History, London, and the Geological Museum at Lausanne, Switzerland. These were not the first fossils from Crete for the British Museum, as previously fossils had been sent to Richard Owen and Hugh Falconer. At the British Museum, Forsyth Major started to work on the primate collection from Madagascar, both extinct and extant. In 1893, he discovered amongst others a new species of extinct giant lemurs (*Megaladapis madagascariensis*) for which he erected a new family (Megaladapidae) and five new species in the genera



ISOLARIO
DI BENEDETTO BORDONE
Nel qual ſi ragiona di tutte l'Iſole del mondo,
con li lor nomi antichi & moderni, hiſtorie,
fauole, & modi del loro viuere, & in qual
parte del mare ſtanno, & in qual pa-
rallelo & clima giaciono. Ri-
coreto, & di Nuouo
riſtampato.
Con la gionta del Monte del Oro
nouamente ritrouato.
CON IL BREVE DEL PAPA
Et gratia & priuilegio della Illuſtriſſi-
ma Signoria di Venetia co-
me in quelli appare.

M. D. XLVII.

Figure 2.1 Title page of Bordone's *Isolario*, 1547.

Lepilemur and *Cheirogaleus*. A year later, he undertook an expedition to the island, funded by the Royal Society, the banker Lionel Walter Rothschild and others. The expedition lasted two years, during which a very large collection of fossils and zoological specimens was gathered:

> 'it may be remarked that the very large collection was obtained under circumstances of great difficulty and danger. The swampy nature of the deposits made the task of excavating very arduous, and the work was frequently interrupted for days at a time through the growing hostility of the natives. Dr. Forsyth Major and his companion, M. Robert, are therefore the more to be congratulated that, under such unfavourable conditions, they have added so much to our knowledge of the extinct fauna of Central Madagascar.' (Andrews, 1897, p. 358)

Towards the end of the 19th century, a young woman, Dorothea Bate, came to the British Museum to look for a job. Self-educated, she first started to work in the Bird Room to prepare bird skins, but soon her abilities were recognized. Forsyth Major began to tutor her on fossil island faunas and suggested that she should go to Cyprus, to collect materials, fossil as well as extant. He expected her to find fossils of dwarf hippopotamuses and dwarf elephants, just as they had been found on Sicily, Malta and Crete. In 1901 she went for the first time, and explored the greater part of the island, guided by the earlier descriptions. She discovered twelve new fossiliferous caves, and relocated some earlier mentioned sites. Among the fossils that she had sent to the British Museum, Forsyth Major recognized fossils of the expected small hippopotamus, which were extremely similar to those depicted by Georges Cuvier in 1804 as 'hippopotame petit', literally small hippopotamus. He realized that the Paris' material obviously originated from Cyprus, not from southern France as generally thought. A year later, Bate returned to Cyprus, and finally found the remains of a dwarf elephant. The similarity in fossil faunas of the Mediterranean islands, containing dwarf hippopotamuses, elephants and giant rodents, prompted her to go to Majorca and Minorca as well, but this was a great disappointment. In contrast to what she and Forsyth Major had expected, she found nothing else but bizarre goats, dormice and shrews. It took some years before *Myotragus balearicus*, described by her in 1909, was appreciated for what it actually was, a highly adapted insular ruminant with ever-growing incisors that had lived for almost two million years undisturbed on the islands. The picture of fossil island faunas had become more diverse.

The American palaeontologist William Dillon Matthew was the first to observe in 1918 that faunas on oceanic islands are typically unbalanced, which is to say that they only contain a limited and unrepresentative number of elements of the contemporaneous mainland fauna. In 1940, his fellow countryman George Gaylord Simpson established the link between the nature of these unbalanced faunas and the means of colonization of these islands, introducing the term 'sweepstake route', a free translation of Matthew's 'accidents of transportation'. The term, changed into sweepstake dispersal, is today widely applied in cases of 'by chance' arrival across large distances over water.

