OBSERVATIONS ON THE BIOSTRATIGRAPHY OF CRETAN PLEISTOCENE VERTEBRATES

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ABSTRACT - Observations on the biostratigraphy of Cretan Pleistocene vertebrates - II Quaternario, 5(1), 1992, p. 67-76 - The paper considers the systematic and phylogenic problems of the Pleistocenic vertebrates of Crete. The species from the various deposits have been subdivided into the two Mayhew's (1977) Murid zones. These have further divided into a greater number of zones or into subzones on the basis of the murids evolutionary degree and the presence of elephants and hippopotamuses.

RIASSUNTO - Considerazioni sulla biostratigrafia dei vertebrati pleistocenici cretesi - Il Quaternario, 5(1), 1992, p. 67-76 - Sono affrontati i vari problemi sistematici e filogenetici di tutte le faune a vertebrati del Pleistocene cretese. Le varie specie ritrovate nei giacimenti sono collocate nelle due zone a muridi istituite da Mayhew (1977); queste sono poi articolate in un maggior numero di zone o in diverse sottozone in funzione del grado evolutivo degli stessi muridi e delle presenza di diverse specie elefantine e ippopotamine.

Key-words: Pleistocene, biostratigraphy, Crete Parole chiave: Pleistocene, biostratigrafia, Creta

1. INTRODUCTION

The Cretan fossiliferous sites of Pleistocene age are mainly located in cave deposits, and secondarily in fluvio-lacustrine sediments and/or in karstic fissures. To establish any clear correlation between the fossiliferous sites and marine sediments is very hard, unless the fossil remains are contained in continental deposits which are under or over datable beach sediments. An useful tool for a correlation is to analyse the faunal associations or their evolutionary degree; in this way too, a reliable correlation between endemic faunas and Pleistocene continental faunal units may not be easily obtained.

As far as a good correlation is concerned, it is worth noting that the same Cretan endemic species are not present in all the deposits; in many of them, e.g., just one or two species of mammals have been discovered (De Vos, 1984; Dermitzakis & De Vos, 1987). At Milatos 3 fossiliferous deposit the discovered endemic species of Murids are two, however they are not contained in the same stratigraphic level but belong to two different layers (Mayhew, 1977): 1) a lower stalactite level contains Kritimys remains, and fragments of Cervid teeth; whereas; 2) an upper level contains molar teeth of Mus minotaurus.

This situation is of great bearing on the Cretan sites biostratigraphy, in that an earlier *Kritimys* zone and a younger *Mus* zone can thus be discriminated. These two zones may be divided into subzones on the basis of studies on the Murid evolutionary degree (De Vos, 1984; Dermitzakis & De Vos, 1985-86, 1987), while if the phylogeny of endemic hippopotamuses (Kuss, 1975) and elephants (Kuss, 1973; Kotsakis *et al.*, 1979) is considered, a greater number of zones can be established

(Kotsakis, 1987).

In the following pages the biostratigraphical problems of each site are put into relation to the systematic and phylogenic data of all the vertebrate remains found in the Cretan Pleistocene sites.

2. CRETAN PLEISTOCENE VERTE-BRATES: SYSTEMATIC AND PHYLO-GENIC PROBLEMS

Amphibians

The only remains of amphibians belong to a *Bufo* cf. *viridis* (Kotsakis *et al.*, 1976; Kotsakis, 1977) found in Bate Cave and to a *Discoglossus* sp. discovered at Sitia 1 (Kotsakis, 1982). Both the species are still living in Crete.

Reptiles

The only reliable notice about this taxon is in Bachmayer & Symeonidis (1974), who report on *Testudo marginata* remains; and Bachmayer *et al.* (1975) describe two specimens of the subspecies *Testudo marginata cretensis* from Gerani 4 and Zourida, respectively.

Remains of *Mauremys caspica* and *Testudo* sp. from Simonelli Cave are described by Mangili (1980), and Kotsakis (1977) refers on remains of *Testudo marginata cretensis*, *Lacerta* cf. *erhardi* and *Coluber* cf. *gemonensis* as found in Bate Cave.

All these reptiles but *Testudo marginata*, are still living in the island.

