European Association
of Vertebrate Palaeontologists

9th Annual Meeting
Heraklion, Crete, Greece
14-19 June, 2011

Guidebook

Alexandra van der Geer & George Lyras

EAVP

European Association of Vertebrate Palaeontologists

9th Annual Meeting
Heraklion, Crete, Greece
14-19 June, 2011

Field Trip Guidebook

by
Alexandra van der Geer[1] & George Lyras[1]

field trip leaders
John de Vos[1] & Charalambos Fasoulas[2]

[1] Nederlands Centrum voor Biodiversiteit Naturalis
[2] Natural History Museum of Crete

NCB naturalis

Natural
History
Museum
of Crete
University of Crete

Cover figure:
The Katharo basin. Photograph courtesy Charalambos Fassoulas

This field guide is partly based on the book:
Van der Geer A, Lyras G, De Vos J, Dermitzakis M. 2010. *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands*. Oxford: Wiley-Blackwell Publishing

HERACLES
GENERAL CEMENT CO.
A member of LAFARGE

Table of Contents

Palaeogeography of Crete

Crete, the largest island of Greece, is mainly known for its Pleistocene endemic taxa, amongst which are dwarf deer, dwarf proboscideans, dwarf hippopotamuses and large mice. However, Crete was not always an island. Up to the Vallesian age of the Late Miocene, Crete was connected to the mainland. This is evidenced by fossil remains of mainland faunas (van der Made, 1996; Athanassiou, 2004; Poulakakis et al., 2005; see figure 1). Gradually, Crete became fragmented into small pieces during the late Late Miocene and Early Pliocene. The region became largely submerged towards the end of Pliocene Period, during what is known as the Pliocene transgression (Dermitzakis and Sondaar, 1978). As a result, marine deposits and late Tortonian (8–7 million years ago) foraminifera beds overlie the remains of the Miocene faunas. Crete was divided into at least four islands during the Pliocene; the remainder of the former land area was transformed into a shallow sea with shoals, as reported by Sondaar and Dermitzakis (1982). No fossils of terrestrial mammals were found from this period. Later, the region emerged again, and finally, at the end of the Pliocene or in the Early Pleistocene, Crete was formed in its present configuration, and could be colonized only by overseas sweepstake dispersal.
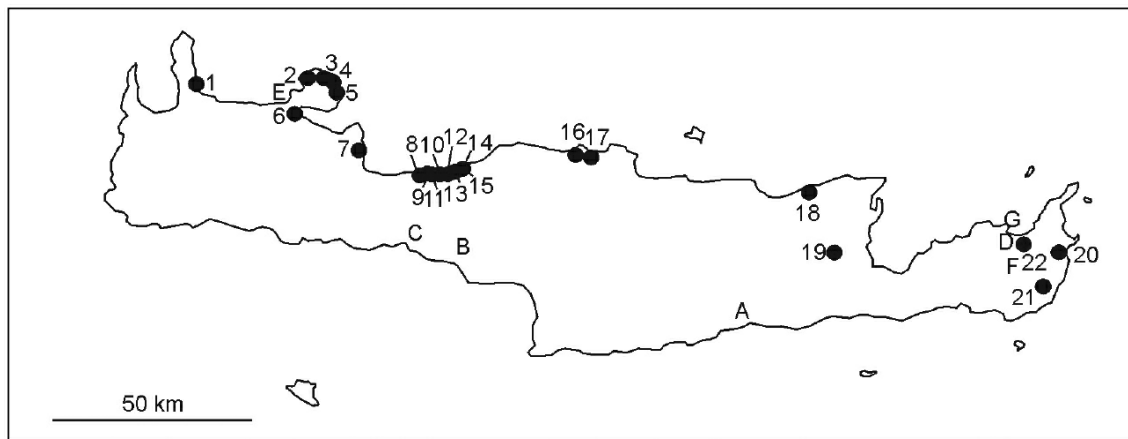

Figure 1. Localities with terrestrial fossil vertebrates in Crete. The pre-Pleistocene localities are indicated with letters. The Pleistocene localities are indicated with numbers. The first five pre-Pleistocene localities (A-E) have been reviewed by van der Made (1996). The material from the sixth locality (F) has been studied by Athanassiou (2004) and from the seventh (G) by Poulakakis et al. (2005).
Pre-Pleistocene localities: (A) Kastellios Hill, (B) Melambes, (C) Plakia, (D) Petras, (E) Vrysses, (F) Maronia, (G) Gela.
Pleistocene localities: (1) Tripiti Cave, (2) Stavros Cave, (3) Agios Georgios Cave, (4) Avlaki, (5) Cape Meleka, (6) Chania/Souda cave deposit, (7) Liko Caves, (8) Gerani Caves, (9) Bate Cave, (10) Zourida Cave, (11) Mavromouri Caves, (12) Simonelli Cave, (13) Koumpes Cave, (14) Panagia Caves, (15) Rethymnon fissure, (16) Mpali Caves, (17) Kalo Choraphi Cave, (18) Milatos Caves, (19) Katharo basin, (20) Karoumpes, (21) Kato Zakro, (22) Siteia I. In total there more than 90 sites with Pleistocene mammals on Crete (Iliopoulos et al., 2010).
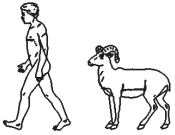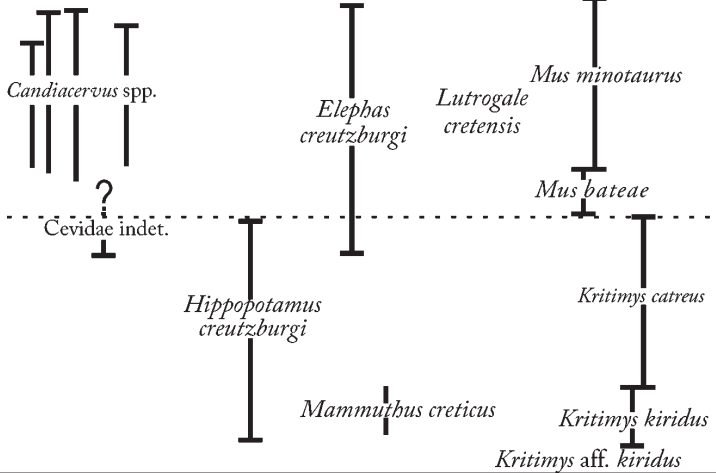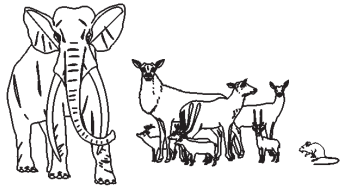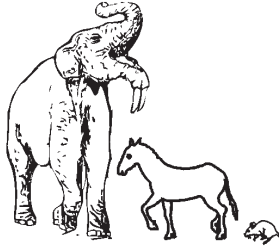
	Faunas	Zones	Faunal evolution overview
Holocene	Humans and accompanying fauna		
Pleistocene	*Candiacervus* spp. ? Cevidae indet. *Elephas creutzburgi* *Lutrogale cretensis* *Mus minotaurus* *Mus bateae* *Hippopotamus creutzburgi* *Mammuthus creticus* *Kritimys catreus* *Kritimys kiridus* *Kritimys* aff. *kiridus*	*Mus* *Kritimys*	
Pliocene			No terrestrial vertebrates
Miocene	MN 9-13 [Maronia and Gela fossil sites] — *Deinotherium giganteum* MN 10/11 [Petras fossil site] — *Microstonyx* cf. *major* Cervidae indet. cf. *Pliocervus pentelici* MN 9/10 [Kastelios fossil sites] — cf. *Doprcabune anthrocotheroides* Carnivora indet *Progonomys cathalai* *Taucanamo?/Yunnanochoerus?* sp. *Hipparion* sp. *Schizogakerix sinapensis* *Muscardinus* cf. *crusafonti* *Progomys woelferi* *Cricetulodon* cf. *sabadellensis* Bovidae indet. *Spermophilinus bredai* MN 8 [Plakia fossil site] — *Spermophilinus* cf. *bredai* *Blackia?* sp. *Forsythia?* sp. *Cotimys* sp. *Glirudinus* sp. *Dermocricetodon affinis cretensis* cf. *Propotamochoerus palaeochoerus* *Glirudinus* sp. MN 6 [Melembes fossil site] — *Dorcatherium naui* Bovidae indet. cf. *Prohyrax hendeyi*	MN 9 -13 MN 6-8	

Figure 2. Stratigraphic scheme, showing the land mammal faunal succession of Crete. Characteristic elements of the successive faunal units are shown to the right. The scheme of the Pleistocene mammals is based on de Vos (1996) with the modifications noted by van der Geer et al. (2010). The scheme for the pre- Pleistocene mammals is based on an overview by van der Made (1996) with the addition of the new findings reported by Athanassiou (2004) and Poulakakis et al. (2005).

Faunal units

The mainland fauna of Middle and Late Miocene

The Miocene faunas of Crete have a clearly continental aspect. There are seven pre-Pleistocene localities in Crete (see figure 1). Most of them can be directly correlated with marine sediments, which makes them ideal for stratigraphy.

The most important Miocene locality is Kastellios hill. It is a section exposed at the slope of a hill, 1 km north of the village Kastelliana. The section is formed by a succession of continental and marine sediments. The vertebrate fauna consists mainly of micromammals (see figure 3). The age, as indicated by foraminifera, is Early Tortonian, while the age of the mammals is Late Vallesian (de Bruijn et al., 1971). Sen et al. (1986) studied the magnetostratigraphy of the section and identified it as part of Chron 5 r of the geomagnetic time scale. According to them, the section is younger than 11.47 My and older than 10.30 My.

