

ALEXANDRA VAN DER GEER ■ GEORGE LYRAS ■ JOHN DE VOS

EVOLUTION OF ISLAND MAMMALS

ADAPTATION AND EXTINCTION OF
PLACENTAL MAMMALS ON ISLANDS



SECOND EDITION



WILEY Blackwell

Evolution of Island Mammals

In memory of Paul Yves Sondaar (1934–2003)

Evolution of Island Mammals

Adaptation and Extinction of Placental
Mammals on Islands

Second Edition

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PREFACE

This is the second edition of our 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. 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. Moreover, since the time of the first edition (2010), many new discoveries were made, and novel techniques and methodologies have been implemented in the study of the fossil record. This edition is substantially modified and offers extensive coverage of the latest developments in the field. It is a comprehensive book that offers an updated concise synthesis of available studies. Our overview of fossil insular faunas provides 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 based on present-day patterns of biodiversity on islands and in fragmented habitats. This means that the available sources are by definition restricted to very short and recent periods of time. To analyse and infer 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 larger 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, elephant birds, and giant lemurs, which are all extinct now. This means that the average body mass of Malagasy taxa is much 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 less than 5% as is the case with the dwarf elephant of Sicily (*Palaeoloxodon falconeri*). As a result, islands today provide a poor example of mammal 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 geographic latitude and altitude with representatives of all trophic levels. In fact, these mega-islands are ecologically 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 focussed, we excluded Australia and South America and restricted ourselves to placental mammals.

The separate chapters of this and/or the previous edition were reviewed by the following experts in the field, in alphabetical order, for which we are grateful: the late Larry Agenbroad, Athanassios Athanassiou, Chiara Angelone, Laura Bonfiglio, Pere Bover, the late Johanna de Visser, Lawrence Heaney, Christine Hertler, Mark Lomolino, Ross MacPhee, Sandra Olsen, Hidetoshi Ota, Hiroyuki Otsuka, Maria Rita Palombo, Lorenzo Rook, Haruo Saegusa, Ian Tattersal, George Theodorou, Gert van den Bergh, Lars van den Hoek Ostende, and Jan van der Made. We thank every one of them for variously commenting on the draft and final material, supplying answers to queries, and sharing with us their most recent papers.

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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 the history 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

Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands, Second Edition.
Alexandra van der Geer, George Lyras and John de Vos.
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Isolated from the continental landmasses, island species evolve novel and often extreme adaptations to new ecological niches. In this book, the past effects of insularity on mammal lineages are discussed, based on more than 300 fossil insular species, which were endemic to about 80 islands all over the world, and ranging from the Eocene to the Holocene, with a few Cretaceous cases.

The evolution of body size change is at first sight 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 herbivores, like elephants (Plate 1) and hippopotamuses, evolved towards miniature forms on islands, while many small mammals, like rodents and pikas, evolved towards giant forms. Since island faunas are highly disharmonic, with many major groups missing, most or all ecologically relevant competitors are absent. Therefore, the colonising species could expand or even change their ecological niche. In fossil species, this can be deduced from observations such as the evolution of hypsodonty – high-crowned cheek teeth – 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, as we shall see. Islands differ amongst each other, and so do their faunas: these may be balanced (mainland ratio between carnivore and herbivore species), unbalanced (ratio between carnivores and herbivores shifted towards the latter), disharmonic or depauperate (poor taxonomic diversity on higher levels), entirely endemic (all species 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 Late Pleistocene–Early Holocene with a few instances from the Cretaceous. 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 tapirs and an opossum. The fauna of Jamaica of the same period contains an early rhinocerotid and a semi-aquatic sea-cow, 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, or the Ice Ages. Especially the Late Pleistocene is known for its wealth of fossil insular mammals

in, for example, the West Indies, Madagascar, and the Mediterranean. When relevant to the discussion, recently extinct and still living but endangered insular mammals are included in our synthesis as well.

Not treated separately in this book is the Eocene of Europe at large. During this geological period, Europe was an archipelago, as inferred from stratigraphy and, for example, findings of fossil marine species. These faunas, such as those of Messel in Germany – one of the richest fossil sites in the world, have been extensively covered elsewhere (see further Box 1.1). Excluded as well is the early Miocene St Bathans fauna of New Zealand (16–19 million years ago). Here, fossils of at least two bat species belonging to the extant endemic family of burrowing bats (Mystacinidae) have been retrieved (described by Suzanne Hand and colleagues, 2015). The St Bathans fauna further includes remains of primitive frogs – *Leiopelma*, still extant and unique to New Zealand – a lizard-like sphenodontine reptile (a relative of the extant tuatara), birds (including kiwi, moa, and waterfowl), an armoured stem turtle (possibly related to *Meiolania* of Australia and New Caledonia), geckos, skinks, a crocodile, and a primitive currently unnamed mammal, as summarised by Trevor Worthy and colleagues (2017). This highly endemic and partly ‘primitive’ fauna confirms the vicariant or ancient dispersal origin of the ‘old endemics’ of New Zealand and refutes the idea of total drowning of Zealandia – a continental fragment of Gondwana – during the late Oligocene–earliest Miocene (22–25 million years ago) high sea level stand.

The European Eocene Archipelago

During the Eocene, much of Europe was under water, forming a kind of archipelago of islands. There was a large Central European Island, which consisted of parts of present-day England, France and Germany, and archipelagos of smaller islands in what is now south-eastern Europe. The islands were inhabited by endemic mammalian faunas – which were different from their contemporaries in North America and Asia – and included various odd-toed ungulates (palaeotheriids and lophiodontids), even-toed ungulates (anoplotheiriids and xiphodontids), and hippopotamus-like even-toed ungulates (choeropotamids and cebochoerids). Most of these faunas, particularly those in Western Europe – such as Messel and Quercy – bear a mainland stamp and have been extensively covered by studies on mainland mammals.

BOX 1.1

The isolation of Europe ended around the Eocene–Oligocene boundary and many European endemic lineages went extinct synchronous with the arrival of new immigrants from Asia. This major faunal turnover, known as the ‘Grande Coupure’, was first recognised and named by the Swiss palaeontologist and geologist Hans Georg Stehlin (1910). It should be noted, however, that remains of the anthracothere *Prominatherium* – a new arrival from Asia – have been found in Late Eocene coastal marine deposits of Croatia, Romania, and Italy, so dating from before the Grande Coupure proper. According to Laureline Scherler and colleagues (2019), this indicates the existence of a maritime path as there was yet no terrestrial connection to Asia. According to them, *Prominatherium* had a sufficiently aquatic lifestyle to allow its dispersal through the archipelago of Southern Europe, but likely not for crossing the Perialpine and Paratethys seas and settle in Western Europe.

One of the islands in the south-east was the Pontide terrane of Central Anatolia, in what is today Turkey. According to Grégoire Métais and colleagues (2017), the terrane hosted a unique combination of Laurasian and Gondwanan mammals. The mammalian fauna of the island included rhino-like paenungulates (embrithopods), stem marsupials (herpetotheriids, anatoliadelphid), and an endemic radiation of archaic ungulates (pleuraspidothériids). Pleuraspidothériids were also present during the Palaeogene in Western Europe, but already went extinct near the Palaeocene–Eocene boundary. Their survival in the Pontide terrane during the mid-Eocene is considered relictual by Métais and colleagues (2017). They may have arrived through land bridges that existed during the Palaeocene. The other taxa, such as embrithopods and metatherians, likely arrived via overwater dispersal, according to Métais and colleagues (2018). The Pontide terrane remained insular until the end of the Eocene.

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 recognised: (i) continental shelf islands, which are islands sitting on a continental plate and may have been (intermittently) connected to the mainland and (ii) oceanic islands, which sit on an oceanic plate and were never connected to the mainland and arose from the sea bottom.

The first type of islands is characterised by a depauperate fauna – consisting of a limited but often representative subset of the continental fauna – with a low degree of endemism. The second type is characterised by a disharmonic fauna – fewer higher order taxa when compared to 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. Thus, many gradations exist within the continental shelf islands, with faunas ranging from balanced and harmonic to balanced but depauperate and disharmonic and endemic, mainly depending on degree, type, and duration of isolation.

Part I of this book forms an introduction to island studies, starting with this general introduction, followed by a short overview of the history of island studies and a chapter on the various factors which 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 a concise overview of the faunas of individual 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, a comprehensive treatment is provided of the history of discoveries, biozones, or faunal units and the peculiarities and evolutionary aspects of individual endemic species or lineages. Here, we define a biozone as a stratigraphic layer characterised 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 species, their time span, arrival to the island, and eventual extinction, where known. Non-mammalian vertebrate species – such as birds, tortoises, and frogs – are included where relevant to the discussion.