Birds

Fossil remains of avifauna in Crete are frequently mentioned in the literature although as scanty and unde-

terminated samples (Kuss, 1965; Kotsakis et al., 1976; Mayhew, 1977). Suriano in Malatesta (1980) described the species Anser albifrons, Sula bassana and ?Athene noctua indigena; the latter species has subsequently been re-determined by Weesie (1982, 1988) as Athene cretensis, a long-legged owl with terrestrial habits, that is found also at Liko. Together with this owl Weesie, in his PhD thesis (Weesie, 1988), describes a rich Pleistocene avifauna from many Cretan localities in which a new endemic subspecies of eagle — Aquila chrysaetos simurgh — stood out. According to Weesie, Athene cretensis preyed murids, and the eagle preyed endemic dwarf megacerini.

Mammais

Soricidae

Remains of *Crocidura zimmermanni* were first found by Bate (1905). Later on, this species was found in association with *Kritimys* by Kuss (1965) and with *Mus minotaurus* by Sondaar (1971). This latter species was found also in Bate Cave (Kotsakis *et al.*, 1977).

Because Soricidae are associated with one another in all the sites, their biostratigraphical value is limited.

Reumer (1987) considered all Cretan remains of *Crocidura* as belonging to *Crocidura zimmermanni* Wettstein.

Chiroptera

Kuss (1973), Kotsakis *et al.* (1976) and Mayhew (1977) refer on undetermined bat remains. Kotsakis (1987) points out the presence of *Rhinolophus ferrume-quinum* and *Miniopterus schreibersi* at Bate Cave.

Mustelidae

Carnivore findings in Crete belong to small- or medium-sized Mustelidae, whose preys were small mammals as shrews or rodents.

Meles meles arcalus Miller — among Melini —and Martes foina bunites Bate — among Mustelini — are described in Caloi (1980). Both the species have been considered as sub-fossils by De Vos (1984) and Dermitzakis & De Vos (1987).

Among Lutrini, Symeonidis and Sondaar (1973) describe *Isolalutra cretensis*. Willemsen (1980) believes that populations of the genus *Lutrogale* may be the ancestors of *Isolalutra cretensis* because of their similar morphology and life habits. Both their continental and Cretan taxa could adapt themselves to different environments, such as open sea, marshy areas and a terrestrial habitat during the dry season. The Cretan otter fitted itself to eat rodents and birds who lived in the island.

Elephantidae

The number of species and the taxonomic position which the many elephant remains found in Creta are to be ascribed to, are still controversial. Bate (1905, 1907) first gives notice of a small-sized elephant at Capo Maleka

and called the species *Elephas creticus*. In the same years remains of *Elephas antiquus*, similar to the continental species, were found at Kharoumes. Simonelli (1907) called *Elephas priscus* a medium-sized elephant from Grida Avlaki. However, Vaufrey (1929) states that *Elephas creticus* and *Elephas priscus* are synonymous of *Elephas melitensis* and *Elephas antiquus*, respectively.

Kuss (1965, 1966) defined Loxodonta creutzburgi as a new species of elephant discovered at Kalo Chorafi. The same Author considered the Elephant priscus from Grida Avlaki as synonymous of this species suggesting that other three species: Elephas antiquus, Loxodonta cretica and Hesperoloxodon antiquus falconeri (?) lived in Crete.

Sondaar & Boekschoten (1967) assume that the Cretan elephants were only two: *Elephas creticus* and *Elephas antiquus*, and do not consider E. *creutzburgi* as a valid species.

In 1970 Kuss changed the taxonomic situation again by stating that only three species existed, *i.e. Elephas creticus* (derived from *E. meridionalis*), *Elephas antiquus* and *Loxodonta creutzburgi* that he renamed as *Elephas creutzburgi* in 1971.

Kotsakis et al. (1979) consider as valid the Maglio's phylogenetic hypothesis (1973), and affirm that the following species were present in Crete: Palaeoloxodon antiquus at Kharoumes, Palaeloxodon creticus at Capo Maleka and Palaeoloxodon creutzburgi at Kalo-chorafi, Simonelli Cave and in other sites near Rethymnon. The same Authors hypothesise that the two latter species descend from Palaeoloxodon antiquus. De Vos (1984) and Dermitzakis & De Vos (1987) agree with them, although if ascribe these three elephants to the genus Elephas (Palaeoloxodon). Phylogenetic problems about these three species have not yet been completely clarified. As a matter of fact, the ancestor of Elephas creticus is considered by Kuss either a species of the genus Loxodonta or a species close to Elephas meridionalis.