Figure 3. The lower jaw of *Deinotherium giganteum* from Gela (close to Agia Fotia, eastern Crete). The University of Crete continued to systematically excavate the area and collected several postcranial elements of this individual (Iliopoulos et al., in press; Fassoulas and Iliopoulos, in press) (photograph courtesy George Iliopoulos).
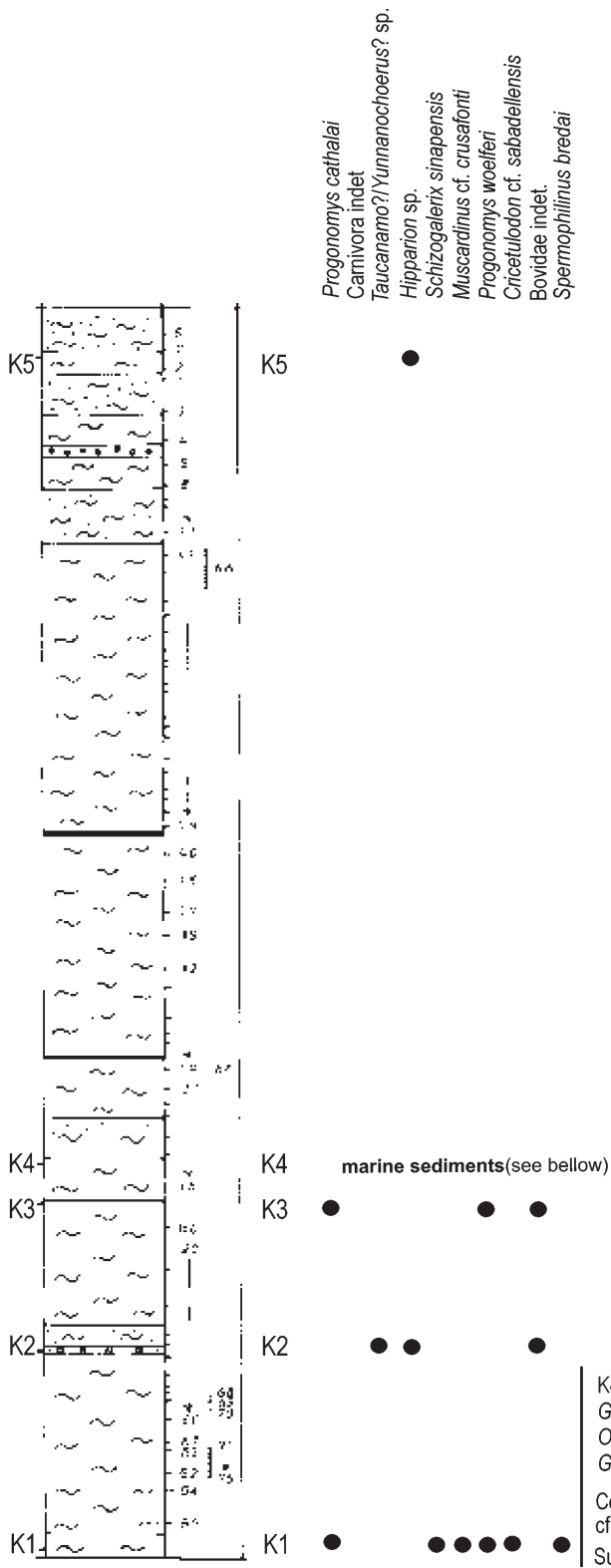
Progonomys cathalai
Carnivora indet
Taucanamo?/Yunnanochoerus? sp.
Hipparion sp.
Schizogalerix sinapensis
Muscardinus cf. crusafonti
Progonomys woelferi
Cricetulodon cf. sabadellensis
Bovidae indet.
Spermophilinus bredai

K5 ●

K4 **marine sediments**(see bellow)

K3 ● ● ●

K2 ● ● ●

K4: *Neogloboquadrina acostaensis; N. falconarae; Globigerina apertura; G. praebulloides; G. quinqueloba; Globigerinoides sacculifera; G. triloba; Orbulina saturalis; O. universa; Globorotalia gigantea; G. ventriosa; G. scitula; Uvigerina selliana.*

Collection at the other side of the hill: Bovidae indet.;Carnivora indet.; cf. *Doprcabune anthrocotheroides*

K1 ● ● ● ● ● ● Surface findings: *Hipparion* sp.; Bovidae indet.

An analysis of pollen collected from Kastellios hill shows that the region was forested in the Upper Miocene (Sen et al., 1986). Forested areas are also indicated by the presence of *Deinotherium*, whose feeding adaptation implies a forested environment. According to Athanassiou (2004), the skeleton of *Deinotherium giganteum* exhibits certain cursorial adaptations, a feature that suggests a landscape more open than that of a forest. Based on this, the same author concludes that it is more plausible to suggest an open forest or woodland landscape for Eastern Crete during the Late Miocene.

The insular fauna of Early-early Middle Pleistocene

Typical elements of the fauna for this period are the Cretan rat (*Kritimys*), the Cretan dwarf mammoth (*Mammuthus creticus*) and Creutzburg's dwarf hippopotamus (*Hippopotamus creutzburgi*), accompanied by a tortoise (*Clemmys* cf. *caspica*) and a frog (*Rana* cf. *ridibunda*). The fauna is generally referred to as the *Kritimys* zone, based upon the presence of the Cretan rat.

The Cretan rat is represented by three species, together forming a lineage from the geologically oldest *Kritimys* cf. *kiridus* to the younger *Kritimys kiridus* and ending with *Kritimys catreus*, as described by Mayhew (1996). The earliest species, restricted to Siteia, is the smallest, but already larger than a brown rat (*Rattus norvegicus*). The different *Kritimys* species are not found together. It has been suggested that the earliest *Kritimys* is an immigrant from Rhodes, via Kassos and Karpathos, based on a similar finding (*Kritimys* aff. *kiridus*) in the Damatria Formation on Rhodes, as reported by Mayhew (1977). The oldest form had relatively low-crowned teeth with a relatively simple cusp morphology.

The earliest finding of the dwarf hippopotamus is at Siteia, the earliest Pleistocene locality. Here also the earliest form of the Cretan rat is found. In younger localities, the dwarf hippopotamus is found together with the intermediate form of the Cretan rat, but never with the largest form, and neither with *Mus*, as observed by Spaan (1996). The most famous dwarf hippopotamus locality is the Katharo basin. This basin is at a height of 1100 m above the sea, which is not exactly a place where one would expect to find hippopotamuses. The other sites with hippopotamus bones are all collapsed coastal caves in which the fossils are found in situ in the limestone. The amount of fossils from these caves is very small, and the material is often badly preserved, with the exception of Kato Zakros on the east coast.

Figure 5. A small block with fossils of *Kritimys* (from van der Geer et al., 2009).

6

Box 1: Simplified evolutionary history of an hypothetical island.
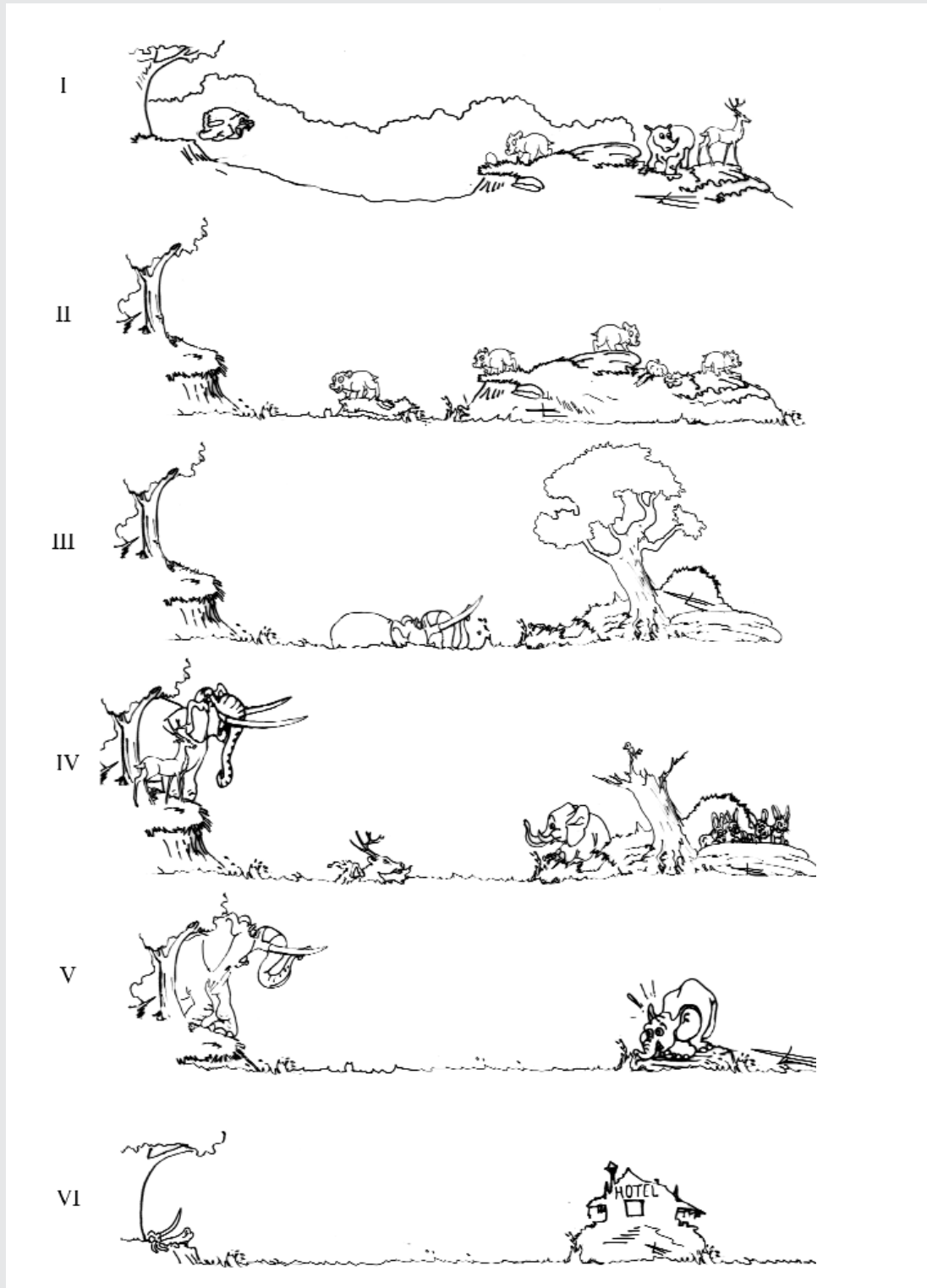
Insular faunas are disturbed in relation to changes in distance to the mainland, area of the island and climate, mainly through extinctions and new arrivals. This figure presents a simplified evolutionary history of an hypothetical island. In stage I the island is still part of the mainland. The fauna 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 (from van der Geer et al., 2010).

