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THE ADAPTIVE RADIATION OF THE ENDEMIC DEER OF CRETE

By

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SUMMARY

The adaptive radiation of island animals is well known. The Darwin finches of the Galapagos islands are a famous example of this. For fossil island animals this phenomenon is hardly discussed. In this paper the speciation of the Cretan endemic island deer is presented as a case of adaptive radiation.

INTRODUCTION

The islands of the Galapagos were very important for the idea of Charles Darwin concerning evolution. It was here that Darwin discovered that, although the animals show signs of a resemblance with the ones of Patagonia, they are different from them. Secondly he realised that species differ from island to island, even if the islands are less than 100 km separated from each other. His attention to that was attracted by the birds and the statement of Mr Lawson, an Englishmen, which was vice govenor of the Archipelago, that he could tell immediately from which island a particular tortoise came. The study of Lack in the nineteenfourties showed that, although the size, plumage and bodies of the birds of the Galapagos islands were superficially seen similar in appearance, the differences in beaks indicates an adaptation to different habitats. It became clear that islands had species which were different from the mainland and were adapted to the different habitats of islands.

Islands are sometimes called the laboratories of evolution.

In so-called oceanic islands, which could only be reached by a few species which can swim (like elephants, hippo's and deer), float or fly to the islands, the species will adapt to the different habitats of that island and adaptive radiation will take place. Such cases are well known for recent island communities, but they are underestimated for fossil communities. The purpose of this paper is to show that the fossil Cretan cervids are an example of such fossil community inwhich adaptive radiation took place.

ADAPTIVE RADIATION

Once an animal settled on a island they underwent changes, adapting to the island conditions. The adaptiations to different habitats is called adaptive radiation. This phenomenon of adaptation is always found in island faunas, provided they are isolated for a sufficiently long period.

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* The adaptive radiation of the endemic deer of Crete.

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The degree of radiation depends on time and the size of the island. In islands which are large and isolated for a very long time, the adaptive radiation will be strong, like in the marsupials of Australia; when the islands are smaller and the time during evolution took place is relatively short, the radiation will be weaker. The most famous exemple of this is the adaptive radiation of the Darwin's Finches, because these birds show a weak developed adaptive radiation, as compared to the Marsupials of Australia.

Darwin's Finches

The fact that all Darwin's finch species are more similar to each other than anyone is to a continental species makes it likely that they were all descended from a single ancestral species of emberizine finch. Grant (1986) wrote:" We can be confident that the ancestral species colonized the Galαpagos or Cocos Island by overwater flight...... But who was the ancestor?". Various candidates have been suggested. In recent times three genera and species have been given special attention: *Melanospiza richardsonii*, *Volatinia jacarina* and *Coereba flaveola*. However, not one of these three candidate species is clearly more closely related to them than are the others (Grant, 1986: 254). So it is difficult to trace the ancestor.

It is generally accepted that in the Darwin's finches a radiation took place, however, concerning their speciation there is no clear picture. Grant (1986) discussed three models of speciation: allopatric speciation, parapatric speciation and sympatric speciation. Further he discussed alternatives to gradual genetic changes. He concluded that gradual genetic changes, like hybridization, may have played a role in speciation through the contribution of new alleles to a population undergoing divergent evolution, but not as a means of producing new species by itself. In addition there is in no case the empirical evidence strong for parapatric speciation on the Galαpagos. The general idea is that the best explanatory scheme for speciation of Darwin's finches is the allopatric model. However, speciation could also occur sympatrically if a more stringent set of conditions were met; this model I consider as more realistic.

Lack (1947: 12) wrote: " Before any discussion of them is possible, Darwin's finches must be named, although this in itself commits one to a partial interpretation of the problems of their evolution". In continental passerine birds, closely related species tend to differ from each other in plumage, and they are usually similar in beak and other structural characters. Differences in beak more usually characterize the broader units, the different genera. In Darwin's finches on the other hand, closely related species differ markedly in beak, but little, if at all, in plumage, and plumage differences are chiefly important in distinguishing the different genera and species on the continent. A further unusual feature in Darwin's finches is that some species are highly variable (Lack 1947: 12).

Six genera and 14 species are recognized (Grant, 1986). They are mostly sparrow-sized, and are all dull in colour. Species are distinguished from each other by bill size and shape, and by body size, and most can be recognized clearly, but some allopatric populations are difficult to classify. Conceivably, therefore, there are one or two species more, or less, than the fourteen currently recognized, according to Grant (1986: 66). All these species are adapted to different habitats and occupy different niches. Patterson (1978: 112) gives a small description of the different groups which follow here. One group, the ground finches, live in the coastal zone and the lowlands, and feed mainly on the ground, on seeds and insects. One species in this group has a long beak and feeds on the flowers of prickly pear cacti. A second group, the tree finches, contains three species with large, parrot-like beaks. They live in the forest zone, feeding in the trees on insects and seeds. The warbler finch, placed in a genus of its own, has a slender beak and feeds only on insects, sometimes taken on the wing. Another species, also placed in a genus of its own, is the vegetarian tree finch, a larger bird living in the forest zone and feeding on fruit, buds and soft seeds. Finally, there are two species with habits like woodpeckers, feeding on insects taken from tree trunks and branches. Unlike woodpeckers, they do not have strong, sharply-pointed beaks and long tongues, but they make up for this using twigs or cactus spines as tools, to poke insects out of crevices. One of these birds, the mangrove finch, ranges up into the forest zone.