Part III starts with a short overview of insular mammals with information about their distribution, range, and dispersal to the islands. Insular species 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 elephants are, for example, found all over the northern hemisphere. Discussing them in relation to each other allows us to highlight similarities and dissimilarities. Furthermore, a number of islands are known only for a single endemic species, and these are limited to this part of the book. The second part of Part III discusses overall patterns and trends – including not only the island

rule of body size evolution but also other parallel evolutionary processes – as well as a treatment of the processes of speciation on islands. The conceptual context for viewing biogeographical patterns is based on the handbooks by Whittaker and Palacios (2007) and Lomolino, Riddle and Whittaker (2017). Part III ends with a discussion on the possible reasons for the extinction of insular mammals.

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CHAPTER TWO

History of Island Studies

*Evolution of Island Mammals: Adaptation and Extinction of Placental
Mammals on Islands*, Second Edition.

Alexandra van der Geer, George Lyras and John de Vos.

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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, and 1880), generations of naturalists and biogeographers have maintained a keen interest in the nature and evolution of insular biotas. The first published 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 *Iso-lario* in the edition of 1534. 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 correct 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') (Figure 2.1), Bordone described a hill at Kyrenia ('Zyrenes'), entirely made of bones of animals and humans. This would lead naturalists in the nineteenth century to investigate these and similar fossiliferous deposits, eventually resulting in the discovery of pygmy hippos 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

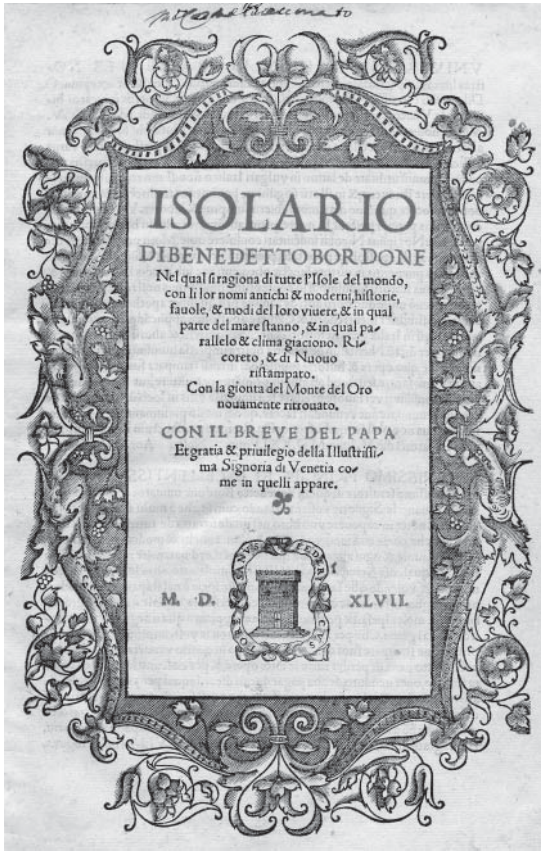


Figure 2.1 Title page of Bordone's *Isolario*, 1547.

genera *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, 358]

Towards the end of the nineteenth 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 recognised. Forsyth Major began to tutor her on fossil island faunas and suggested that she should go to Cyprus, to collect materials for him, fossil as well as extant. He expected her to find fossils of dwarf hippos and dwarf elephants, just as they had been found on Sicily, and Malta. In 1901, she went for the first time and explored the greater part of the island, guided by the earlier descriptions. She discovered 12 new fossiliferous caves and relocated some earlier mentioned sites. Amongst the fossils that she had sent to the British Museum, Forsyth Major recognised fossils of the expected small hippo, which were extremely similar to those depicted by Georges Cuvier (1804) as 'hippopotame petit', literally small hippo. He realised that the material curated in Paris 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 hippos, elephants, and giant rodents prompted her to go to Mallorca and Minorca as well, but this turned out a great disappointment. In contrast to what she and Forsyth Major had expected, she found nothing else but bizarre goats, giant dormice, and shrews. It took some years before *Myotragus balearicus*, described by her (1909), was appreciated for what it actually was, a peculiar insular dwarf ruminant with ever-growing incisors like a rodent that had lived for some 5 million years undisturbed on the islands. The picture of fossil island faunas had become more diverse.

The American palaeontologist, William Dillon Matthew (1918), was the first to observe 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. Later, his fellow countryman George Gaylord Simpson (1940) established the link between the nature of these unbalanced faunas and the means of colonisation 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 long-distance overseas dispersal was initially not commonly accepted. A prevalent explanation for the presence of elephants, hippopotamuses, and small mammals on islands was dispersal across ancient but now submerged land bridges. Elephants were believed not to be able to swim (see especially Bourlière, 1970), and thus, these islands had been connected to the nearest mainland by the time of arrival of the ancestors of the insular species. The findings of elephants and hyenas in 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.)

Despite Matthew (1918) and Simpson (1940), the land bridge idea remained a mainstream explanation for island faunas for decades. The Dutch palaeontologist Dirk Hooijer, for example, explained (Hooijer, 1964) the presence of similar-sized dwarf elephants in Sulawesi, Timor, Flores, and Java by a large landmass that included these islands during the Pleistocene. He referred to this immense landmass as ‘Stegoland’. Now we know that the first three islands were never connected to each other or the continent and belong to Wallacea, while Java, on the other hand, was indeed intermittently connected to the mainland and part of the Sunda Shelf.

The Dutch palaeontologist and geologist Paul Yves Sondaar was one of the first to embrace the hypothesis of swimming and rafting as main modes of dispersal to the islands. Sondaar (1977) noticed that the Pleistocene fossil faunas of islands worldwide often consisted of a few genera and species only – mainly elephants, hippopotamuses, deer, and rats – and no terrestrial carnivores and referred to these as *unbalanced endemic island faunas*. He also noticed that, on many islands, fauna with a very small dwarf elephant (pygmy elephants in his terminology) was often replaced at the start of the mid-Pleistocene by fauna with a larger elephant and the presence of Palaeolithic stone tools. He attributed these ‘dramatic faunal turnovers’ to the arrival of humans, and the absence of extreme dwarfism in these new elephants to the presence of a large carnivore species: humans. Today, the long-distance swimming and rafting abilities of several species (see Chapter 3), including hominins, are widely acknowledged, and sweepstake dispersal is an accepted theory. We now also know that early humans on islands had a wider distribution indeed, not only in maritime Southeast Asia but also in the Mediterranean and elsewhere. In some cases, however, land connections are still the best explanation for the

occurrence on islands of unlikely overseas dispersers like rabbits and frogs, or in the case of a species-rich balanced fauna on the island, such as the Late Pleistocene rainforest fauna of Java.

A few early authors, including Piero Leonardi (1954) and Sigfried Kuss (1965), explained the presence of these pygmy herbivores on islands as the result of inbreeding or genetic degeneration in the absence of selective pressure exerted by large terrestrial carnivores. This model was never widely accepted, though from time to time, it is revived, such as in the case of the Late Pleistocene diminutive human of Flores, *Homo floresiensis*, whose small stature and low brain capacity are considered by some as evidence of a pathological condition (see Chapter 13). Leonardi (1954) 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* [= *Palaeoloxodon*] *falconeri*). This mistake survived well into the mid-70s, with several unrelated island dwarf elephants worldwide being referred to *E. falconeri*, simply based on size.

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, J. Bristol Foster (1964) was the first who noted that there are different tendencies in body size evolution amongst taxonomic groups. Whereas insular even-toed ruminants, lagomorphs, and carnivores tend to become smaller, insular rodents and possibly insular marsupials as well tend to become larger. Leigh Van Valen (1973) dubbed this observation a 'rule' (quotation marks his), not directly referring to Foster but indirectly through his own 1970 publication. Later authors, e.g. Lawrence Heaney (1978) and Mark Lomolino (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 under optimal conditions, as suggested by Ted Case (1978).

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* (1963), and later in a monograph (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

purely morphological data with the results presented as plots and graphs. The equilibrium theory of MacArthur and Wilson, based on extant species and populations only, suggests that species diversity on islands is the sum of new arrivals 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 include surface area of the island, its distance to the mainland, limited resources on the island, decreased inter-species competition, and absence of predation by mammalian carnivores. For example, the greater the distance, or the more difficult the passage or filter, the lower the species richness, and the more prevalent ecological release and tendencies towards body size shifts.