The Cretan dwarf hippopotamus is smaller than the one from Malta, but larger than the one from Cyprus. The most likely ancestor of the Cretan dwarf hippopotamus is *Hippopotamus antiquus.* This species – described as *H. major* by Cuvier because of its large size – lived in Europe during the Early and early Middle Pleistocene and was replaced by *H. amphibius* (= *H. incognitus*) in the late Middle and Late Pleistocene, perhaps with a small overlap in time.

Figure 6. Mandible fragment with m3 and m2 of the Cretan dwarf hippopotamus (*Hippopotamus creutzburgi*), occlusal view. Katharo. Scale bar 5 cm (from van der Geer et al., 2010).

The only site with dwarf mammoth remains is Akrotiri Melekas 1, or Cape Melekas (= Cape Kiamou), discovered by Dorothea Bate in 1905. In 1973, Sondaar found here a lower molar with an attached *Kritimys kiridus* jaw (figure 5.6; reported in Mol et al., 1996), which indicates that the dwarf mammoth was already present at the beginning of this period. The deposits here are somewhat younger in age than those of Siteia, based upon the evolutionary stage of *Kritimys*.

Figure 7. Lower molar of the Cretan pygmy mammoth (*Mammuthus creticus*), Cape Meleka, occlusal view.
(from van der Geer et al., 2009).

The dwarf mammoth is really a pygmy form compared with mainland mammoths. Most molars of this mammoth have a low and wide crown with broad cement areas and thick and simple enamel ridges. Its most likely mainland ancestor is the southern mammoth (*Mammuthus meridionalis*), as suggested by Mol and colleagues (1996).

During the Middle Pleistocene two new taxa appeared for the first time on Crete: Creutzburg's elephant (*Elephas creutzburgi*, *Elephas antiquus creutzburgi* or *Elephas* cf. *antiquus*- depending on the taxonomy that each author follows) and a medium-sized deer. The mainland ancestor of Creutzburg's elephant is *Elephas antiquus*. This elephant, which is approximately 20% smaller than its mainland ancestor, survived well in to the next biozone. The Middle Pleistocene deer has not yet been attributed to a particular species. Dermitzakis et al. (2007) have speculated that it is the ancestor of the several deer species that flourished on Crete during the next biozone.

The insular fauna of late Middle - Late Pleistocene

The typical faunal elements of this biozone are two species of common mice (*Mus bateae, M. minotaurus*), Creutzburg's elephant, Cretan deer (*Candiacervus*, with the eight species *ropalophorus*, sp. IIa, b and c, *cretensis, rethymnensis, dorothensis* and *major*), the Cretan otter (*Lutrogale cretensis*), and the Cretan shrew (*Crocidura zimmermanni*). The herpetofauna contains the endemic Cretan tortoise (*Testudo marginata cretensis*). The faunal unit of this period is generally referred to as the *Mus* zone.

The common mouse is represented by two species, of which the earlier is *Mus bateae*, which is slightly smaller than the later *Mus minotaurus*, but slightly larger
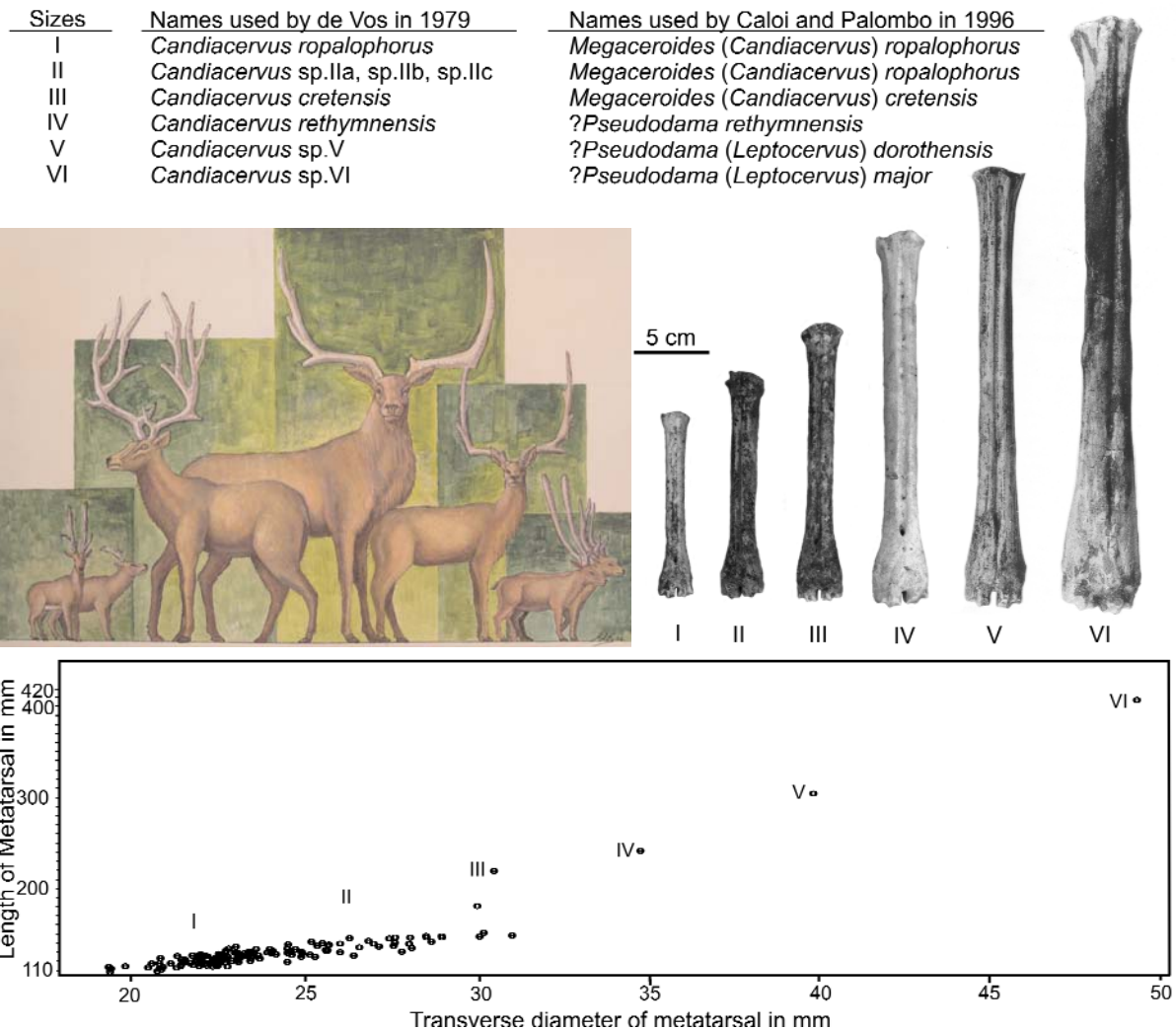
Sizes	Names used by de Vos in 1979	Names used by Caloi and Palombo in 1996
I	*Candiacervus ropalophorus*	*Megaceroides (Candiacervus) ropalophorus*
II	*Candiacervus sp.IIa, sp.IIb, sp.IIc*	*Megaceroides (Candiacervus) ropalophorus*
III	*Candiacervus cretensis*	*Megaceroides (Candiacervus) cretensis*
IV	*Candiacervus rethymnensis*	*?Pseudodama rethymnensis*
V	*Candiacervus sp.V*	*?Pseudodama (Leptocervus) dorothensis*
VI	*Candiacervus sp.VI*	*?Pseudodama (Leptocervus) major*

Figure 8. Reconstruction of the various species of the Cretan deer and metatarsals of the different size groups (from van der Geer et al., 2010).

than the common house mouse (*Mus musculus*). The two species belong to a single lineage. As in the case of the Cretan mouse of the previous biozone, a long-term trend for increasing size is attested. The Cretan white-toothed shrew managed to survive on Crete till the present day. The fossil and the living *Crocidura zimmermanni* are the same species as shown by Jelle Reumer (1986). Apart from this species, two more shrews live today on Crete.