Other examples of adaptive radiation

Besides the Darwin's Finches there are a lot of more cases known to science, like:

- The honeycreeper finches (Drepaniidae) of Hawaii. In this group there is a much more differentiation in morphology than in the Darwin's Finches. The radiation is so extreme that it is not possible anymore to tell which group is the ancestor. Lack thought that a Finch may be the ancestor, like in the Darwin's Finches, while for others the honeycreeper or a tanagra is the ancestor. Nine genera with 22 species are distinguished. Some genera do feed on honey and insects, in others is the main food honey, while in others again the insects are the main food. All kind of species are developed, comparable with parots, finches, etc., with different kinds of beaks.
- Birds of Paradise from New Guinea.
- Not only in birds, but also in Marsupials from Australia which can been seen as an adaptive radiation. The tanrects and the lemuren of Madagascar, a landsnail in the Galapagos islands (Nesiotus) which developed about 53 species. From Hawaii is known an Achatina-like giantlandsnail with more than 500 different morphotypes, which must be not considered as species, but it shows that it is possible to give a lot of forms, originating from one ancestor.
- Adaptive radiation is not only the case in islands which are isolated, but also in lakes which are isolated. The adaptive radiation of chiclid fishes (Haplochromine cichlid fishes) in Lake Malawi (Afrika) is an example of this. They differ particular in the mouth, which is adapted to all kinds of food.

CERVIDS OF CRETE

The Pleistocene fauna of Crete

From the literature (Bate 1905, 1907; Simonelli 1907, 1908; Kuss 1965, 1966, 1973, 1975a and b; De Vos 1979, 1984; Capasso Barbato and Petronio 1986; Capasso Barbato 1989, 1990, 1992 a and b; Boekschoten and Sondaar 1966; Kuss and Misonne 1968; Mayhew 1977; Reumer 1986; Reumer and Payne, 1986; Symeonidis and Sondaar 1971; Weesie 1982, 1987; Willemsen, 1980; Bachmayer et al. 1975) it is clear that the fauna of Crete only contains cervids, hippos, murids, shrews, elephants, birds and reptiles, while large carnivores, with the exception of the otter, are lacking. A fauna with a restricted group of mammal species (mostly endemic) is designated as an unbalanced fauna (Sondaar 1971, 1977). The mammals found in Crete were endemic, which means that they were restricted to Crete itself. The endemic unbalanced fauna points to isolation of Crete during the Pleistocene (Sondaar 1971, 1977). According to Sondaar & Boekschoten (1967) and Dermitzakis & Sondaar (1978) the mammals, including the cervids, reached the island by swimming or drifting.

The biostratigraphy

The Vos (1979) published a table with the biostratigraphy for the Pleistocene of Crete. Based on the data given in that table he suggested that there were two invasions of cervids. This idea was followed by Capasso Barbato (1992b). Recently De Vos (in press), based on literature study and own observations, concluded that there was only one invasion. He suggested in Crete a faunal turnover (fig. 1), inwhich a fauna with pygmy elephant and pygmy hippo and large murids are succeeded with a fauna with cervids, a large elephant and a small murid.

Ancestors

In the past different hypotheses have been postulated concerning the relation of the fossil Cretan deer with mainland species. It has been suggested (Azzaroli 1953a, 1961, 1977; Kuss 1965, 1966, 1967; Kuss & Misonne 1968; Kurtın 1968; Sondaar 1971; Accordi 1972; Malatesta 1980; Capasso Barbato, 1989, 1990, 1992a and b) that there is a relationship between the various dwarfed deer of the Mediterranean islands, including Crete, as a group and the large continental cervids of the Pleistocene: *Eucladoceros* of the Villafranchian, *Praemegaceros* of the Middle Pleistocene and *Megaceros* of the Upper Pleistocene.

Kuss (1975b) already rejected a relationship of the Cretan deer with the megacerines. He created a new genus, *Candiacervus*, with two species in Crete, a small one (*Candiacervus cretensis*) and a large one (*Candiacervus rethymnensis*).

Sickenberg (1975) described a deer Cervus peloponnesiacus from the Megalopolis Basin (Peloponnensis, Greece), and believed that it was the ancestor of the Cretan deer for the following reasons:

1) the great resemblance in morphology of the antlers;
2) the tendency towards hypsodonty in the teeth;
3) the variability in the size of the extremities;
4) the paleogeographical and paleoecological situation.

At variance with this hypothesis are the facts that the antlers of *Cervus peloponnesiacus* are too fragmentary for an exhausting comparison, and the browtine is placed too low. Furthermore, the variability in size of the extremities is absent in the Cretan deer as is indicated in the study of De Vos (1979). There is too little teeth material for measuring the hypsodonty in *Cervus peloponnesiacus*, and finally the paleogeography and paleoecology are not very strong arguments for phylogeny.