Even if the molars of the endemic species are archaic, Kotsakis *et al.* (1979) believe that the ancestor of *Elephas creticus* can be taken as an archaic form of *Elephas antiquus*. According to Dermitzakis & De Vos (1987) the low lamellar frequency and the thick enamel may be explained with a cranial and mandibular reduction.

Dermitzakis & De Vos (1987) such as Maglio (1973) does, consider that the ancestor of *Elephas creticus* might descend from an elephas of the *Elephas namadicus* group, which includes also *Elephas antiquus*.

Kotsakis (1987) and Palombo & Petronio (1989) ascribe the two Cretan endemic species to the genus *Elephas* and subgenus *Palaeoloxodon*, respectively.

Hippopotamidae

Owen (1845), Blainville (1847), Spratt (1865) and

Raulin (1867-69) were the first to report on Hippopotamus remains in Crete. Also Lydekker (1886) listed Cretan hippopotamuses in the fossil mammals catalogue of the British Museum of London.

While all these Authors had assimilated the Crete hippopotamuses to the endemic species of Sicily and Cyprus, Bate (1905) ascribed them to *Hippopotamus* sp.

Vaufrey (1929), Creutzburg (1958), Melentis (1965) ascribed the Cretan hippopotamus remains to endemic species of other islands, and Boekschoten and Sondaar (1966) put together all Cretan remains (especially those from the Katharo basin) into one taxon only, and defined *Hippopotamus creutzburgi* as a new species.

Kuss (1975), on the basis of still smaller bones found in Kato-Zakro 1 and Stavros (Kuss & Missone, 1968), defined *Hippopotamus creutzburgi parvus* as a smaller and younger chrono-subspecies by distinguishing it from the older *Hippopotamus creutzburgi* creutzburgi which was of a slightly greater size.

While Boekschoten and Sondaar (1966) believed that *Hippopotamus amphibius* is the ancestor of *Hippopotamus creutzburgi*, Kuss (1975) supposes that the ancestor could be *Hippopotamus antiquus*.

Capasso Barbato et al. (1982) studied Hippopotamus creutzburgi remains from the Katharo basin, and suggested Hippopotamus antiquus Desmarest as its possible ancestor. In the same paper (p. 63-66) the authors listed both the morphological differences discriminating Hippopotamus creutzburgi from the fossil and still living Hippopotamus amphibius, and the similarities between Hippopotamus creutzburgi and Hippopotamus antiquus.

Hippopotamus creutzburgi (Petronio, 1986) had developed apomorphies allowing him to move easily on the rough morphology of the island during the migration from plateaux towards more peripheric and coastal territories. This endemic species, in fact, had thinner and longer bones than the continental form and strong muscular insertions. In particular, it had broad astragalus-navicular articulation surfaces permitting a wide front-rear flexibility. Hippopotamus creutzburgi had a narrow, short and elongated skull with less prominent orbits and ipsodont molars than the continental species. These features are typical of a less aquatic specialization and of a more herbivorous diet.

Faure (1983, 1984, 1985) also considers *Hip-popotamus antiquus* (that she erroneously calls *H. major*)—and not *Hippopotamus incognitus* (=*H. amphibius*)— as the *Hippopotamus creutzburgi* ancestor.

Later on, Dermitzakis & De Vos (1985-86, 1987) expressed the same opinion.

Cervidae

In 1865 Spratt for the first time reported the presence of Cervid bones in the fossiliferous sites of Gonia, Monastiry and Suda. Additional undetermined Cervid remains were discovered in 1894 by Simonelli at Koulouridi, Aghios Antonios, Bali and near Rethymnon, and in 1905 by Bate (from 13 fossiliferous sites).

In 1907 Simonelli for the first time gave a complete diagnosis of small dwarf cervid remains, discoverd near Grida Avlacki, and defined the species *Anaglochis cretensis*. On the other hand, Vaufrey (1929) ascribed the same Cretan remains, to the genus *Cervus* (subgenus *Eucladoceros*) and to the new species *creticus*.