The white-toothed shrew *Crocidura suaveolens caneae* was introduced around 3700–3550 years ago and the red-toothed shrew *Suncus etruscus* is found in sites dated to as early as 3370– 3200 years ago. There is no genetic relation between the Cretan shrew and the later introduced white-toothed shrew, according to Vogel (1980), nor between the Cretan shrew and the other living European species. Most likely, the Cretan shrew is related to an Early or Middle Pleistocene
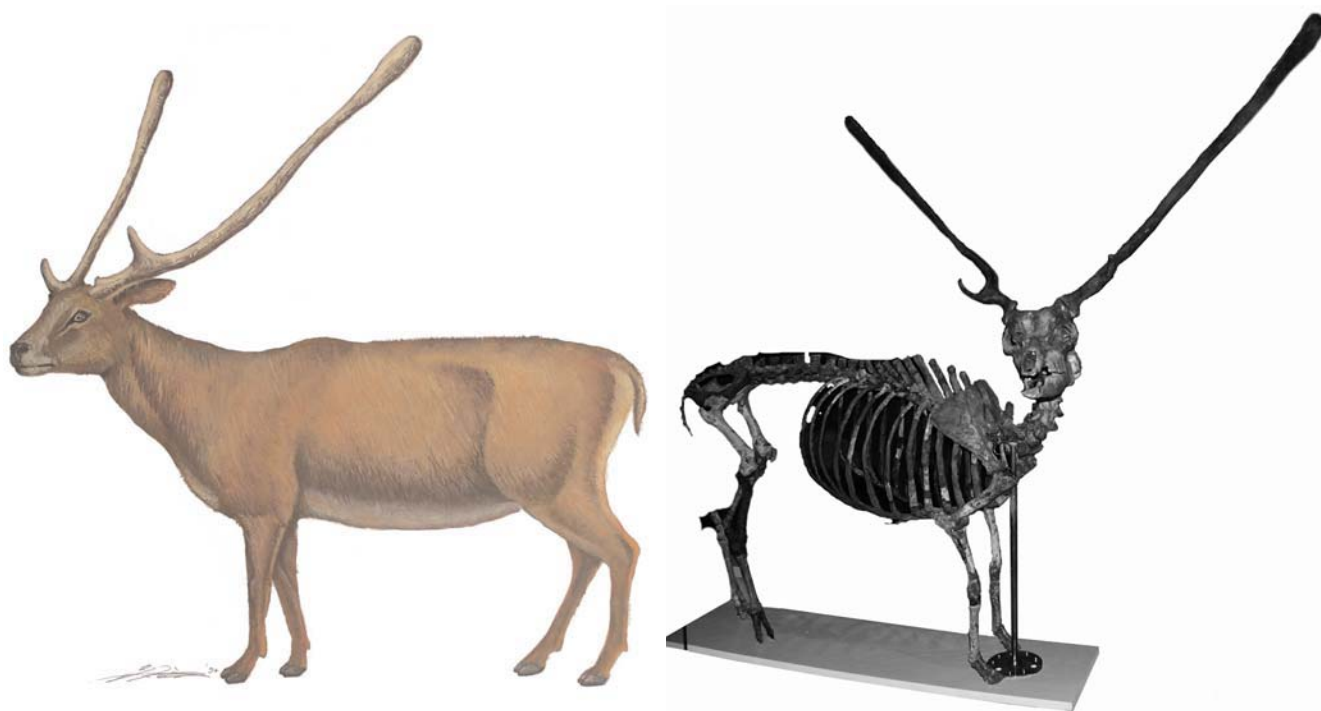
Figure 9. Skeleton and reconstruction of a small-sized *Candiacervus* species (from van der Geer et al., 2009)

species, for example *Crocidura kornfeldi*. Unfortunately, the Cretan shrew lives today only in two elevated regions of Crete. It is a unique relict species, being the only survivor of a once existing completely different world of endemic species, and deserves therefore active conservation.

Most literature of the previous century dealing with the elephants of the late Middle and Late Pleistocene of Crete mentions either two separate species –*E. antiquus* of mainland proportions and *E. creutzburgi,* which is a little smaller – or just one, *E.* cf. *antiquus*. To this a slightly larger species, *Elephas chaniensis*, was added in 2000 by Symeonidis and his colleagues. It is about 20% smaller than the mainland form, and overlaps in size with *creutzburgi*. The average body mass of the Cretan elephant(s) has been estimated at 3200 kg by Burness et al. (2001).

The earliest find of the Cretan deer is in Charoumbes 2 (not dated); the youngest is Simonelli Cave I (about 21,500 years ago). The Cretan deer is represented by no less than eight different morphotypes, ranging from dwarf size with withers height of about 0.40 m for the smallest species, to very large with withers height of about 1.65 m for the largest species. De Vos (1996) and de Vos and van der Geer (2002) explain this phenomenon as sympatric speciation followed by an adaptive radiation to occupy all possible empty niches ranging from dense forest to jagged rocks. The coexistence of various environments has been confirmed by studies on the rich fossil avifauna by Weesie (1988). The avifauna consists of, among others, an endemic long-legged walking owl (*Athena cretensis*), which is most abundant, and an endemic very large golden eagle (*Aquila chrysaetos simurgh*), next to continental birds.

Box 2: The island rule
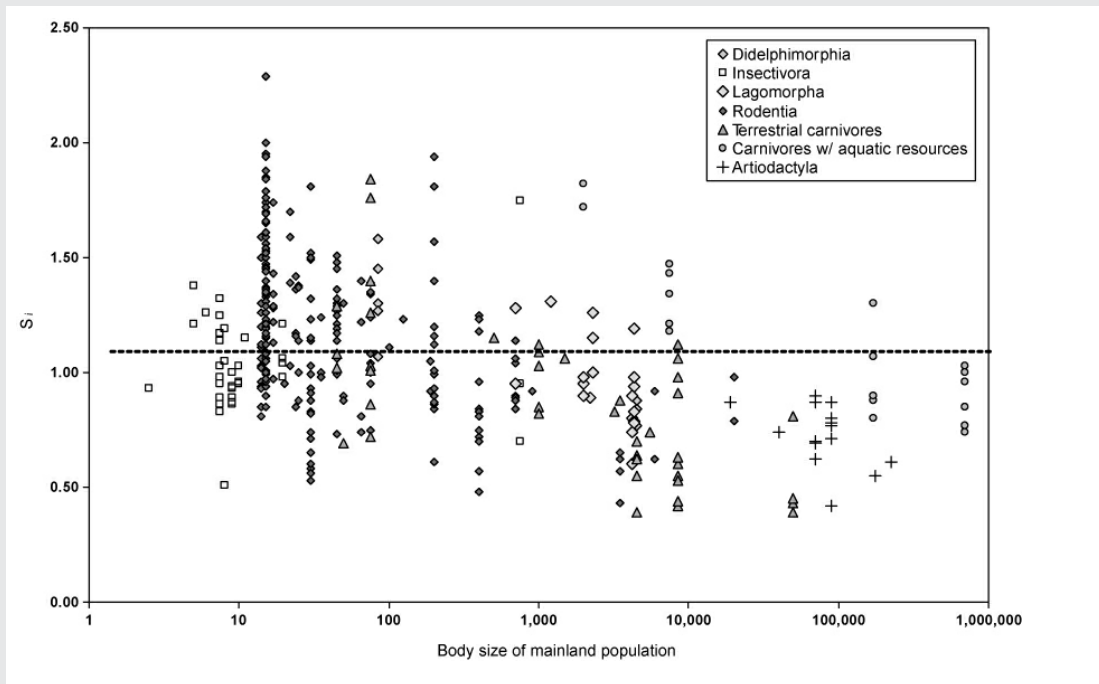
Body-mass trends for populations of insular mammals. Si = relative mass of insular forms expressed as a proportion of body mass of their mainland relative.

On islands small vertebrates tend to increase in body mass whereas large vertebrates tend to decrease in body mass. This trend is particularly evident in the fossil record, which provides some of the best examples: some insular elephant species were almost 100 times smaller than their mainland ancestors and some micromammals were over five times larger. The trend is so common in island species, that it has been dubbed the island rule. Lomolino (2005) suggested that the major factor behind these body-mass changes is the shift towards an optimal body mass for a particular design and ecological resource exploitation strategy.

The most typical Cretan deer are the two smallest species (figure 9). They have not only relatively and absolutely short limbs, but also long and simplified antlers. These species occupied a niche close to that of the wild goat of Crete today: barren rocks with thorny bushes, as shown by features of their osteology and goat-like body proportions. Fossils of males and females of the smallest sizes are found in the ratio 1:1, indicating a gregarious species with mixed herds. A further taphonomic peculiarity is that all ontogenetic ages are represented, from very young to very old.

The massivity of the limbs of the smaller sizes of the Cretan deer led Falconer and Bate to assume that the fossils belonged to goats or antelopes. Goats, however, made their first appearance on Crete with the colonization by human settlers, and are unknown from the fossil record. The roebuck that Falconer identified from

12

Figure 10. The fossil site Gerani Cave. Most of the Pleistocene fossil sites of Crete are in caves , collapsed caves or fissure fillings (from van der Geer et al., 2009)

Tripiti cave is probably based on the small-sized deer teeth or antler fragments. He could not combine the deer cranial remains with the 'bovid' postcranials because the existence of insular deer with robust limbs was still unknown to science. The only insular dwarfs that Falconer was aware of were the elephants and hippopotamuses from Sicily and Malta.

The largest species are equally bizarre. They developed extremely thin and elongated metapodials and do not resemble any known mainland form. Their limbs were even longer than those of the giant deer *Megaloceros giganteus*. Probably the larger forms were typically browsers, based on the molars which show more ridges. Both the small and the large forms deviated so much from mainland deer that it is impossible to indicate with certainty their ancestors. The most likely candidates are the giant deer from the *Megaloceros verticornis* group.

The Cretan otter is the only carnivore known from the Pleistocene of Crete; the other fossil carnivores (beech marten and badger) are of a Holocene age. Its only remains consist of a nearly complete skeleton found in the deer layer. Later, a left mandible, two left first molars and a left femur were added to this species, as reported by Willemsen (1996). The Cretan otter was less aquatic than both the common otter (*Lutra lutra*) and the smooth-coated otter *Lutrogale perspicillata*) and comparable in this aspect to the African clawless otter (*Aonyx capensis*). This is explained as a secondary development as the result of adaptation to the different conditions on Crete. Its diet consisted mainly of fish, with crustaceans as an important addition and possibly also small land vertebrates such as mice. The most likely ancestor is, according to Willemsen (1992), *Lutrogale perspicillata*. At

13

Figure 11. Carapax of the endemic Cretan tortoise (*Testudo marginata cretensis*).