In the past decades, various models have been proposed to explain the underlying processes influencing patterns of diversity and evolution on islands. These models, which are mainly based 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 (2007) provide a comprehensive overview of all these previous works. Application of rules and methods from these and similar works to fossil insular taxa became a new trend in the early 2000s, for example, Pasquale Raia and colleagues (2003) on life-history traits of the dwarf elephant from Sicily; Raia and Shai Meiri (2006) on body size in fossil ungulates and carnivores; Virginie Millien (2006) on the speed of evolution on islands, calculated from the fossil record; Maria Rita Palombo (2007) on evolution of insular elephants from the Mediterranean; and our contributions in the 2010s with quantification of body size evolution in island populations worldwide, extinct, extant as well as introduced (Lyras and colleagues, 2010; Lomolino and colleagues, 2012, 2013; van der Geer and colleagues 2013, 2016, 2017). The number of these studies is increasing, as we will see in the coming chapters, 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 species only, those occurring within tens of thousands of years at most, more integrative and insightful island studies nowadays include time spans ranging from hundreds of thousands to even millions of years.

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CHAPTER THREE

Island Faunas: Types and Origins

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*Evolution of Island Mammals: Adaptation and Extinction of Placental
Mammals on Islands*, Second Edition.

Alexandra van der Geer, George Lyras and John de Vos.

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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: 396.)

The composition of island faunas regarding type and number of species and their ecological specialisation depends on many variables. These are, amongst others, the geology and age of the island, the dispersal abilities of the colonising species, the distance to the mainland and island area, the faunal composition as a whole and characteristics of its elements, and the physiography and climate of the island. Naturally, these variables 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 puts a heavy stamp on island size in terms of suitable surface area.

Types of Islands

Early studies on fossil island faunas often presented a rather artificial but convenient categorisation of island types, based on palaeo-zoogeographic evidence and urged by the wish to compare fossil faunas mutually and with extant insular faunas. Two types of islands were recognised by Philip Darlington (1957) – continental versus oceanic islands – to which Josep Alcover and colleagues (1998) added a third type – 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 the following text). In addition, the palaeogeography of many islands is complex, and the same island may belong to different classes through time. The only clear distinction between oceanic islands and the other islands is perhaps that saltwater intolerant taxa – such as salamanders – are unlikely to occur on oceanic islands.

The geological history of an area is in principle reflected in the faunal evolution of that area. For example, when a highly disharmonic fossil fauna consisting of few endemic taxa is found at a site on the mainland, then this area might very well have been an island in the past. Fossil faunas are thus useful as a palaeogeographic tool.

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 low lowering of the sea level through a land bridge or land span. Many islands with fossil endemic faunas belong to this category, such as Sardinia, Sumatra, and the Californian Channel Islands. Continental islands sometimes drift away due to tectonics and are never reconnected again, such as the Balearics.

Oceanic and Oceanic-like Islands

Oceanic islands arise beneath the sea and are surrounded by water since their origin. Oceanic-like islands, on the other hand, are continental islands that were connected to the mainland in a very remote past and have since remained isolated (Box 3.1). Both types of island – oceanic and oceanic-like – are colonised overseas. Only very few taxa will be successful enough to found a new population because terrestrial mammals are poor dispersers across wide water barriers. Because of the observed similarity in faunal composition, Alcover and colleagues refer to these two types of island as true islands. Examples of oceanic islands are Cyprus, Flores, and the Galápagos. An example of an oceanic-like island is Madagascar, which got separated from Africa already early in the Cretaceous. Subsequent tectonic and volcanic processes may minimise the distance to continent or in rare cases even lead to a connection with the latter. This is the case with Java, which consisted of one or several small oceanic islands in the Early Pleistocene but was large and connected to the mainland in the Late Pleistocene. After this point in geological time, such islands behave like continental islands and are separated again with rising sea levels, such as today (see below).

BOX 3.1

Oceanic-like Islands

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. Mallorca, one of the Balearic Islands in the Mediterranean, 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 could be reached overland from the

mainland. Since then, a long-term isolation started, lasting up to the present day. Its lineages of highly endemic bovids (*Myotragus*) and giant dormice (*Hypnomys*) stem from the period of the Late Miocene land connection and thus represent a vicariance effect, not overseas dispersal. Apparently, despite its long-term isolation, Mallorca cannot be considered an oceanic-like island. Crete, on the other hand, with its much shorter isolation, is often classified as an oceanic-like island. Crete was still part of the mainland during the Miocene. During the Pliocene, it submerged for the greater part. During the Pleistocene, the emerged island is considered an oceanic-like island, based on the composition of its faunas which suggest that the colonising populations came overseas and not by land connection.

From Oceanic to Continental

The opposite – the change from oceanic to continental island – is known as well. For example, Gargano, now a peninsula of Italy, and Las Murchas, now part of the mainland of Spain, were islands in the Late Miocene. Tectonics led to collision of their microplates with continental areas, resulting in the extinction of the islands. The process can be less dramatic or can be intermittent. Java, for example, started its geological history in the Pliocene as an oceanic island through volcanic activity. Gradually, the distance to the continental shelf – the Sunda Shelf – decreased through tectonic movements, while the island grew through continuing volcanic eruptions and tectonic uplift. Eventually, the distance was sufficiently small in the early Middle Pleistocene to form a corridor connection with the mainland during colder periods when the sea level was lower. During subsequent warmer periods, sea levels rose again, and Java was again isolated. The last complete connection was during the Late Pleistocene, when a tropical rainforest fauna – shared with Borneo, Sumatra, and mainland Southeast Asia – entered Java. Today, Java is again an (continental) island.

Dispersals to Islands

There are several ways for vertebrates, including mammals, to reach an island and maintain a viable population. Naturally, the different species may disperse differently, and not all dispersal types are available to all species.

Roughly speaking, three main types of dispersal routes to the islands can be distinguished, respectively, over land, over water, and through the air. The first type has in principal no restrictions – except for obligate aquatic taxa – depending on the habitats available on the connecting land corridor (Box 3.2). The second type is available for taxa that can swim, float, or raft on a floating mass across wide water barriers, while the last type is restricted to bats and birds. For invertebrate taxa, hitchhiking on a host during the journey has been recorded, for example, freshwater snails sticking to the feathers of a bird, but this kind of dispersal seems irrelevant for mammals. The total distance may be broken up into smaller units, for which the popular term *island hopping* is sometimes used.

Corridor and Filter Dispersal

The first type of dispersal – over land – is on its turn artificially divided into two routes, corridor dispersal and filter dispersal. The corridor route applies to cases in which faunal interchange between two areas is possible; this is probable for some animals but improbable for others in the case of a filter route or filter bridge. The former route is by definition over land (land bridge), whereas the latter may include (very) short distances over water ('stepping stones', not to be confused with island hopping). Land bridges are supposed to provide the only possible way of dispersal for groups that are intolerant to saltwater, such as freshwater fishes and amphibians.

Continental islands are typically colonised by a normal mainland fauna through corridors (at low sea level) or filters (at higher sea levels). During further disconnection and isolation, the filter becomes stronger and eventually no new direct influx takes place anymore. At this point, the taxa are confined to the island and from here on undergo so-called vicariance, the effect of being separated from the rest of the original group by a geographic barrier, in this case, a body of water. This separation often results in a differentiation into new varieties or species (anagenesis). In case an array of new species arises (cladogenesis), the term *adaptive radiation* is applied. An example of such a vicariance phenomenon is provided by the Pleistocene fauna of the Balearics and perhaps by the ground sloths of the West Indies. Isolation not necessarily leads to speciation. In some rare cases, hardly or no change takes place at all, and some sort of living fossil, or relic taxon, is preserved on the island, often amidst species that did evolve and radiate. This seems the case with the monotremes of Australia but also with the primitive Amami rabbit (*Pentalagus furnessi*) of the central Ryukyu Islands. Paradoxically, islands often function as laboratories for speciation, as we will see, sometimes to the

absurd, and at the same time as sanctuaries for the preservation of rare and primitive taxa.

The opposite situation takes place when an island gradually becomes connected to the mainland, and a mainland fauna arrives, first through filter dispersal and later through corridor dispersal. This is seen in Japan where during the Late Pleistocene, a mainland fauna with a large Chinese deer (*Sinomegaceros*) met the endemic dwarf elephant (*Palaeoloxodon naumanni*) and its accompanying fauna, resulting in the latter's extinction.