Sigogneau (1960) classified the Cretan deer as Cervus cretensis.

Azzaroli (1952, 1953, 1961) considers the Cretan deer to be both morphologically and phylogenetically close to *Megaceros*. KUSS (1965, 1966, 1967) and Kuss & Missone (1968) are of the same opinion. Kuss reported also the presence of fossil deer populations having a greater variability than those discovered until then, and assumed that only one species descending from primitive Megacerinus populations had lived there.

Radulesco & Samson (1967) introduced the new genus *Nesoleipoceros* as one of the cervids of the Mediterranean area, including *Nesoleipoceros cretensis*. Furthermore, they hypothesised a lineage of *Nesoleipoceros* from the *Allocenelaphus* from the Rumania basins.

Sondaar & Boekschoten (1967) and Sondaar (1971) associate Cretan deers with the genus *Megaceros s.l.*, and classify them as *Megaceros cretensis*.

Also Kurten (1968) considers megacerini as the ancestors of Cretan deers and calls them as *Praemegaceros cretensis*.

Kuss in his recent papers (1970; 1973) resumes old theories of him about the lineage of endemic deer by hypothesising a tertiary "Cervus" as the possible ancestor, which would have given origin to the Cervid groups of the island through three different evolutionary phases. According to this Author the remains of bigger size are to be classify as the new genus *Cervus* sp.

In 1975 Kuss defined the new genus *Candiacervus* including four morphological species of increasing size from *C. cretensis* (synonymous of *Anaglochis cretensis* Simonellil) through *Candiacervus rethymnensis* Kuss, to *C. cerigensis* Kuss and *C. pigadiensis* Kuss, the two latter species being present only at Karpathos and Kasos.

Accordi (1972) in his preliminary note on the Simonelli Cave, referred to *Megaceros cretensis* the fossil remains of this cave, such as Melentis (1974) seems to do.

In 1975 Sickenberg, in describing a fauna from Marathusa, defined the new species *Cervus peloponnesiacus*, and pointed out morphological features of this *Cervus* which suggest a possible lineage of *Cervus cretensis* from this continental species.

Kotsakis et al. (1976) faced the problem after the finding out of deer remains in Bate Cave. They recognized there Cervids of at least three different sizes: a group of small size, and two other groups of much greater

size than the first one. Of such latter groups, the one of smaller size is bigger than the common still living red deer, and the other has a size greater than that of present elk.

In 1980 Malatesta described the rich deer fauna from Simonelli Cave, and attributed all remains to *Praemegaceros cretensis* (Simonelli). Malatesta explains the great variability in size, that is well evident in the transverse values of the limb bones, as a result of a kind of marked sexual dimorphism which would not affect skulls, as it usually happens with Cervids. The constant presence of antlers or pedicles in the more than 70 skulls found in the cave is explained with the hypothesis of the presence of antlers-bearing female skulls as the effect of an endocrine disequilibrium affecting females.

De Vos (1979, 1984) analyzed the Cervid populations from various caves (in particular, Gerani 4 and Liko) and compared his own data with those by all the other authors concerned with this subject. As a first step, he discriminated six size ranks on the basis of biometrical studies of the postrcranial skeleton. Then, he determined 8 distinct taxa basing on the morphological study of skulls, teeth and antlers. Although if he accepted the genus *Candiacervus* as defined by Kuss (1975), however he completely changed the meaning and limits of the species as fixed by Kuss with revising the Cretan cervids systematics by defining the following taxa (De Vos, 1979, 1984; De Vos & Dermitzakis, 1987):

- Candiacervus ropalophorus De Vos; it is the smallest species (about 40 cm at withers). On the contrary antlers are anomalously long (about 70 cm) compared to the animal size. The species had ipsodont teeth with flat occlusal surfaces.
- Candiacervus sp. Ila, Candiacervus sp. Ilb and Candiacervus sp. Ilc are 3 species slightly bigger in size than the above mentioned one (50 cm at withers), which differentiate from one another for the skulls and antlers typology.
- 3) Candiacervus cretensis: this species which is still bigger than 1) and 2) species (65 cm at withers), corresponds with remains of this species as defined by Simonelli (1907), the lectotype of which is a metacarpus exposed in the Museum of Paleontology in Bologna.
- Candiacervus rethymnensis: it is similar in size to the red deer and is known only through its postcranial skeleton.
- 5) Candiacervus sp. V: it has only been found in Bate Cave by Kotsakis et al. (1976), and was 120 cm high at withers.
- 6) Candiacervus sp. VI: it is the biggest Cretan species (165 cm at withers); it is present mainly at Bate Cave (Kotsakis et al., 1976) and only for a few fragments at Liko.