Figure 12. Skull and lower jaw of the Cretan otter (*Lutrogale cretensis*). Scale bar 5 cm (from van der Geer et al. 2010)

present this species is restricted to Asia, but it is thought to have had a much wider distribution – including Asia Minor or even Greece – in the past. Fossils of *Lutrogale*, however, are very rare and the only fossils species known so far are two Javanese species and the Cretan species. No fossils are known from the extant species, so conclusions about its Pleistocene distribution are based on very weak evidence. The main reason to attribute the Cretan otter to *Lutrogale* is found in peculiarities of the dentition and the thoracic vertebra.

The faunal turnover between this period and the previous was not sudden, because a molar and a tusk fragment of the elephant and an antler fragment of the deer are found close to the hippopotamus remains at Katharo, as briefly reported by Dermitzakis et al. (2007). Remains of the Cretan shrew were found together with fossils of the last *Kritimys* species at Xeros, as reported by Lax (1996). This implies that there was an overlap between the biozones to an unknown extent. The second faunal zone of the Pleistocene Period went extinct just before or after the arrival of the first humans on the island.

Problems of dating and the lack of Palaeolithic artefacts and human remains obscure this point. In 2009, Kopaka and Matzanas reported Paleolithic tools in situ, dating back to perhaps ca. 120–75 kyr, from the island of Gavdos, off the south coast of Crete, a first indication that humans may have colonized Crete before the Holocene. In 2010, Strasser and colleagues reported paleolithic tools from Plakias (Southern Crete). In any case the fauna of the second biozone was already completely extinct at the Aceramic Neolithic level of Knossos, and replaced by newcomers who came together, or along, with the humans. The new fauna included ancestors of the extant endemic species, such as the beech
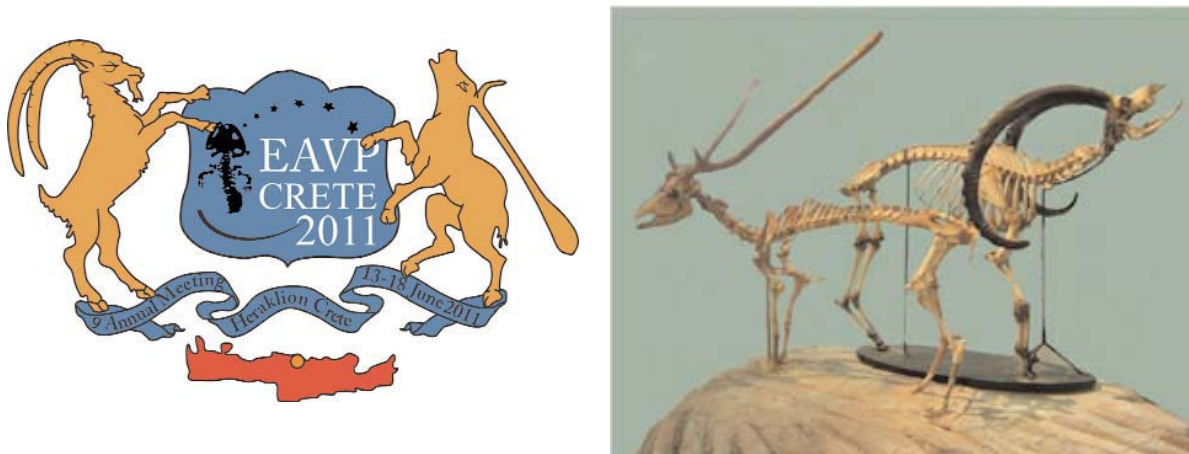

Figure 13.. The most typical element of the Late Pleistocene fauna of Crete is the small-sized *Candiacervus* (=Cretan deer). In the Holocene, the deer was ecologically replaced by the wild goat (*Capra aegagrus*), which arrived on the island sometime in the Holocene and still occurs in some uninhabited parts of Crete. The logo depicts the deer and the goat of Crete, the island itself and the official logo of EAVP. Logo design and photograph of the skeletons George Lyras.

marten (*Martes foina bunites*) and the badger (*Meles meles arcalus*). The Holocene fossils of these mustelids are intermediate between the recent endemic species and their Near Eastern relatives, as pointed out by Steensma and Reese (1996). This indicates an eastern origin of the human settlers and the accompanying fauna, as suggested previously by Evans (1968).

Katharo Plateau

Geology of Katharo

The Katharo basin is a level depression on the Dhikti mountains, at 1100 meters above the sea. According to Psarianos (1961) the basin is a polje, formed by limestone at the rims and crystalline schists at the bottom. The Pleistocene sediments of Katharo consist mainly of clays, clayey sands and angular gravels. Boekschoten and Sondaar studied the sedimentology of the basin in 1966. According to them, the sediments contained no limestone grains with the exception of some limestone pebbles in the gravels and the strata with fossils. The same authors explained the sediments as lacustrine deposits. Boekschoten and Sondaar also sampled the sediments for pollen, however, they found pollen in only one sample, which contained "some badly corroded pollen grains of *Pinus, Quercus, Liquliflorae* and Gramineae".
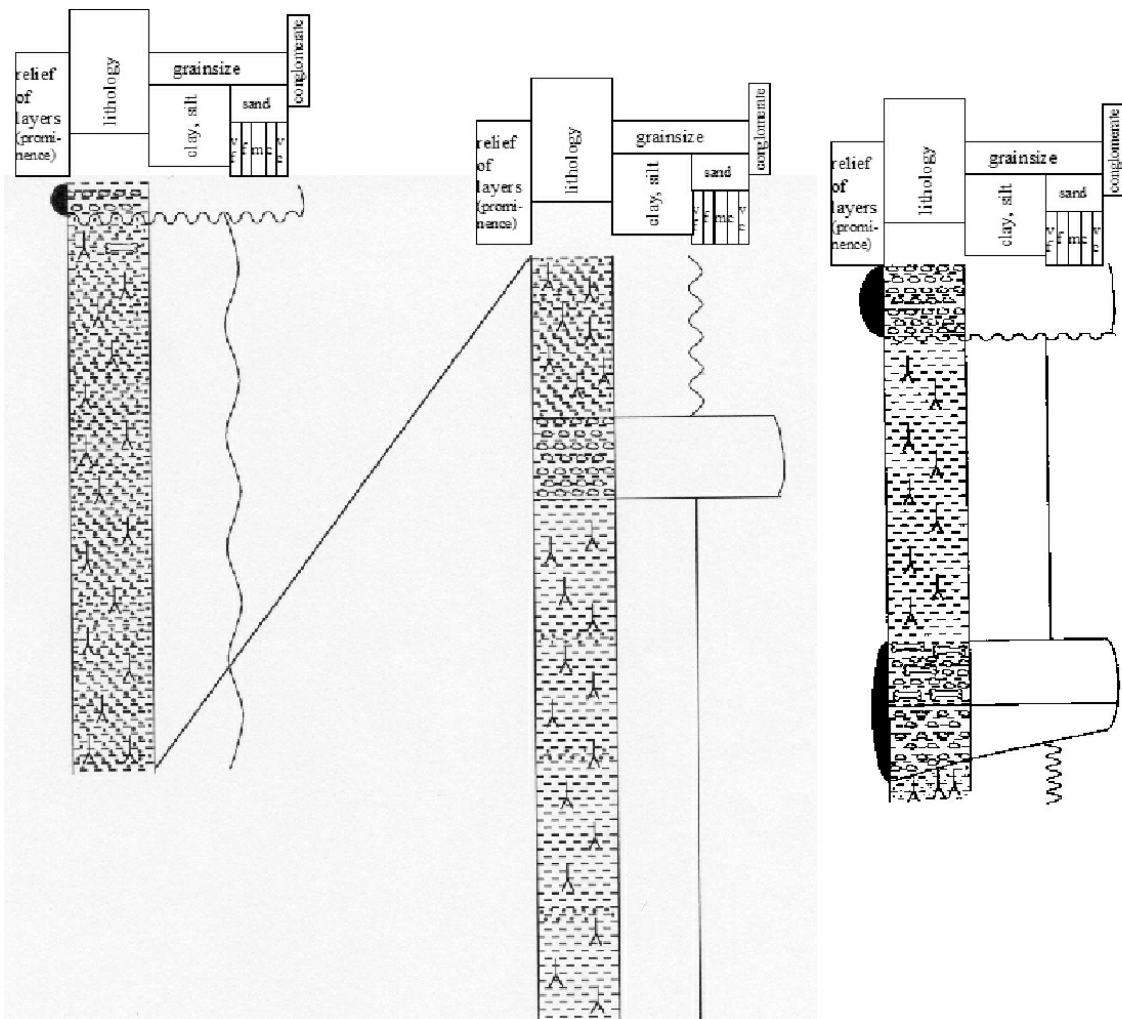
Figure 14. Profiles close to the site Digenis Anaspa in Katharo basin. The profiles were drawn by Hannie de Visser in 2001.

Palaeontology of Katharo basin

The majority of the fossils found on Katharo belong to *Hippopotamus creutzburgi*. According to Boekschoten and Sondaar (1966), who named the species, it is a small-sized *Hippopotamus* with considerable anteroposterior flexibility on its foot articulations. The later feature was explained by the authors as an adaptation to a less-aquatic life in the rockier and mountainous terrain of Crete (see box 4). The body proportions of the Cretan dwarf hippopotamus differed slightly from those of *H. antiquus*. The humerus was relatively long whereas the radius was relatively short. Also the pes and manus were relatively shorter. With regard to the morphology of the knee, the femur and tibia seem to have been less vertically arranged than in the extant hippopotamus, as described by Spaan (1996).