Land Bridges and Land Spans

The theory of vanished intercontinental land bridges and island arcs across ocean basins in order to explain the distribution of species, held in vogue in the early days by, amongst others, Scharff (1912) and Schuchert (1935), became discredited since the acceptance of plate tectonics in the latter part of the twentieth century. Land bridges as explanation behind the presence of organisms on islands are entirely dismissed by some authors, while others hold on to it. The reality lies, as often, most likely somewhere in the middle. A dry land connection is a very reasonable explanation for cases like Sicily during the Late Pleistocene, while it is a totally impossible option for cases like the Galápagos. For Madagascar, though, Robert McCall (1997) suggested the existence of an at least partially exposed land bridge in the Mozambique Channel during the mid-Eocene to the Early Miocene, which consisted of uplifted crustal blocks along the activated fault of the Davie Ridge. In this way, large areas of dry land in the Channel could have functioned as step stones to Madagascar's north-east margin. These areas subsided in the Early Miocene, separating the Malagasy mammals from their African relatives. Extensive ocean floor research, however, could not detect terrestrial deposits along the ridge, indicating that the uplifted blocks were never exposed above the water. In addition, such a bridge would have allowed the dispersal of a far richer fauna than actually took place. Also, this Miocene bridge fails to explain the arrival of Late Pleistocene hippos.

A more likely land bridge, or land span, is found in the Caribbean region. The Aves Ridge, now almost entirely submerged, may have formed a land bridge at the Eocene–Oligocene transition. This theory, the land span theory, is promoted by Ross MacPhee and Manuel Iturralde-Vinent since 1994. Holcombe and Edgar (1990)

discussed the Aves Ridge in great detail and showed what the ridge would look like if it were 600 m and 1000 m higher, exposing many islands, or a land bridge if subsidence had been even greater. The ridge would have provided a filter in the first case, as followed by Pindell (1994) and Droxler and colleagues (1998), and a corridor in the latter case, as followed by MacPhee and Iturralde-Vinent.

‘Pendel’ Dispersal

Closely related to corridor and filter dispersals – and often not distinguishable from these – is the ‘pendel’ route, named thus by Michael Dermitzakis and Paul Sondaar (1978) after the Dutch word for pendulum, as it swings back and forth. The distance is now easily crossed by some mammals, and subsequent invasions of the island by the same species take place. Genetic exchange with mainland populations takes place on a regular basis (rescue effect). As in the case of filter dispersal, the term *pendel route* actually applies to the taxon itself, because the same distance during the same period may form an insurmountable barrier for other taxa. The main difference between pendel route on one side and corridor and filter dispersal on the other side is that, in the former case, overseas dispersal over a very short distance is assumed.

Sweepstake Dispersal

Long-distance overseas dispersal is generally referred to as *sweepstake dispersal* – the chance crossing of large bodies of water – which proves to be a highly efficient filter. The idea derives from the work done by William Diller Matthew (1918),

‘These [= the mammalian faunas] I conceive to have arrived at various times during the Tertiary [...], by accidents of transportation, of which the most probable for the mammals would perhaps be the so-called “natural rafts” or masses of vegetation dislodged from the banks of great rivers during floods and drifted out to sea’. (Matthew 1918, 665)

Matthew’s idea was reformulated by Gaylord Simpson (1940, 1965) (Figure 3.1) and adopted by Paul Sondaar (1977) and subsequent palaeontologists. Simpson added, ‘spread is impossible for the most and very improbable for some, but does occur accidentally’. A sweepstake dispersal is thus on itself not limited to overseas dispersal over large distances – filter dispersal can also provide a case – but the opposite is always true – overseas dispersal over large distances is always a sweepstake dispersal. That is the reason why terrestrial mammals have colonised so

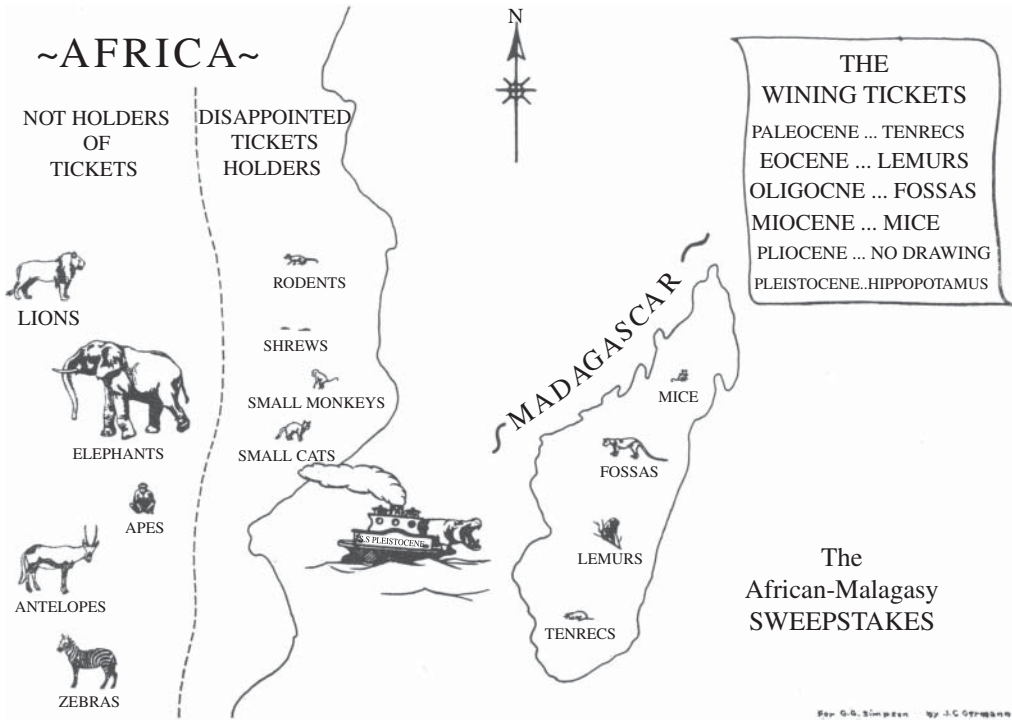


Figure 3.1 Conceptional sketch by Gaylord Simpson (1940) explaining the principles of sweepstake dispersal. Source: From Simpson G.G. 1940, Figure 6. Mammals and Land Bridges. *Journal of the Washington Academy of Sciences* 30 (1940): 137-163. © Washington Academy of Sciences. Reprinted with permissions of Washington Academy of Sciences.

few isolated islands, as concluded by Lawlor (1986). Natural phenomena such as hurricanes may increase the chance, as Matthew (1918) noted in a footnote ‘Tropical storms, as Wallace pointed out years ago, probably play a principal part in transportation of very small animals or their eggs’. (Matthew 1918, 665). Today, this is rarely observed given the extremely short window we live in compared to geological periods spanning thousands or millions of years. A case of cows accidentally dispersing in this way has been reported from Cedar Island in North Carolina. Here, three feral cows were swept into the ocean by Hurricane Dorian in 2019. They were considered lost, until they were rediscovered, happily grazing in good health, a month later on one of the Outer Banks islands, about 6.4 km away. The only way they could have reached their new home was by swimming, being pushed along in the right direction by the storm.

Regarding the water mass to be crossed, the greater the distance and the more challenging the crossing is – unfavourable currents, wave types, temperatures, etc. – the lower the chance is to make it safely to the other site (Box 3.3). That is why, the only large herbivorous animals are giant tortoises instead of ruminants and elephants on remote oceanic islands like the

Galapágos, Mauritius, and the Seychelles. On nearby islands, on the other hand, several herbivores of different size classes may be found together, proboscideans as well as ruminants. This is the case with the central Ryukyu Islands and Honshu, Japan, during the Pleistocene. Where the return voyage is practically impossible, adaptive radiations may evolve from the single coloniser – as seen in the two to four genera of Late Pleistocene giant rats of Flores, all descendants from the earlier middle-sized *Hooijeromys nusatenggara* – or, more commonly, a single lineage undergoing progressive change – as seen in many species of dwarf elephant, for example, the four-tusked stegodon (*Stegolophodon pseudolatidens*) of the late Early and early Middle Pleistocene of Honshu, Japan.

BOX 3.3

Transatlantic Boats?