The idea of overseas dispersal was initially not commonly accepted. A prevalent explanation for the presence of elephants, hippopotamuses and micromammals on islands was dispersal across ancient, but now submerged land bridges. Elephants were believed not to be able to swim (see especially Bourlière in 1970) and thus these islands had been connected to the nearest mainland by the time of arrival of the ancestors of the insular taxa. The findings of elephants and hyenas on Sicily were accordingly considered proof of the connection between Sicily and North Africa, as Hugh Falconer wrote to Darwin on 9 July 1860:

> 'What I want to tell you now is quite a different affair – but one which I am sure will interest you very much. Baron Anca a Sicilian Friend, who followed up my inquiries in the Sicilian caves, has brought over from Sicily two molars of the Existing African Elephant and upwards of 20 jaws of the Existing Spotted Hyæna (*Hyæna Crocuta*), of the Cape – from the Caves! Admiral Smyth laid down 'Adventure Bank' 'a shoal with a narrow channel, between Trapani the Western End of Sicily & Capo Bono – the promontory of Tunis. We can now show that the division of Sicily from the African Continent is quite as late – if not later than the separation of England from France.' (Letter 2863, the Darwin Correspondence Project)

Today, the swimming abilities of several taxa (see Chapter 3) are generally acknowledged, and sweepstake dispersal is an accepted theory. In some cases, however, land connections are still the best explanation for the occurrence on islands of non-natatorial taxa, such as lagomorphs and amphibians.

A few early authors explained the pygmy ungulates on islands as the result of inbreeding or genetic degeneration in the absence of selective pressure exerted by large terrestrial carnivores. Examples are Piero Leonardi in 1954 and Sigfried Kuss in 1965, both focusing on the Mediterranean dwarfs. This model was never widely accepted, although from time to time it is revived, such as in the case of *Homo floresiensis* whose small stature and low brain capacity is considered by some as evidence of a pathological condition (see Chapter 13). Leonardi also provided an alternative theory, according to which the dwarfs had evolved elsewhere and had migrated to the various islands. According to that view, the various dwarf elephants found on Mediterranean islands were considered conspecific with the Sicilian pygmy elephant (*Elephas falconeri*). This theory was partly based on a misinterpreted fossil milk molar from the mainland.

Body size evolution is not only one of the most fundamental responses to island environments, but also the easiest response to quantify and compare. This explains the almost unique focus on body size changes in island studies. In his comprehensive review published in 1964, J. Bristol Foster was the first who noted that there are different tendencies in body size evolution among taxonomic groups. Whereas insular artiodactyls, lagomorphs and carnivores tend to become smaller, insular rodents and possibly insular marsupials as well tend to become larger. Leigh Van Valen in 1973 dubbed this observation a 'rule' (his quotation marks), not directly referring to Foster but indirectly through his own 1970 publication. Later authors, e.g. Lawrence Heaney in 1978 and Mark Lomolino in 1985, refined this island rule and interpreted the pattern as a graded trend across as well as within taxa, from dwarfism in the larger species to gigantism in the smaller species. The intersection point is then a crude estimate of an 'optimal' body size for a species of a particular design or Bauplan and ecological strategy, as suggested by Ted Case in 1978. To go one step further, similar ecomorphs from different phylogenetic lineages evolve towards a similar body mass in time under optimal conditions.

One of the key driving forces for these evolutionary trends is interspecific interactions, or release from those interactions on unbalanced and species-poor islands. Therefore, a general theory of body size evolution on islands also needs to explain the paucity of competitors and predators on those islands, along with the subsequent evolutionary responses of the island's endemics. In a paper published in the journal *Evolution* in 1963, and later in a monograph published in 1967, Robert MacArthur and Edward Wilson developed a quantitative mathematical model to predict the species diversity in a given isolated area. Since then, most island studies use quantitative data instead of morphological data and the results are presented as plots and graphs. The equilibrium theory of MacArthur and Wilson suggests that species diversity on islands is the sum of new arrivals and newly evolved species *in situ* minus the number of extinctions.

Thus, the factors that are used in these quantitative studies to calculate or predict species diversity and body mass of endemic species comprise surface area of the island, distance to the mainland, limited food on the island, decreased interspecies competition, and absence of predation by mammalian carnivores. For example, the greater the distance is, or the more difficult the passage or filter, the lower the species richness, and the more prevalent ecological release and tendencies toward body size extremes.