Absolute dates (AAR and ESR) were provided for hippopotamus molar fragments from Katharo, and range between 850,000 and 375,000 years ago. A ^{14}C date on hippopotamus bone from the Katharo indicated a much younger age of only about 12,500 years ago, but these were considered unreliable by Reese et al. (1996) and are in conflict with the tooth enamel dating.

The majority of the fossils from Katharo belong to hippopotamuses. However, a few fossils of a dwarf elephant (Poulakakis et al., 2002) and a medium-sized deer (Dermitzakis et al. 2007) have also been discovered. The elephant fossils are a lower third molar (Herridge, 2010) and a tusk fragment. Poulakakis et al. (2006) gave a detailed description of the material, together with its importance for our understanding on the faunal evolution on Crete. The deer fossils (an antler fragment and some postcranials) have not yet been studied in detail. Dermitzakis et al. (2007) attributed the specimens to a Megacerini and hypothesized a direct phylogenetic relationship between the Katharo deer and the *Candiacervus* species of the Late Pleistocene.
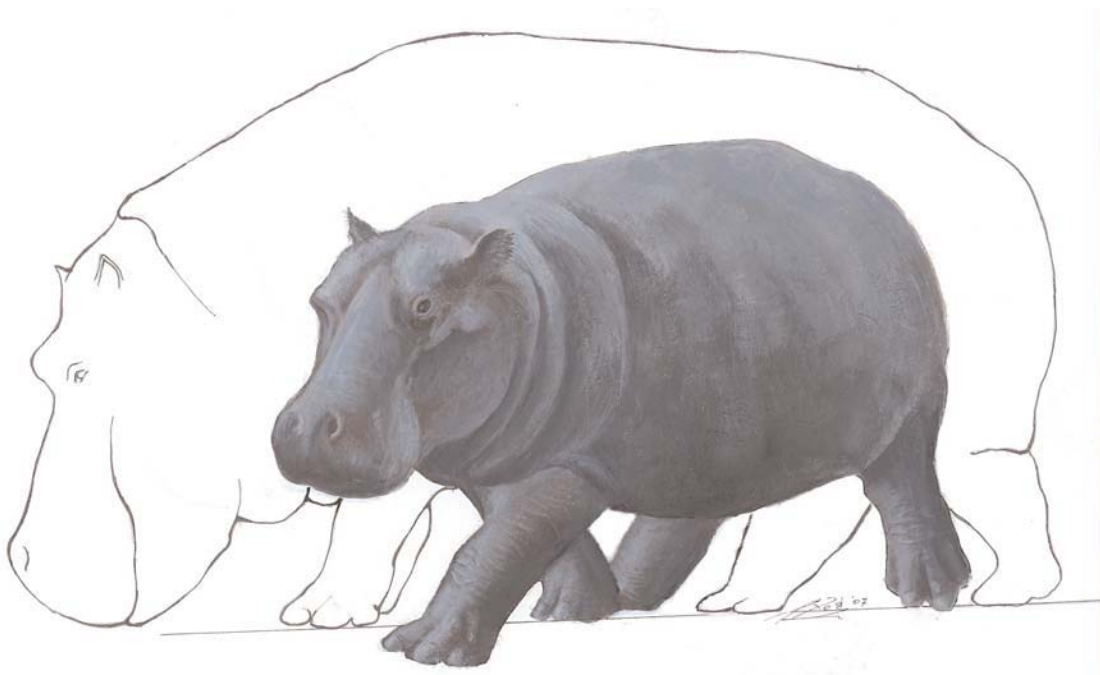

Figure 15. Reconstruction of the Cretan dwarf hippopotamus. The outline in the background is of its mainland ancestor (from van der Geer, 2009).
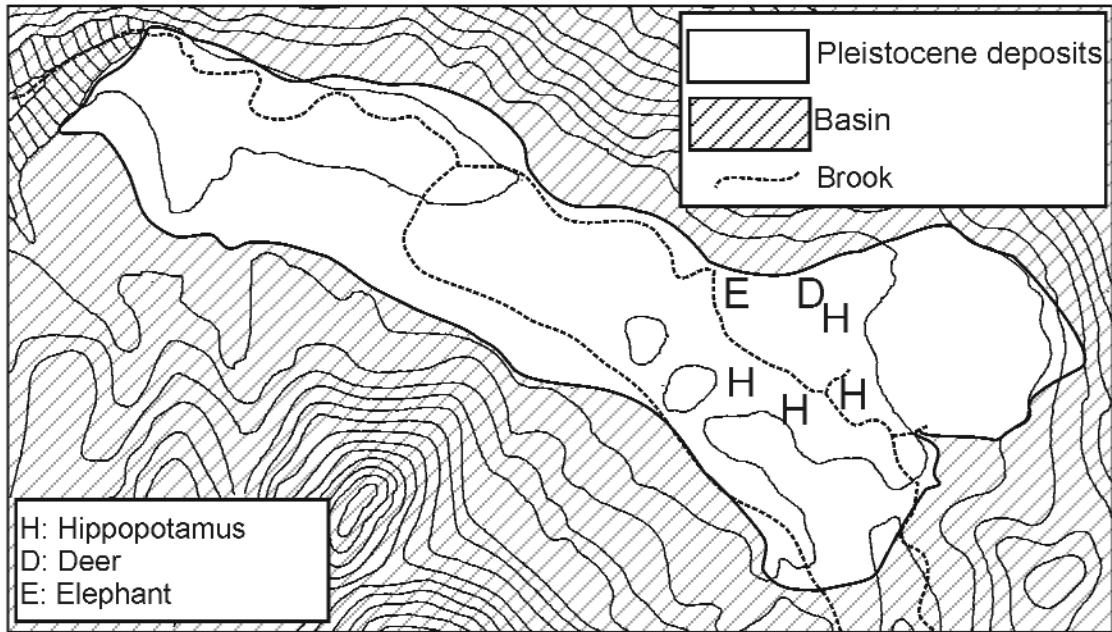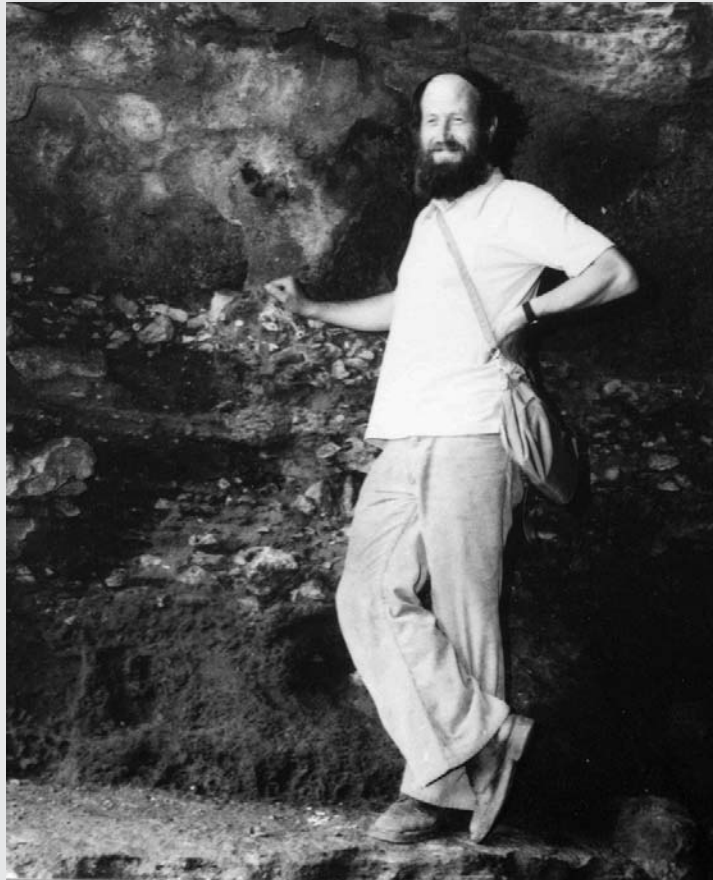
Figure 16. Map of Katharo basin and location of the fossil sites.

Figure 17. Profile of the Pleistocene deposits in the Katharo basin. The vertebrate fossils are found within the lower levels of the deposits. They are gray to brown poorly-sorted terrigeneous sediments that consist of sand in a muddy matrix, clays and sands.

The Dutch palaeontologist Paul Yves Sondaar (1934-2003) wrote many unpublished autobiographic anecdotes. In one of them he described his very first discovery of fossils of insular mammals, being a tibia and an astragal from the dwarf hippo of Crete. This discovery had a big impact on him, as from that moment on, he switched his scientific focus from horses to insular mammals.

He wrote (in translation):

"It was more a professional routine than real interest which played a role, when I compared the two bones from the hind foot [of the Cretan dwarf hippo] with those of an extant hippo. They were much smaller, but what arose my interest most was that they had a different shape. It was pure coincidence that I found just two bones from the ankle joint that fitted each other perfectly well. It appeared to me that the ankle joint of the dwarf hippo had been much more mobile than that of its large continental ancestor. They could walk much better and more tiptoed. Very different from all hippos from the past and present, in fact more like a goat. After having made the walk to the mountain of Katharo myself, I thought, of course, a normal hippo would never have made it. No degeneration but adaptation to the landscape of Crete! Besides, land bridges are also geologically unlikely, and offer no explanation for why only elephants,

hippopotamuses and deer crossed them. The very same animals, elephants, hippos and deer, happen to be good swimmers, and because of their digestion system where gasses develop, they are at the same time good floaters. The trunk of an elephant is comparable to a snorkel. Predators do swim, but hardly ever in herds, besides, their buoyancy is very poor. Deer, elephants and hippos came to the uninhabited islands and evolved. The evolutionary changes are to be considered adaptations to a predator-free island environment, where it turned out that being small was advantageous. Deer developed short legs in time; being fast was not important, in contrast to increased stability in the mountains. Short legs as the first gear in a jeep..".