Rafting was presumably the means of migration of the ancestors of the New World monkeys (Platyrrhini) and the caviomorph rodents from Africa to South America across the Atlantic Ocean some 40 million years ago (Middle Eocene), as suggested by Alain Houle (1999). At that time, the ocean was much less wide, but still between 1000 (50 million years ago) and almost 2000 km (30 million years ago) wide. Recently, Erik Seiffert and colleagues (2020) discovered a third taxon in South America that undertook this almost improbable transatlantic journey: *Ucayalipithecus perdita*, a very small monkey, closely related to Oligocene parapithecoid primates of Africa. They estimate the migration might have occurred at the Eocene–Oligocene boundary around 34 million years ago when the sea level lowered.

The raft could have consisted of a vast piece of floating mangrove forests that storms occasionally break off from the tropical African coast. Houle (1998), in his review of oceanic rafting by small vertebrates in the tropical Atlantic, mentioned a floating island measuring 60 m by 23 m, with trees as high as 15 m. Equatorial currents can transport larger floating objects with wind-exposed surfaces in less than two weeks from the river deltas to the South American coast, as summarised by Susanne Renner (2004). In the Early Tertiary, when the Atlantic was narrower than today, such transport probably took less time, increasing survival chances of the passengers.

Evidence of long-distance over-water rafting in the past is limited to small-bodied mammals. Not only do they need less resources and water, but several of these species are able to go into torpor or hibernation, thus drastically reducing their metabolic needs.

Two-way Tickets

No matter how low the changes may be for successful colonisation of an island, and the more so for a subsequent adaptive radiation into a number of new species, even more unlikely is recolonisation of the mainland of one of these new lineages and subsequent radiation into, again, new species (Box 3.4).

Successful Returns

Recolonisation of the mainland has been proposed to explain the present distribution of *Anolis*, a group of Caribbean lizards. One group of these lizards has successfully colonised the Americas, as explained by Glor and colleagues (2005) and Nicholson and colleagues (2005). The former concluded that one *Anolis* species of Florida can be traced back to the pre-Pleistocene of Cuba. The latter showed that several dozen *Anolis* species in the continental Neotropics descend from a single Caribbean coloniser. Two-way invasions were also used to explain the phylogeny of a bird lineage in Polynesia and New Guinea by Filardi and Moyle (2005). Dávalos (2007) followed the same line of thinking regarding the phylogeny of extant short-faced fruit bats of the Caribbean and of Central and South America. The latter group of species shares a more recent common ancestor than does the former, which indicates evidence for colonisation from the West Indies and not vice versa. The bats invaded the island prior to the Pleistocene and radiated into several lineages of which one returned to the continent. The way back to the continent has even been brought to the fore in the case of Madagascar and Africa by Raxworthy and colleagues (2002) in respect to chameleons, assuming the common ancestor to crown chameleons had dispersed from Africa to Madagascar in the Late Cretaceous, evolved there, and dispersed back between 90 and 47 million years ago. This study was based on mitochondrial markers of about 40% of chameleon species, using molecular clocks to estimate the time of divergence. A broader analysis of over 90% named chameleon species using dated phylogenies led by Krystal Tolley and colleagues (2013), however, concluded the opposite, namely that chameleons originated in Africa and rafted twice to Madagascar, once some 65 million years ago in the Early Palaeocene, and once in the Oligocene, and not vice versa. During the late Cretaceous and the Oligocene, the oceanic currents flowed from Africa towards Madagascar, so opposite of the situation today.

BOX 3.4

Reverse colonisation is propagated by Eva Bellemain and Robert Ricklefs (2008). Their basic assumption is that adaptation to island life does not necessarily result in reduced dispersal ability, and that island inhabitants are thus capable to undertake the journey back. However, the examples provided throughout this book demonstrate that most fossil insular taxa clearly had lost their dispersal ability – e.g. flightlessness in birds and short-leggedness in large mammals. The hypothesis of reverse colonisation will not be considered further, as the fossil record lacks any substantial evidence.

Time of the Dispersal

Apart from the dispersal itself – the way in which the founder population reaches the island – there is another interesting aspect of dispersal: time, or when did the dispersal take place. One way to approach the time range, or dispersal window, is by dating the fossiliferous deposit in which fossils of the most primitive form of the endemic lineage are found. This is in most cases impossible, either because no primitive form – that is, closest to the founder species – has been recovered or because no reliable dating can be done. Another method is by using the so-called molecular clock on the basis of DNA or RNA in the living endemic species of the island. The idea was first proposed by Linus Pauling and Emile Zuckerkandl (1962). The working principle, the mechanics of the clock as it were, is based on stochastic events or randomness. Molecular clocks track minor mutations in the cell's DNA or RNA, which not only occur at a constant rate but also randomly. The pattern of randomness can be quantified and used as a predictor. The genetic mutations occurring over time are compared against the fossil record, and the time of split of a species along the evolutionary tree can thus be 'calculated'. At present, molecular clocks are amongst the standard tools for evolutionary biologists, especially when calibrated with dated fossils or deposits.

A possible error though lies in the choice of protein used for the clock. A discrepancy in the clocks based on RNA and DNA, respectively, led to a difference of at least 11 million years in dispersal dates for the Malagasy rodents (Nesomyinae). Jean-Yves Du Bois and colleagues (1996) calculated the arrival of these mice at around 12 million years ago, based on DNA hybridisation. Céline Poux and colleagues (2005), however, calculated a much earlier colonisation (20–25 million years ago) based on RNA. This early date is unlikely because advanced cricetids and murids do not appear in the fossil record before 14 million years ago. Why then their clock gives such an early timing? Du Bois showed that there is a huge difference between

the clocks. The 12S rRNA clock indeed suggests an age of 20 million years ago for the dispersal, but the DNA hybridisation clock tells that this happened much later, at ca 8–9 million years ago. The 12S rRNA gene appears to evolve faster in the Nesomyinae than in other tested murids.

The Candidate Species

Few taxa appear to be successful islanders in the long term. The first filter consists of the way of dispersal to the island. For continental islands, this filter is not particularly strong, and, practically, all taxa may pass it. For oceanic islands, the filter is very strong. Practically, only some large herbivores (deer, hippos, and proboscideans), rodents, small primates, bats, birds, and some reptiles (tortoises and crocodiles) are potentially successful over-water dispersers, as we will see. They swim, float, fly, or travel by floating masses. In addition, they have a relatively high potential to survive for prolonged time in open sea.

The second filter that the aspirant colonisers have to pass is simply to survive long enough within a restricted area, often in an entirely different habitat than the one which they were used to. Eventually, only very few taxa survive long enough to become successful colonisers, gradually adapt to their new environment, and evolve into endemic forms.

The Holdovers

In principle, the original founding population of a gradually disconnecting area (corridor and filter dispersals) is identical to the mainland population. Soon after the disruptive event, however, taxa gradually go extinct, either because they are outcompeted by fitter species or simply because of lack of resources and suitable habitat. Resource limitation applies, first of all, to the top predators; they are the first to disappear from the record. Only few taxa, especially small herbivores, are able to survive for a longer time. Other taxa typically found on continental islands that were populated through corridor or filter dispersal are pigs, moles, and lagomorphs. The Middle Pliocene to Early Pleistocene fauna of Sardinia, for example, is mainly characterised by a pig, a mole, a rabbit, and a profusion of bovids, indicators of dispersal over land, and subsequent vicariance. Other typical overland dispersers of this fauna are a hyena and a macaque.

The Swimmers

Fossil faunas of oceanic and oceanic-like islands show that especially elephants, deer, water buffaloes, and less so, hippos were successful in reaching these islands. This is best

explained by their shared characters: they swim very well in open sea, and their digestive systems produce gasses which add to their buoyancy. In addition, the trunk of an elephant serves as a snorkel, further enhancing their potential to survive for longer periods in the water. Finally, these animals live and swim in herds. Carnivores, too, can swim, but they do not have the above described floating capacity. Furthermore, if they reach the island, it is often not in a group, and, therefore, the founder population may be too small to establish a viable population. Exceptions are otters, which are frequently found as part of fossil insular faunas. Other taxa are limited to one or two islands only: e.g. wolf-like canids (*Xenocyon*) on Sardinia and Java and tigers on Java.

Especially proboscideans are notoriously good swimmers, as documented by Donald Lee Johnson (1980). This is further confirmed by the presence of their fossils on several islands that were not connected to the mainland by the time of dispersal. For example, extinct stegodons are reported from the Philippines, Sulawesi, Flores, Timor, and Sumba; mammoths from the Californian Channel Islands, Japan, and Crete; and elephants from many Mediterranean islands, the Philippines, and Java. Practically, all islands with a fossil record of the Northern Hemisphere contain a proboscidean species. Deer colonised amongst others Crete, Karpathos, Sardinia, the central Ryukyu Islands, Japan, Java, and the Philippines, while hippopotami managed to reach Cyprus, Crete, Sicily, Malta, Madagascar, and Java (for details, see the relevant chapters). On the latter island, they may even have arrived twice, once overseas during the Early Pleistocene when Java was an oceanic island and once via filter dispersal during the Middle Pleistocene when Java was intermittently connected to the mainland.