In the past 30 years, various models have been proposed to explain the underlying processes influencing patterns of diversity and evolution on islands. These models, which are based mainly on studies of living biotas, attempt to explain the arrival, evolution and extinction in both single islands and archipelagos. Robert Whittaker and José María Fernández-Palacios provided in 2007 a comprehensive overview of all these works. Application of rules and methods from these and similar works to fossil insular taxa is a new trend, for example Pasquale Raia and colleagues in 2003 on life-history traits of *Elephas falconeri* from Sicily, Raia and Shai Meiri in 2006 on body size in fossil ungulates and carnivores, Virginie Millien in 2006 on the speed of evolution on islands, calculated from the fossil record, and Maria Rita Palombo in 2007 on evolution of insular proboscideans from the Mediterranean. The number of these studies is increasing, contributing fundamentally to our understanding of evolution on islands in a broader context. The important factor in this new trend is time. Where most island studies are based on recent or extant taxa only, i.e. those occurring within a thousand years at most, more integrative and insightful island studies will include time spans ranging from thousands to even millions of years.

CHAPTER THREE

Factors that Influence Island Faunas

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> 'I do not deny that there are many and grave difficulties in understanding how several of the inhabitants of the more remote islands, whether still retaining the same specific form or modified since their arrival, could have reached their present homes.' (Charles Darwin, 1859, p. 396)

Island faunas are influenced by several factors. These are, amongst others, the various types of islands, the ways of dispersal to the island, the distance to the mainland and island area, the faunal composition as a whole and characteristics of its elements, and physiography of the island. Naturally, these factors are interwoven and subject to changes over time, influencing each other constantly. For example, the physical geography of the island together with local and global climate place a significant control on island size in terms of suitable surface area.

Types of Islands

Many studies on fossil island faunas present a rather artificial categorization of island types, based on palaeozoographic evidence and the wish to compare fossil faunas mutually and with extant insular faunas. Two types of islands were recognized by Philip Darlington in 1957 – continental versus oceanic islands – to which Josep Alcover and colleagues added a third type in 1998 – oceanic-like islands. The usefulness of such a classification is limited, partly because of the interchangeability of the terms continental and oceanic-like islands (see below). The only distinctiveness between oceanic islands and the other islands is that absolutely no saltwater-intolerant taxa, such as salamanders, are found on the former.

Continental islands

Continental islands are part of a continental shelf. Generally, they become isolated from the mainland through subsidence of the isthmus of a peninsula. Often they are separated from the mainland by relatively shallow water. Continental islands are subject to being reconnected with the mainland by a relatively small lowering of the sea level through a land bridge or land span. The majority of islands with fossil endemic faunas belong to this category. Examples of continental islands are Sardinia, Sicily and Japan.

Oceanic and oceanic-like islands

Oceanic islands arise beneath the sea and from their origin are surrounded by water. Subsequent tectonic and volcanic processes

BOX 3.1

Oceanic-Like Islands or Not

The term oceanic-like is somewhat unfortunate without a clear indication of the duration of the isolation to distinguish a continental island from an oceanic-like island. Majorca, one of the Balearic Islands, for example, began its existence as part of the Iberian Peninsula from which it broke off in the Early Oligocene as a continental island, in parallel with the Sardinia–Corsica block. During the Messinian salinity crisis of the terminal Miocene, the island came into some sort of contact with the mainland. Since then a long-term isolation started, lasting up to the present day. Its lineage of highly endemic bovids (*Myotragus*) seems to originate from the period of the Late Miocene land connection, and thus represents a vicariance effect, not overseas dispersal. The same is true for the island's giant dormice. To conclude, despite its long-term isolation, Majorca cannot be considered an oceanic-like island. Crete on the other hand, with its much shorter isolation, is classified as an oceanic-like island, based on its fauna with elephants, deer and hippopotamuses and lack of vicariant taxa.

may minimize the distance to a continent, or in rare cases even lead to a connection with the latter. Oceanic-like islands on the other hand are continental islands that were connected to the mainland in the very remote past, and have since remained isolated. Both types of island – oceanic and oceanic-like – are colonized by oversea dispersal. Only very few mammal taxa will be successful enough to found a new population though, because terrestrial mammals are poor dispersers across wide water barriers. The main exceptions are elephants and deer. Because of the observed similarity in faunal composition, Alcover et al. (1998) refer to these two types of island as true islands (see box 3.1). Examples of oceanic islands are Cyprus, Flores and the Galapagos. An example of an oceanic-like island is Madagascar, which became separated from Africa early in the Cretaceous.

Changes through time

The palaeogeography of many islands is, however, complex and the same island may belong to different classes through time. For example, Crete was still part of the mainland during the Miocene. During the Pliocene, however, it was partly submerged and became a continental island. Since the Pleistocene