Capasso Barbato & Petronio (1986) ascribed this latter species to the genus *Cervus* (l.s.) whose ancestor,

in the Authors' opinion, might be the *Cervus peloponnesiacus* found at Megalopoli (Peloponnesus) (Sickenberg, 1975). The hypothesis is supported by a cladistic analysis (Capasso Barbato, 1988) applied to the holotype (metatarsus n° 30). The writer, in her Ph. D. thesis (1989) revised the systematic position of Cretan cervid, and demonstrated that the phylogenetic origin of Cervid of small size is indipendent of that of the Cervids of bigger size.

Small Cervids (Capasso Barbato, 1989) would descend from the Megacerini of the "verticornis" group (sensu Azzaroli) and are: i) Megaloceros (Candiacervus) ropalophorus (De Vos) and ii) Megaloceros (Candiacervus) cretensis (Simonelli). Big Cervids would derive from Cervid populations with thin limb bones of lower Middle Pleistocene times. These latter Cretan Cervids have been defined as the new subgenus Leptocervus. The species are: Cervus (Leptocervus) rethymnensis (Kuss), Cervus (Leptocervus) dorothensis Capasso Barbato and Cervus (Leptocervus) major Capasso Barbato & Petronio.

Bovidae

The various findings of bones attributed to this family (Bate (1905) and Vaufrey (1929): antelope remains; Simonelli (1907): Bos remains that Kuss (1975) identified as Candiacervus rethymnensis; Spratt (1865): goat remains; Kuss (1970): bovine remains) are not reliable determinations so that Bovidae cannot be included in the Cretan fauna, because they are subfossils of Neolithic Age (Kotsakis et al. 1979).

Gliridae

Spratt (1865) attributed to *Myoxus* fragmentary rodent remains found at Gonia Cave. Afterwards, only Mayhew (1977) found an undetermined glirid at Stavros Micro.

Muridae

Bate (1905) was the first to find murid remains at Capo Maleka, Sphinari and Chania-Souda. As to the Sphinari fossils Bate (1912) defined the new species *Mus catreus* and recognized two more species: *Acomys* sp. and *Rattus rattus*.

In 1942 Bate renamed Rattus rattus as Rattus kiridus and identified Acomys sp. with the new species Mus minotaurus.

Kuss (1965) reconsidered the systematic position of the murids from Kalo-Chorafi, Capo Maleka II, Stavros, Bali, Milato, Grida Avlachi, Gumbes I, and Skaleta.

Kuss & Missone (1968) recognized the validity of the species *Mus minotaurus* and defined the new genus *Kritimys* attributing to it the species "*Rattus*" *kiridus* and "*Mus*" *catreus*. The Authors suggested also that the genus *Praomys* may be the African ancestor of *Kritimys*. Whereas, Kuss (1973) hypothesised a tertiary ancestor

for this genus.

Jaeger (1975), Mayhew (1977), Kotsakis *et al.* (1979), De Vos (1984) do not agree with this hypothesis, and assume a murid which arrived to Crete from Rhodos through Karpathos and Kasos islands as the possible ancestor of *Kritimys*. This hypothesis is based on murid remains found in the Damatria Formation (Rhodos) which were very similar to remains of *Kritimys* cf. *kiridus* from Sitia 1, that is of Early Villanian times (Van Der Meulen & Kolfschoten, 1986).

Mayhew (1977), in rearranging the Cretan sites biostratigraphy, assumed that there were four Murid species *i.e.*, *Kritimys kiridus*, *Kritimys catreus*, *Mus bateae*, and *Mus minotaurus*. For these species, Mayhew established a precise chronological succession, based on the Milatos III stratigraphy.