Hippos are semi-aquatic but do not swim. Instead, they ‘walk’ over the bottom of the river or lake in which they live. Only calves aged up to about one year swim actively. In the sea, however, adults would likely float, and swimming hippos have indeed been reported by Frädrich (1968) (see for discussion on hippo dispersal, van der Geer, Anastasakis and Lyras, 2015).

The situation with the pigs is not entirely clear. Generally, pigs were considered evidence of a land connection and, thus, indicators of a corridor or filter dispersal, as in the case of Sardinia. The extant babirusa, however, is an excellent swimmer. This endemic pig is known to often swim in the sea to reach small islands. Roland Melisch (1994) reported that they swam across the 10-km-wide Lake Poso. Presumably, the endemic Pleistocene pigs (*Celebochoerus*) of Sulawesi and the Philippines – which were never connected to the

Asian mainland – had thus reached these islands by swimming. This might theoretically also have been the case for the Antillean sloths, because some sloths seem to have been adapted to marine habitats (*Thalassocnus*), as demonstrated by Muizon and McDonald (1995). The two extant sloth species are excellent swimmers and regularly cross rivers.

Excellent swimmers amongst the rodents are the capybaras (*Hydrochoerus hydrochaeris*), which readily take to water and lead an aquatic life. Their fossils have been recovered from Curacao in the West Indies. Most rodents, however, are unlikely long-distance swimmers, though the extant common or black-bellied hamster (*Cricetus cricetus*) occasionally swims and crosses large rivers in the event of mass population movements forced by food shortages. Before taking to the water, it inflates its cheek pouches with air for greater buoyancy. In addition, the common hamster is large, with a body mass of almost a kilo and a head and body length of up to 340 mm. It can be imagined that at least part of such a migrating group is swept away by the river and ends up in the open sea, eventually perhaps landing on an island, though the changes are undoubtedly extremely limited. The survival changes increase somewhat by the ability of hamsters to enter torpor for up to seven to ten days. Fossil giant island hamsters have been reported only from the Late Miocene of Gargano (*Hattomys* and *Mystemys*) and Tuscany (*Kowalskia*) and the early Early and late Early Pliocene of Mallorca (*Apocricetus darderi* and *Tragomys macpheeii*). The latter, however, likely arrived over land during the Messinian Salinity Crisis, and not overseas.

The Rafters

Most proficient amongst mammals in crossing long stretches of open seas are without doubt rodents, found on most oceanic islands, including even the Galapagos Archipelago, 972 km off the shore of continental Ecuador, as shown by Robert Dowler and colleagues (2000). They did not arrive there by swimming, but likely travelled on a floating mass or vegetation mats, known as flotsam. Flotsams, consisting of tree logs, bushes, grasses, and floral detritus, are regularly seen in river mouths where they drift into the open sea, as reported by Guppy (1917), King (1962), and Heatwole and Levins (1972). Currents may push these floral ‘boats’ further sea inward and eventually lead them to an island where they wash ashore. This is supposed to be the way of transport of insects and small vertebrates such as lizards, mice, and shrews. The distance covered may be huge, for example, the endemic Cuban *Tarentola* lizards are supposed to have rafted all the way from Africa, according to Blair Hedges

(1996). Actual rafting has only been observed in the case of green lizards in the West Indies. A flotsam, which had landed on a beach in Anguilla in October 1995, contained green iguanas, as reported by Censky and colleagues (1998). The journey was supposed to have started in Guadeloupe a month earlier as a result of hurricanes. Hurricanes in the Caribbean are by no means rare, and hundreds of thousands of hurricanes likely occurred since the onset of the Miocene. If only a small fraction, say 0.01%, of these hurricanes caused the transportation of mammals between the islands, even then, tenths of possibilities for dispersal occurred. Within these, only a fraction may eventually have led to successful colonisation.

The past record of endemic island mammals shows that such long-distance over-water rafting was an extremely rare event indeed and has been confirmed only for Madagascar (Box 3.5), Galápagos, Canaries, São Tomé and Príncipe, Christmas Island, and Enggano near Sumatra, as summarised by Jason Ali and Miguel Vences (2019) in a letter to the editor in defence of the possibility of such dispersal. They excluded arrivals in complex areas as the Mediterranean, the West Indies, insular Southeast Asia, and the western Pacific, as these likely involve island hopping, thus reducing the covered distance.

Perhaps, the most extreme evidence of long-distance rafting is that of the Galápagos. It appears that two or three independent colonisations by New World rats and mice (Sigmodontinae) took place, being the extinct, Late Pleistocene giant rice rat *Megaoryzomys*, the extant rice rats *Nesoryzomys indefessus* and *Aegialomys galapagoensis*, and the recently extinct *Nesoryzomys darwini*. Molecular data seems to resolve these latter two genera as sister taxa, in which case, there were only two successful colonisations.

BOX 3.5

Lemurs on a Boat

The theory of rafting on flotsams has been brought to the fore to explain the presence of lemurs on Madagascar, first mentioned by Simpson (1940; Figure 3.1). The resolved lemur phylogeny of the team of Julie Horvath (2008), based on nuclear and mitochondrial DNA, clearly indicates that the time of lemuriform divergence postdates the separation of Madagascar from Africa and India by many millions of years. They calculated the time of dispersal to Madagascar to between 50 and 80 million years ago, which confirm earlier calculations by Anne Yoder and Yang (2004) and Céline Poux and colleagues (2005). This means that lemurs

must have arrived by overseas sweepstake dispersal. The same applies to the Malagasy latecomers – the tenrecs, the rodents, and the fossas, – which arrived during the Middle Miocene, as calculated by Poux and colleagues (2005), based on nuclear genes. The prevailing ocean currents ran from Africa to Madagascar in these periods, contrary to today, greatly increasing the chance of a successful trip.

Hibernation may have made the long journey more endurable to the ancestral lemurs. Today, the only hibernation primate worldwide is the fat-tailed dwarf lemur (*Cheirogaleus medius*) of Madagascar. When the season becomes cool and dry, they huddle together in tree holes and go into a winter sleep for up to seven months. Their metabolic activity drops to about 2%, and their body temperature assumes the ambient temperature, as low as about 5°C. This unique feature may have been inherited from an ancestral form, and if so, it may have enabled the overseas journey.

A very peculiar sweepstake dispersal – in the sense of a chance dispersal – by long-distance rafting is provided by the Falkland wolf or fox (*Dusicyon australis*). Its ancestors likely did neither swim or float to the islands nor crossed a persistent land bridge between South America's southern tip and the island group. Darwin held a different explanation for the enigmatic presence of a wolf-like animal on these remote islands:

‘The Falkland Islands, which are inhabited by a wolf-like fox, come nearest to an exception; but this group cannot be considered as oceanic, as it lies on a bank connected with the mainland; moreover, icebergs formerly brought boulders to its western shores, and they may have formerly transported foxes, as so frequently now happens in the arctic regions’ (Charles Darwin 1859, 394).

Instead of drifting on an iceberg on the move, ‘land’ bridges made of ice could have shortened the distance considerably, or even have connected the Falkland Islands with South America's southern tip. Dispersal over such an icy bridge seems to have been the case elsewhere as well, such as for reindeer to Svalbard (= Spitzbergen) (*Rangifer tarandus platyrhynchus*), which got isolated and evolved dwarf size when the ice bridge disappeared at the end of the last ice age.

Composition of Island Faunas

The depauperate or disharmonic taxonomic composition of the fauna – with poor diversity at higher levels and impressive adaptive radiations at lower levels – of several islands or island groups was already noted by Wallace as early as 1881. Similar observations were done by Matthew (1918), Simpson (1956), and Darlington (1957). In the case of the West Indies, this observation was termed the *central problem* in Caribbean biogeography by Ernest Williams (1989), because he could not explain this taxonomic composition by vicariance alone. The great radiation and morphological diversity seen in, for example, the hystricognath rodents – now filling niches normally occupied by other orders of mammals – is best explained by assuming that these other orders were absent. In the case of vicariance alone, the founder fauna would have been balanced, including all orders that were present at the mainland at that particular time.