Figure 18.. Astragals of mainland hippopotamus (left) compared with an astragal of *Hippopotamus creutzburgi* (right) . Scale bar 5 cm (from van der Geer et al 2010).
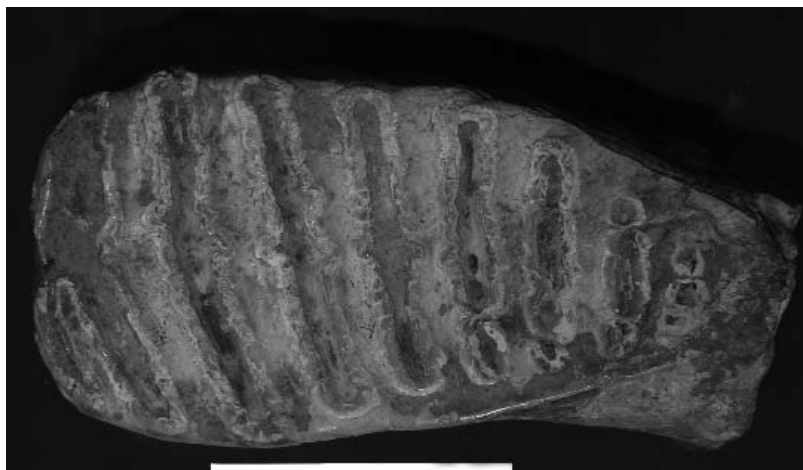

Figure 19. Occlusal view of a lower third molar of *Elephas antiquus creutzburgi* found on Katharo (from Poulakakis et al., 2002).

Box 5: Chronology of the palaeontological research on Katharo

The French geologist F lix Victor Raulin visited Crete in 1869. During his stay, Raulin received some hippopotamus fossils from the people of Kritsa village at the foot of the Dikti Mountains. They had been found at Katharo. He forwarded the fossils to the French anatomist and zoologist Henri Marie Ducrotay de Blainville, who ascribed them in 1847 to *Hippopotamus amphibius*, the extant hippopotamus. Two years before, Richard Owen had mentioned fossil teeth of *Hippopotamus medius* from the same Katharo basin. They had been given by Mr Ittas from Heraklion to Captain Graves, who in turn gave them to Owen. The species name *medius* had been applied by the French naturalist Anselme Ga tan Desmarest in 1822 to remains of what he and his teacher Georges Cuvier had considered a fossil medium sized hippopotamus ('moyen Hippopotame fossile') from Saint- Michel-en-Chasine, western France. In reality, the remains belonged to the Miocene sea cow *Metaxytherium medium*. Owen simply applied the same name to the Cretan species, based upon the illustration of a left lower jaw by Cuvier in 1804.

In 1865 the British navy officer Thomas Abel Spratt explored Crete, after his successful excavations on Malta a few years before. One of his motives was to explore the Katharo basin, the locality of dwarf hippopotamuses. He applied the name *Hippopotamus minor* to the Katharo fossils, using the name Desmarest had given in 1822 to the dwarf hippopotamus which Cuvier had illustrated in 1804 as 'hippopotame petit'; neither Cuvier, Desmarest nor Spratt knew that the fossils on which the drawing was based originated from Cyprus.

In 1904, the British palaeontologist Dorothea Bate went to Crete to relocate the deposits described by Spratt and Raulin in order to find fossils of dwarf elephants and dwarf hippopotamuses. The trip was not easy, travelling by foot and on horseback in cold and windy weather and sleeping in flea-infested rooms. Against official regulations, she managed to ship a lot of material back to London. Her account of the travels was published in 1905.

The Cretan dwarf hippopotamus had to wait for its own specific name until 1966 when Bert Boekschoten and Paul Sondaar named it *Hippopotamus creutzburgi*, based on material from the Katharo collected by Bate 60 years earlier, together with some new material. Before 1966, the hippopotamus had been given the names of the Sicilian, Maltese and Cypriot dwarf hippopotamuses, respectively *H. pentlandi, H. melitensis* and *H. minor* or *minutus.*

Since then, several scientists visited Katharo and collected fossils of hippopotamuses. So far the most extensive collection has been done by Paris Pavlakis and Michael Dermitzakis of the Univ. of Athens (Dermitzakis et al., 2005).

Hippos however, is not the only taxon known from Katharo. Nikos Poulakakis and his colleagues described a molar of the Cretan dwarf elephant (*E. creutzburgi*). Although just a molar, this is a rather important finding, since it provided stratigraphic evidence that elephants were present in Crete already since the middle Pleistocene.

Figure 20. Although there are several sites with fossil hippos on the Katharo, the most important one is at Digenis Anaspa. The site was discovered by Giannis Siganos and was excavated for three seasons by Paris Pavlakis and Michael Dermitzakis of the University of Athens (Dermitzakis et al., 2005). In this site, the remains of several hippopotamus individuals were discovered.

Prassas section

Prassas section is located 6 km east of Heraklion. This locality is known for its marine fish fauna. The site has been dated between 2.6-2.1 Ma (Late Pliocene). According to Gaudant et al. (1994) the majority of the fossils (53,7%) are *Spratelloides gracilis.* Other fishes collected from this section are *Boops*, *Blennius*, *Bregmaceros* and an undetermined Percoid. These are all fishes that inhabited the neritic zone. Therefore during the Late Pliocene the region was a shallow sea near the sea-shore (Gaudant et al., 1994).
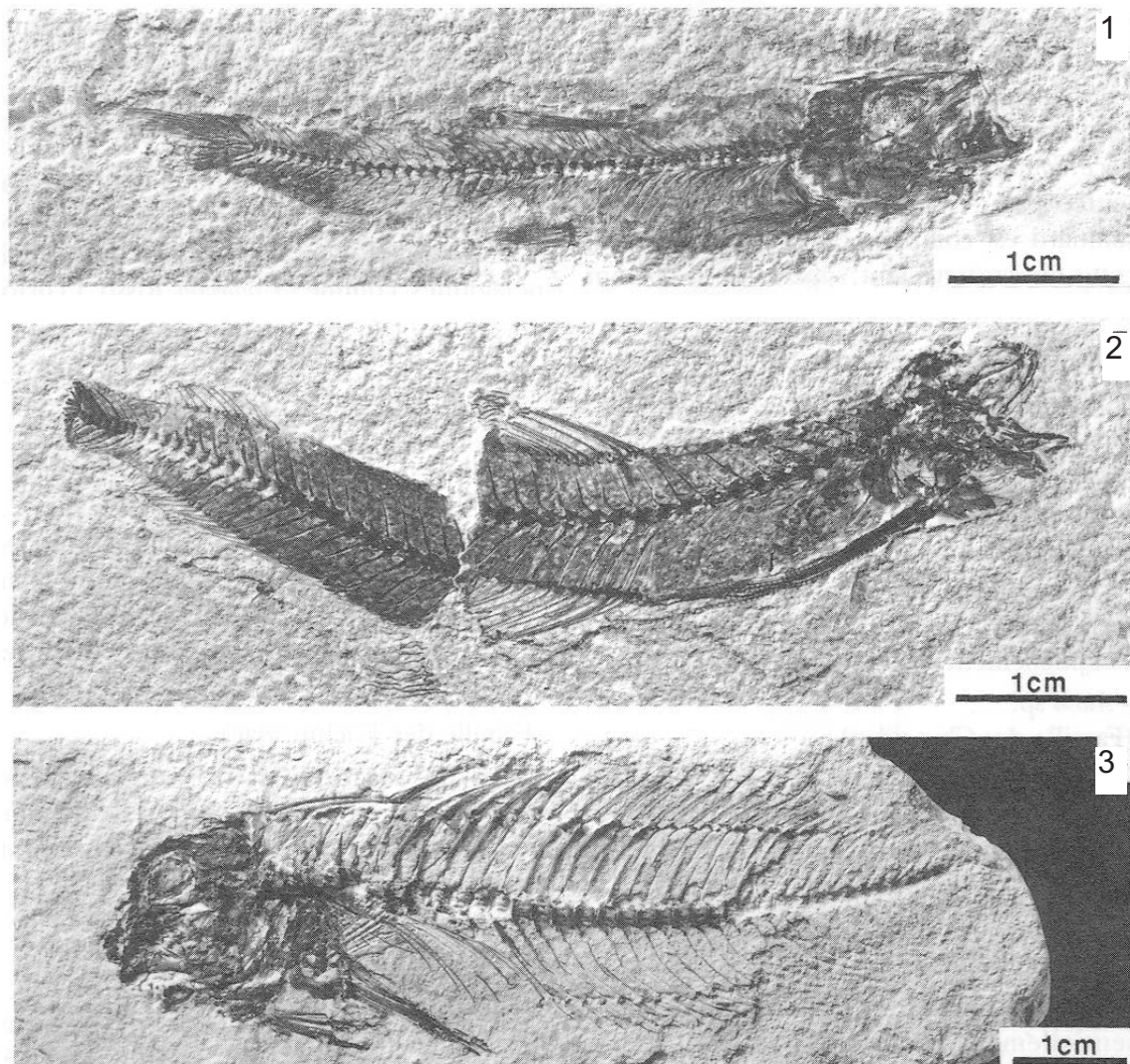

Figure 21. Pliocene fishes from Prassas cross section: (1) *Spratelloides gracilis*, (2) *Bregmaceros albyi*, (3) *Blennius* cf. *pavo* (from Gaudant et al., 1994).