As for *Mus minotaurus*, Mayhew (1977) took as valid the Jaeger's hypothesis (1975) about the origin of this Murid from an ancestor close to *Mus musculus*, which went from Peloponnesus through Kythera and Antikithera to Crete during Middle Pleistocene.

3 BIOSTRATIGRAPHIC SCHEME OF CRE-TAN SITES (see Table 1)

Sitia I

Mammals: Kritimys aff. kiridus (Bate), (?)Apodemus sp.

Age: Early Pleistocene (Upper Villafranchian)

Phylogeny: As mentioned, Mayhew (1977) considered the genus *Kritimys* similar to a Murid found at Rhodos in the Damatria Formation. Kuss (1977) regarded this Murid as a Cretan tertiary relict.

Zone I - Kritimys kiridus

Locality: Capo Maleka I, Capo Maleka 3

Mammals: Crocidura zimmermanni Wettstein, Elephas creticus Bate, Kritimys kiridus (Bate)

Age: Lower Middle Pleistocene

Phylogeny: *Kritimys kiridus* may be considered as descending from the Sitia I form. The origin of *Elephas creticus* is controversial, as it could be phylogenetically linked to archaic palaeoloxodontine forms (Kotsakis *et al.*, 1979).

Zone Ila - Kritimys catreus, Hippopotamus creutzburgi creutzburgi

Locality: Kharoumbes 4-5, Katharo, ? Karoumbes I Mammals: Crocidura zimmermanni Wettstein, Hippopotamus creutzburgi creutzburgi Boekshoten & Sondaar, Megaloceros (Candiacervus) sp. undet'd., Kritimys catreus (Bate).

Age: Middle Pleistocene

Phylogeny: Acc. to Mayhew (1977) Kritimys catreus descends from Kritimys kiridus. The subspecies of

hippopotamus of bigger size probably derives from *Hippopotamus antiquus* (Capasso Barbato *et al.*, 1982).

Any phylogenetic hypothesis cannot be made on the basis of the few Megacerinus available remains.

Zone II b - Kritimys catreus, Hippopotamus creutzburgi parvus

Locality: Kato Zakros, Stavros, Stavros Macro.

Mammals: Crocidura zimmermanni Wettstein, Hippopotamus creutzburgi parvus Kuss, Megaloceros (Candiacervus) ropalophorus (De Vos), Kritimys catreus (Bate).

Age: Middle Pleistocene.

Phylogeny: The Hippopotamus subspecies "parvus" is the last step towards the size reduction from Hippopotamus creutzburgi creutzburgi Boekschoten & Sondaar; M. (C.) ropalophorus (= Candiacervus sp. II De Vos, 1984) is a reduced megacerine form of the verticornis group which underwent a simplification and a variation of the antlers structure. M. (C.) ropalophorus, however, maintained similar morphological features of skull, teeth and postcranial skeleton even if metapodials were proportionally thinner than those of the continental forms.

Kritimys faunas from the sites where Hippopotamus was not found, are also included in Zone II (Sphinari, Bali 2, Milatos 1, Milatos 3 lower layers, Milatos 3 stalactite layers, Kharoumbes A, Xeros).

The Kharoumbes 3 deposit in which *E. (P.) antiquus* (Falconer & Cautley) and *M. (Candiacervus) cretensis* (Simonelli) were found, is referred to a not well-identified Middle Pleistocene zone. The *E. (P.) antiquus* size and morphology approach those of continental forms, whereas *M. (C.) cretensis* is the type-species of the subgenus *Candiacervus*, and was slightly bigger than the species *ropalophorus*. *M. (C.) cretensis* may be the possible ancestor of *M. (C.) ropalophorus*, although if it may also be the result of a size reduction from Megacerinus forms of a subsequent immigration.

Zone III - Mus bateae

Locality: Stavros Micro.

Mammals: *Crocidura zimmermanni* Wettstein, Gliridae gen. and sp. undet'd., *Kritimys catreus* (Bate), *Mus bateae* Mayhew.

Age: Late Middle Pleistocene.

Phylogeny: The genus *Mus* and Glirids appeared for the first time in this zone, both of them descending from European faunas. In this zone also *Kritimys* relict populations were found.