Several types of fossil insular faunas are mentioned in the palaeontological literature. These are generally referred to as *balanced mainland faunas*, *balanced depauperate (or impoverished) faunas*, *unbalanced depauperate faunas*, and *unbalanced endemic faunas*. Such classification is artificial though practical, as any classification.

A typical feature of depauperate faunas is that taxonomic diversity is poor, with many major groups absent. At the same time, though, some of the insular genera or species may have undergone radiations to fill in the ecological gaps. The lack of diversity on higher taxonomic levels is balanced as it were by higher than normal diversity on lower taxonomic levels, as compared to the mainland. A further typical feature of a depauperate fauna is the occupation of some endotherm niches by ectotherms, for example, giant tortoises as megaherbivores instead of ruminants. The terms *balanced* and *unbalanced* are applied in relation to the number of carnivore species in relation to herbivore species. A typical mainland fauna is considered balanced, whereas typical insular faunas are devoid of (larger) terrestrial mammalian carnivores and are thus named unbalanced. This lack of mammalian carnivores (see, however, Box 3.6) leaves the niche of top predator open, which is subsequently filled by birds of prey, such as the giant eagles (*Garganoaetus freudenthali*) in Gargano and Haast's eagle (*Harpagornis moorei*) in New Zealand, or reptiles, such as the Komodo dragon (*Varanus komodensis*) in Flores, Rinca, and Komodo. There is a difference in the understanding of the

term *balanced* between palaeontology and ecology. The way the term is used by most palaeontologists only means that large carnivores are present and that thus major trophic niches are occupied. In ecology, a balanced fauna means it is ecologically stable, for instance, the trophic niches are not only occupied but also occupied in ratios which do not encourage transitions.

Insular Carnivores

In some cases, a large or medium-sized canid species – foxes, dogs, and wolves – forms part of an otherwise typical (unbalanced) Pleistocene Island fauna. These exceptions are just a few, including two large fossil species (*Chasmaporthetes melei* from Sardinia and *Xenocyon merriami* from Java), two medium-sized fossil species (*Cynotherium sardous* from Sardinia and *Xenocyon trinilensis* from Java), one still living species (*Urocyon littoralis* from the Californian Channel Islands), one undescribed and possibly already extinct species (*Urocyon* sp. n. from Cozumel Island of Mexico), and one recently extinct species (*D. australis* from the Falkland Islands). The two Sardinian species – a hyena and a dog from subsequent geological periods – likely arrived through filter dispersal over land, whereas the other species presumably arrived overseas. The dispersal of the Falkland species – a large South-American fox – is still unresolved, and hypotheses so far are a land bridge to Argentina during the last Ice Age, or, more likely, transport on a floating ice berg during the same period as mentioned by Darwin (1859), or, most unlikely, introduction as a pet by the first visitors to the islands. In any case, the extreme rarity of carnivores on islands, except for otters, underlines the stochastic, though taxon-dependent, nature of sweepstake dispersals and vicariance.

BOX 3.6

Once an insular fauna is established, it has the tendency to remain stable in composition through time. A striking example is the five-million-year long faunal history of the Balearic Islands during which the faunal composition was not affected by intermittent global climatologic changes. On the mainland, on the contrary, dramatic changes took place – extinctions, immigrations, and evolution of new taxa – during the very same period. The arrival of humans on the Balearic Islands approximately 8000 years ago finally caused dramatic changes to the fauna and flora, as on most Mediterranean islands. Generally, insular faunas are only disturbed through extinctions and new arrivals in relation to changes in distance to the mainland, area of the island, human arrival, and, less so, climate (Figure 3.2).

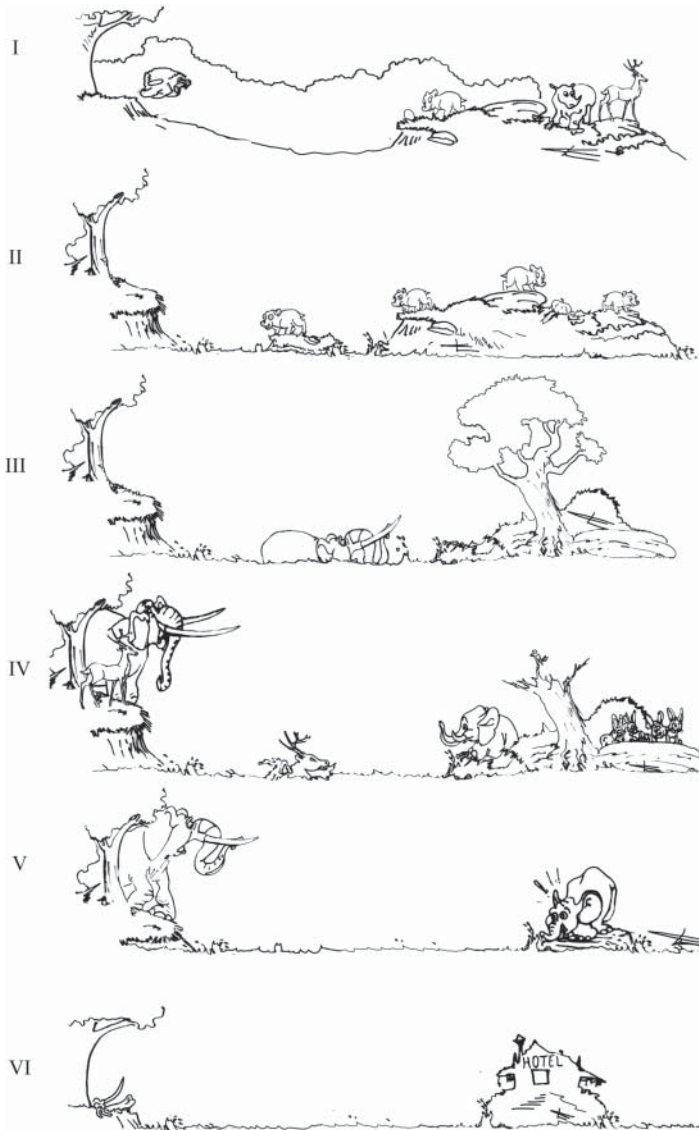


Figure 3.2 Simplified evolutionary history of a hypothetical island. In Stage I, the island is still part of the mainland. The fauna is balanced and of mainland character. In Stage II, the island is formed. The fauna of the newly formed island is at the beginning a subset of the continental fauna of Stage I. However, soon, the fauna melts down and only a few (if any) mammalian species survive. In Stage III, new mammalian species of mainland origin colonise the island. In Stage IV, the island is inhabited by endemic species. Meanwhile, more colonisers arrive from the mainland. In Stage V, the successful establishment of new colonisers to the island, as well as other factors, such as the reduction of the island size or its habitats, leads to extinction of many insular species. In Stage VI, the arrival of humans and the subsequent habitat alternation and introduction of alien species eventually leads to the extinction of the majority (if not all) of the native mammalian species. The sequence of these stages does not need to be a straightforward line. For example, the extinction of insular species of Stage V increases the chance of successful colonisation by mainland species and thus Stages II and III may be repeated. Also, the island may, at a particular time, reconnect to the mainland and thus start again from Stage I. (Drawing George Lyras.)

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PART II

The Islands and Their Faunas

In this part, island faunas are presented per island or island group. Each chapter starts with a short introduction on geology and palaeogeography, followed by an overview of the island's history of palaeontology, a geochronological treatment of the insular faunas – biozones and faunal units – and ending with a section on the peculiarities and evolution of the most important endemic species. Madagascar and the West Indies are treated somewhat different, due to the lack of a fossil record with sufficient depth. Their faunas are treated taxonomically. Only those islands are discussed in detail that either yielded several faunas of different ages or a single fauna with a number of elements. Islands from which only one taxon is known are briefly mentioned elsewhere. The discussed islands are, in this order, Cyprus, Crete, Gargano, Sicily, Malta, Sardinia, the Balearics, Madagascar, Java, Flores, Sulawesi, the Philippines, Japan, the Ryukyu Islands, the Californian Channel Islands, and the Greater and the Lesser Antilles.

The chronology of the Cenozoic era. The listed numerical ages follows the chart drafted for the International Commission on Stratigraphy by Kim Mikkelsen and colleagues in January 2020 (Cohen and colleagues, 2013; updated). In June 2009, the International Commission on Stratigraphy agreed upon lowering the base of the Pleistocene Epoch such that it includes the Gelasian Age. This book follows the new scheme. However, the older cited literature (prior to 2009) follows the old definition of the Plio-Pleistocene boundary and thus often cite as Late Pliocene what we now define as part of Early Pleistocene.