Acknowledgements

PART 3: LITERATURE

Athanassiou A. 2004. On a *Deinotherium* (Proboscidea) finding in the Neogene of Crete.- Carnets de Géologie / Notebooks on Geology, Brest, Letter 2004/05

Bate D.M.A. 1905. Four and a half months in Crete in search of Pleistocene mammalian remains. Geological Magazine (Decade 5), 2 (5): 193–202.

Boekschoten G. J., Sondaar P.Y. 1966. The Pleistocene of the Katharo Basin (Crete) and its Hippopotamus. Bijdragen tot de Dierkunde, 36(8): 17–44.

Burness G.P., Diamond J., Flannery T. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proceedings of the National Academy of Science of the United States of America, 98: 14518–23.

Caloi L., Palombo M.R. 1996. Functional aspects and ecological implications in Hippopotami and cervids of Crete. In: Reese D. (ed.), Pleistocene and Holocene Fauna of Crete and its First Settlers. Monographs in world Archaeology, 28: 125–51. Prehistory Press, Madison, Wisconsin.

Cuvier G. 1804. Sur les ossement fossiles d'hippopotame. Annales du Museum National d'Histoire Naturelle, Paris, 5: 99–122.

De Blainville H.M.D. 1847. Sur les Hippotames (Buffon) (*Hippopotamus* L.) et les cochons (Buffon) (*Sus* L.). In: Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie, A (22): 1–248. J.B. Bailliere, Paris.

De Bruijn H., Sondaar P.Y. & Zachariasse W.J. (1971).- Mammalia and Foraminifera from the Neogene of Kastellios Hill (Crete). A correlation of continental and marine biozones – I.- Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam: 74(5): 1-22.

De Vos J. 1979. The endemic Pleistocene deer of Crete. Proceedings of the Koninklijke Akademie van Wetenschappen (Series B), 82(1): 59–90.

De Vos J. 1996. Taxonomy, Ancestry and Speciation of the Endemic Pleistocene Deer of Crete compared with the Taxonomy, Ancestry and Speciation of Darwin's Finches. In: Reese D. (ed.), Pleistocene and Holocene Fauna of Crete and its First Settlers. Monographs in World Archaeology 28: 111–24. Prehistory Press, Madison, Wisconsin.

De Vos J., van der Geer A.A.E. 2002. Major patterns and processes in biodiversity: taxonomic diversity on islands explained in terms of sympatric speciation. In: Waldren B., Ensenyat J.A. (eds.), World Islands in Prehistory, International Insular Investigations, V Deia International Conference of Prehistory. BAR International Series 1095: 395–405.

Dermitzakis M., Iliopoulos G., van der Geer A., Lyras G. 2007. The Rise and Fall of the Cretan Deer. XVII INQUA Congress, July 28–August 3 2007, Cairns, Australia. Quaternary International, 167–8 (suppl.1): 97.

Dermitzakis M., Pavlakis P., Drinia H. 2005. The Pleistocene hippopotamuses of the Katharo Plateau, Lasithi, Crete. Preliminary report. Proceedings of the 2nd Pancretian Speleological Symposium, Herakleion, 53-59.

Dermitzakis M.D., Sondaar P.Y. 1978. The importance of fossil mammals in reconstruction paleogeography with special reference to the Pleistocene Aegean Archipelago. Annales Géologiques des Pays Helléniques, 46: 808–40.

Desmarest A.G. 1822. Mammalogie ou description des espèces de mammifères. Supplement. Agasse, Paris.

Evans J.D. 1968. Knossos Neolithic, Part II: Summary and Conclusion. The Annual of the British School of Archaeology at Athens, 63: 267–76.

Fassoulas Ch., Iliopoulos G., in press. The excavations of *Deinotherium giganteum* from Siteia: Life and environment in Crete during the Miocene, Proceedings of the 10th International Cretological Congress, Chania 1-8/10/2006.

Gaudant J., Delrieu B., Dermitzakis M.D, Symeonidis N.K . 1994. Découverte d'une ichthyofaune marine dans les diatomites du Pliocène superieur (Plaisancien) des environs d'Heraklion (Crete centrale, Grece). Comptes Rendus de l'Académie des Sciences, Série II. Sciences de la Terre et des Planètes 319: 589-596.

Herridge V. 2010. Dwarf elephants on Mediterranean islands: a natural experiment in parallel evolution. Upublished Ph.D. Thesis. University College, London.

Iliopoulos G., Eikamp H., Fassouls Ch. 2010. A new Pleistocene mammal locality from Western Crete. Bulletin of the Geological Society of Greece 5:918-925.

Iliopoulos G., Fassoulas Ch., Lyberakis P., Poulakakis N. in press. A complete skeleton of *Deinotherium giganteum* (Proboscidea, Mammalia) from the Late Miocene of Siteia (Crete Island, Greece). Proceedings of the 6th European Geoparks Meeting, Lesvos Island 5-8/10/2005.

Kopaka K, Matzanas C. 2009. Palaeolithic industries from the island of Gavdos, near neighbor to Crete in Greece. Antiquity, 83 (321).

Lax E.M. 1996. A gazetteer of Cretan paleontological localities. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 1–32. Prehistory Press, 1996.

Lomolino M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography, 32: 1683–99.

Mayhew D.F. 1977. The endemic Pleistocene murids of Crete I-II. Proceedings of

the Koninklijke Akademie van Wetenschappen (Series B), 80(3): 182–214.

Mayhew D.F. 1996. The extinct murids of Crete. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 167–71. Prehistory Press, Madison.

Mol D., de Vos J., van den Bergh G.D., Sondaar P.Y. 1996. The taxonomy and ancestry of the fossil elephants of Crete. Faunal turnover and comparison with Proboscidean faunas of Indonesian islands. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 1–32. Prehistory Press, Madison.

Poulakakis N., Lymberakis P., Fassoulas C. A. 2005. *Deinotherium giganteum* (Proboscidea, Deinotheriidae) from the Late Miocene of Crete. Journal of Vertebrate Paleontology 25(3), 732-736.

Poulakakis N., Mylonas M., Lymberakis P., Fassoulas C. 2002. Origin and taxonomy of the fossil elephants of the island of Crete (Greece): Problems and perspectives. Palaeogeography Palaeoclimatology Palaeoecology, 186(1–2):163–83.

Psarianos P. 1961. Karstphänomenen Griechenlands. II. Die Polje von Lassithi (Kreta). Annales Geologiques des Pays Helleniques, 12: 105-121.

Reese D.S., Belluomini G., Ikeya M. 1996. Absolute Dates for the Pleistocene Fauna of Crete. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in world Archaeology 28: 47–52. Prehistory Press, Madison.

Reumer J.W.F. 1986. Notes on the Soricidae (Insectivora, Mammalia) from Crete, part I. The Pleistocene species Crocidura zimmermanni. Bonner zoologische Beiträge, 37: 3.

Sen S., Valet J.V., Ioakim Ch. 1986. Magnetostratigraphy and biostratigraphy of the Neogene deposits of Kastellios Hill (Central Crete, Greece). Palaeogeography, Palaeoclimatology, Palaeoecology 53(2-4): Pages 321-334.

Sondaar P.Y., Dermitzakis M.D. 1982. Relation Migration Landvertebrates, Paleogeography and Tectonics. In: Pichon X.L., Augustidis S.S., MascleJ. (eds), International Symposium on the Hellenic Arc and Trench (H.E.A.T.), April 8–10 1981, Athens, 2: 283–308.

Spaan A. 1996. *Hippopotamus creutzburgi*: the case of the Cretan *Hippopotamus*. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 99–111. Prehistory Press, Madison.

Spratt T.A.B. 1865. Travels and Researches in Crete. 2 vols. John van Voorst, London.

Steensma K.J., Reese D.S. 1996. The mustelins of Crete. In: Reese D. (ed.), Pleistocene and Holocene Fauna of Crete and its First Settlers. Monographs in

World Archaeology, 28. Madison, Wisconsin: Prehistory Press, pp. 159–66.

Strasser T.F., Panagopoulou E., Runnels C.N., Murray P.M., Thompson N., Karkanas P., McCoy F.W., Wegmann K.W. 2010. Stone age seafaring in the Mediterranean: Evidence from the Plakias region for Lower Palaeolithic and Mesolithic habitation of Crete. Hesperia 79: 145-190.

Symeonidis N.K., Theodorou G., Giannopoulos B. 2000. The new species *Elephas chaniensis* from the submerged Pleistocene deposits of Vamos Cave at Chania, Crete. Bulletin, Society for Speleology of Greece, 22: 95–108. [in Greek with English abstract.]

Van der Geer A., Lyras G., de Vos J., Dermitzakis M. 2010. Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands. Oxford: Wiley-Blackwell Publishing.

Van der Geer A.A.E., de Vos J., Dermitzakis M., Lyras G. 2009. Hoe dieren op eilanden evolueren. Majorca, Ibiza, Kreta, Sardiniie, Sicilie, Japan, Madagaskar, Malta. Utrecht: Veen Magazines.

Van der Made J. 1996. Pre-Pleistocene land mammals from Crete. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 69–79. Prehistory Press, Madison.

Vogel P. 1980. Metabolic levels and biological strategies in shrews. In: Schmidt-Nielsen K., Bolis L., Tayler C.R. (eds.), Comparative physiology: primitive mammals: 170–80. Cambridge University Press, Cambridge.

Weesie P.D.M. 1988. The Quaternary Avifauna of Crete, Greece. Palaeovertebrata, 18(1): 1–94.

Willemsen G.F. 1992. A revision of the Pliocene and Quaternary Lutrinae from Europe. Scripta Geologica, 101: 1–115.

Willemsen G.F. 1996. The Cretan otter *Lutrogale cretensis*. In: Reese D.S. (ed.), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 153–7 . Prehistory Press, Madison.