Zone IV - Mus minotaurus

Locality: Stavros Cave (upper layers), Milatos 2, Milatos 3 (upper layers), Milatos 4, Simonelli Cave, Kalo Khorafi, Rethymnon fissure, Zourida, Mavro Mouri IV

TABLE 1

AGE		ZONE	MAMMALS	CERVIDES	C. (L.) major C. (L.) dorothensis C. (L.) rethymnensis M. (C.) cretensis M. (C.) ropalophorus M. (C.) indet.
PLEISTOCENE	Middle	IV Mus minotaurus	Crocidura zimmermanni Rhinolophus ferrumequinum Miiniopterus sc hreibersi Isolalutra cretensis Elephas (P.) creutzburgi Megaloceros (C.) ropalo- phorus Megaloceros (C.) cretensis Cerv us (L.) rethymnensis Cervus (L.) dorothensis Cervus (L.) major	Grotta Stavros Miulatos 2 Milatos 3 Milatos 4 Grotta Simonelli Kalo Chorafi Fessura Rethymnon Zourida Mavro Mouri IV C Liko Grotta Bate Gerani 2 Gerani 4 Gernai 5 Gerani 6 (?) Chania e Souda Gumbes 1 Gumbes 2 (= Grida Avlaki) Skaleta	* * * * * * * * * * * * * * * * *
		III Mus bateae	Crocidura zimmermanni Kritimys catreus Gliridae indet.	Stavros Micro	
		Kritimys catreus b Hippopotamus creutzburgi parvus	Crocidura zimmermanni Megaloceros (C.) ropalo- . phorus	Kato Zakros Stavros (esterno) Stavros Macro	*
		Kritimys catreus a Hippopotamus cr. creutzburgi	Crocidura zimmermanni Megaloceros (C.) sp. indet.	Kharoumbes 4-5 Katharo Kharoumbes 1 (?)	*
		l Kritimys kiridus	Crocidura zimmermanni Elephas creticus	Capo Maleka 1 Capo Maleka 3	
	,	Sitia 1	Kritimys aff. kiridus Apodemus sp.	Sitia 1	
Lower					

C, Liko, Bate Cave, Gerani 2 (levels 2, 3, 4), Gerani 4, Gerani 5, ? Gerani 6, sourroundings of Chania and Souda, Gumbes 1, Gumbes 2 (= Grida Avlachi), Skaleta.

Mammals: Crocidura zimmermanni Wettstein, Rhinolophus ferrumequinum (Schreber), Miniopterus schreibersi (Natterer), Isolalutra cretensis Symeonidis & Sondaar, Elephas (Palaeoloxodon) creutzburgi KUSS, M. (Candiacervus) ropalophorus (De Vos), M. (C.) cretensis (Simonelli), Cervus (Leptocervus) rethymnensis (Kuss), C. (L.) dorothensis Capasso Barbato, C. (L.) major Capasso Barbato & Petronio, Mus minotaurus Bate. Caloi (1980) refers on two subfossil specimens of Carnivores (Meles meles arcalus Miller and Martes foina bunites Bate).

Age Late Pleistocene.

Phylogeny: Small elephants appear to be phylogenetically linked to *E. (P.) antiquus*, as it still keeps many morphological (Kotsakis *et al.*, 1979; Dermitzakis & De Vos, 1987) and morphostructural features similar to *E. (P.) antiquus* (Palombo & Petronio, 1989).

In this zone, the two Cervid species derived from the Middle Pleistocenic Megacerini, are present together with 3 Cervine species probably phylogenetically linked to populations of the genus *Pseudodama* (*sensu* Masini *et al.*, 1990). Among the Cervine species, *C.* (*L.*) rethymnensis is the most similar in proportions to *C. elaphus*, whereas the two bigger species resemble more Cervine thin-limbed populations of the European Lower Pleistocene (*Cervus rhenanus* = *Pseudodama philisi* acc. to Masini *et al.*, 1990).

Mus minotaurus, who descended from Mus bateae, replaced this latter and was in its turn replaced by Rattus rattus (Linnaeus), which was taken to the island together with domestic animals in Neolithic Age. In that period M. (C.) ropalophorus was still living.

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