CHART before June 30, 2009			CHART January, 2020		
Age	Epoch		Age	Time in millions of years	
	Late	Pleistocene	Late		0.0117
	Middle		Middle	Chibanian	0.129
Calabrian	Early		Early	Calabrian	0.774
Gelasian	Late	Pliocene		Gelasian	1.80
Piacenzian	Middle		Late	Piacenzian	2.58
Zanclean	Early		Early	Zanclean	3.600
					5.333

Epoch		Age	Time in millions of years
Miocene	Late	Messinian	5.333
		Tortonian	7.246
	Middle	Serravallian	11.63
		Langhian	13.82
			15.97
	Early	Burdigalian	20.44
		Aquitanian	23.03
Oligocene	Late	Chattian	27.82
	Early	Rupelian	33.9
Eocene	Late	Priambonian	37.8
	Middle	Bartonian	41.2
		Lutetian	47.8
	Early	Ypresian	56.0
Palaeocene	Late	Thanetian	59.2
	Middle	Selandian	61.6
	Early	Danian	66.0

CHAPTER FOUR

Cyprus

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Cyprus is the largest oceanic island of the Mediterranean and had a unique fossil fauna. This fauna, Pleistocene in age, was extremely depauperate, consisting only of the world's smallest hippopotamus, a dwarf elephant, and likely bats. The time of arrival of the genet and mouse is unknown. The faunal stasis was dramatically interrupted in the Early Holocene with the extinction of all Pleistocene species.

Geology and Palaeogeography

Cyprus is the third largest Mediterranean island, situated opposite the coasts of Turkey and Syria, and one of its few oceanic islands. The island owes its existence entirely to volcanism, which explains the many copper mines from which the name of the island is said to have been derived. During the Cretaceous – about 120 million years ago, Cyprus was a mountain range on the bottom of the Tethys Sea. Much later, during the Miocene, this part of the oceanic crust was gradually uplifted when the African and the Eurasian plates collided. This resulted amongst others in the emergence of the island's main mountainous area, the Tróodos Massif, and later, near the end of the Miocene, the Pentadaktylos Range. Eventually, around the beginning of the Pleistocene, Cyprus emerged above the water and formed the present-day island. Cyprus was thus never connected to the mainland and has a long history of isolation since the Miocene, as evidenced by geological data.

Historical Palaeontology

The first recorded discovery of vertebrate fossils was by the fifteenth-century Cypriot historian Leontios Machairas. His *Chronicle of Cyprus* is known from two manuscripts only: one from the Oxford Library, copied in 1555 at Paphos, Cyprus, and one from Venice, Italy, printed in 1873 by Sathas. In this extensive work, Machairas (1555) mentioned petrified bones, visible at the surface at Casa Epifani (=Kazaphani) on Mount Pentadaktylos, south-east of Kyrenia (Figure 4.1). The bones were said to be locally known as the remains of 300 Maronites – members of one of the Syrian Eastern Catholic Churches – who had fled from Syria to escape persecution, but shipwrecked at Cyprus' inhospitable coast. The villagers referred to them as the *Manifested Saints* (Agioi Fanentes).

The next report that survived is the one from the astronomer and cartographer Benedetto Bordone from Padua, Italy (see also Chapter 2). In his *Isolario* (1528), he described a hill at Kyrenia at the foot of Mount Pentadaktylos, which entirely consisted of

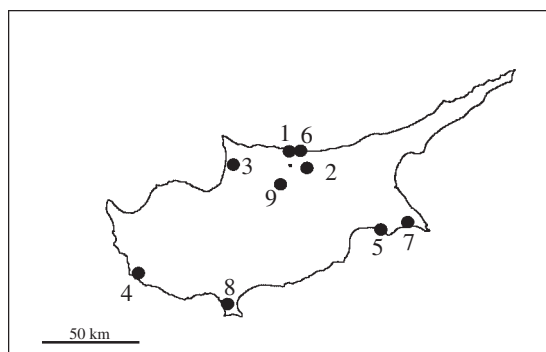


Figure 4.1 The most important Pleistocene localities of Cyprus: (1) Kyrenia, (2) Kazaphani Agios, Chrystostomos and Bellapais (3) Agia Irini, (4) Paphos, (5) Xylophagos, (6) Agios Georgios, (7) Agia Napa and Cape Pyla, and (8) Akrotiri Aetokremnos.

the bones of animals and humans. The book was an illustrated guide about the then known islands for seafarers. Bordone wrote that the local population powdered the bones from the hill to make a potion against all sorts of diseases. Likely, Makhairas and Bordone had seen similar deposits.

The French traveller André Thevet (1554) and the English traveller Fynes Moryson (1617) both mentioned a cave dedicated to the Seven Sleepers at Paphos at the south-western coast. The latter wrote:

‘On Sunday the nineteenth of May, we came to the first Promontory of the Iland Cyprus, towards the West, and after eight houres sayling, we came to the old City Paphos (or Paphia), now called Baffo, and the wind failing us, and gently breathing upon this Castle of Venus, we hovered here all the next night, gaining little or nothing on our way. This place is most pleasant, with fruitful hills, and was of old consecrated to the Goddess Venus, Qgeene of this Iland [.]. A mile from this place is the Cave, wherein they faigne the seven sleepers to have slept, I know not how many hundred yeeres’. (F. Moryson, 1617, Part 1, Book 3, Chapter 1)

The ancient legend about the Seven Sleepers stems from the sixth century or perhaps earlier. According to one variety of the story, once, seven young Christians were locked up in a cave at Ephesus by the non-Christian emperor in order to die. By miraculous intervention, however, they did not die but slept for two or three hundred years. One day, a shepherd passed nearby and discovered the cave. He opened the cave and saved the young men who had not even aged in the meantime. The legend is known in Asia Minor, and also on Cyprus.

The Cypriot monk and philosopher Neophytos Rhodinos, though, wrote in his book on the heroes, warriors, and saints of Cyprus, published posthumous in 1659, that the petrified

remains in the cave at Paphos did not belong to the Seven Sleepers but to the Seven New Martyrs instead, local Cypriot saints who have nothing to do with those of Ephesus.

The Dutch traveller Cornelius de Bruyn (1698) also mentioned a bone deposit in the Pentadactylos range with petrified remains of animals and humans. One of his plates figures a human upper arm, which in reality is a fossil of the extinct Pleistocene dwarf hippopotamus. De Bruyn considered these remains as evidence of the biblical Flood, a common explanation for fossils in that time. This view was shared by some Cypriots as well, because an exposed fossiliferous layer – in reality, a collapsed rock shelter and perhaps the same as de Bruyn's deposit – at Agia Irini in the Pentadactylos range is locally known as Dragondovounari, literally the Dragon Hill. According to local myth, dragons had drowned here during the Flood and got petrified thereafter. De Bruyn noticed similar petrified bone remains at Agios Chrysostomos near Koutsovendi, not far from Kazaphani and possibly the same as noticed earlier by Makhairas.

A variation on the theme of 300 Marionites who had fled from Syria was recorded by the British consul Alexander Drummond (1754). The coastal bone breccia, locally known as Agios Fanentis (Manifested Saints), not far from the ruins of the Bellapais monastery at the foot of the Pentadactylos, was believed to consist entirely of the petrified remains of pirates or barbarians, who had come to the island for plunder but shipwrecked. As punishment for their planned crime, their bones turned into stone. Some good-hearted fellows though were converted to the Christian faith and lived happily thereafter on the island and eventually became saints.

Luigi Palma di Cesnola (1877), who visited Cape Pyla between 1872 and 1875, published a description of two caves with bones at the village Xylophagos, one of which he said was dedicated to Forty Saints (Agioi Saranda).

In 1901, Dorothea Bate went on her own, without formal training and with minimal support, to explore the island for fossils and zoological specimens. Her attention was drawn to several regions, such as the Pentadactylos range, by the earlier descriptions of others. She was successful because she discovered 12 new fossiliferous caves, for the greater part near Kyrenia. She also relocated earlier mentioned sites, such as the cave of the Forty Saints at Cape Pyla, already mentioned by Cesnola.

A year later, Bate returned to Cyprus with funding from the Royal Academy of Sciences. This time, she found remains of a dwarf elephant, which she (Bate, 1903a) described as *Elephas cypriotes*. In the same year (1903b), she described subfossil remains of a genet as *Genetta plesictoides*. Part of the material she collected was purchased by Dr F. Krantz Rheinisches