Capasso Barbato and Petronio (1986) attributed the large species in the genus *Cervus* again, based only on the resemblances of postcranial elements, with *Cervus Peloponnesiacus and Cervus philisi*. The difference they (Capasso Barbato and Petronio, 1986) speak of is the fact that the metapodials are much slender than any continental form. However, this is no good argument, as the taxonomy of cervids is based on antlers, and sometimes cervids with identical postcranial elements in size and morphology, but different in antlers, are put in different genera (like *Cervus perrieri* and *Arvernoceros ardei*; Heintz, 1970). In 1989 Capasso Barbato created a new subgenus (*Leptocervus*) for the large species.

Capasso Barbato (1992b) follows the opinion that the ancestor of the larger Cretan species might be the *Cervus peloponnesiacus* found at Megalopoli (Peloponnesus) (Sickenberg, 1975). The large cervids would be derived from cervid populations with thin limb bones of lower Middle Pleistocene times.

Capasso Barbato (1989, 1990, 1992a and b) considered the smaller species to be Megacerini of the "verticornis" group (sensu Azzaroli) and put them in the subgenus *Candiacervus* of the genus *Megaloceros* (in the paper of 1989 and 1990 indicated as Megaceros).

I still hold the opinion that the now available data are insufficient to conclude firm phylogenetic relationship between the mainland forms and the Cretan cervids. Adopting the genus name *Candiacervus* for all the Cretan species is still the best solution.

Concluding we may say that there are no known relatives of the Cretan deer on the mainland although various candidates have been suggested as ancestor. Two genera and two species have been given special attention: *Cervus peloponnesiacus* and *Megaceros verticornis*. However, not one of these candidate species is clearly more closely related to them than are other cervids of the continent.

The number of species

It was Simonelli (1907, 1908) who was the first to describe the cervid fossils of Crete under the species name cretensis. Till 1975 only one species of deer was considered to be present in Crete, although Kuss (1965, 1967, 1970, 1973) already reported that a large variability in size and morphology existed within the species cretensis and that there were a few specimens with sizes going beyond the variation of the species cretensis. In 1975 Kuss, on basis of size, considered the material from Crete to belong to two species, a small one (cretensis) and a large one, for which he erected a new name, rethymnensis. The large size range in the material from different localities of the small species, Kuss (1975b) explained as a consequence of diminution in size of the deer in the course of time. Also in the larger species rethymnensis there was a diminution in size, according to Kuss (1975b: 46). Kotsakis et al. (1976) considered the deer remains originating from the locality Bate Cave to belong to one species, cretensis, with the exception of a few very large bones, which they described as " Cervo taglia media" and " Cervo taglia grande". In 1979, Kotsakis et al. again acknowledged the difference in length between the bones, but they thought that this quantitative aspect not sufficient to establish a new species. However, the variation within the material from Bate Cave went far beyond the range of variation of both species cretensis and rethymnensis in the sense of Kuss (1975b). Malatesta (1980), who described the material from Simonelli Cave, considered the fossil deer from this cave to belong to a single species. He observed a large variation in the thickness of the metapodials of the same length. He stated (p. 53) that the differences between thicker and thinner metacarpals were so long that it would be hard to believe that these bones could have belonged to a single species. He suggested, however, that the difference between the thicker and thinner metapodials was due to sexual dimorphism. This explanation is not very likely, because in recent cervids the sexual dimorphism is reflected not only in the thickness, but also in the length of the metapodials. Bones from males are in general longer and heavier than bones from females, although the distribution of sizes may show overlap (Bosold 1968). Such a distribution of sizes, which may be attributed to sexual dimorphism, has been found for the robustness of the metacarpals of the fossil deer from Gerani 4 (Crete, De Vos 1979: fig. 3). The more robust metacarpals of the same length, mentioned by Malatesta (1980), may indicate that the material originates from older and younger animals. For example, the first two metatarsals illustrated by Malatesta (1980) in his plate XXII, and attributed by him to females, actually represent juvenile animals, as indicated by the absence of epiphyses. In addition, Malatesta (1980: 91) mentioned that among the material from Simonelli Cave some bone fragments were found (metatarsal and calcaneum), the size of which went beyond the variation range of his cretensis. As an explanation for the presence of such large elements, Malatesta (1980: 91) stated: " probably they represent exceptional cases of reappearance of ancestral genetic configuration". But as many of such large elements are found at different localities (De Vos 1979), the largest metatarsal being of about four times the length of the smallest (De Vos 1979: table 12), it is more realistic to suppose that we are dealing with different taxonomic units.

In a biometrical approach of postcranial and cranial material from several sites, De Vos (1979) distinguished six size groups (fig. 2) in the fossil remains of the Pleistocene deer from Crete. In one of the size-groups he distinguished three morphotypes of skulls and antlers, leading to eight taxonomic units:

Candiacervus ropalophorus De Vos, 1984
Candiacervus spp. II, including three taxonomic units
Candiacervus cretensis (Simonelli, 1907)

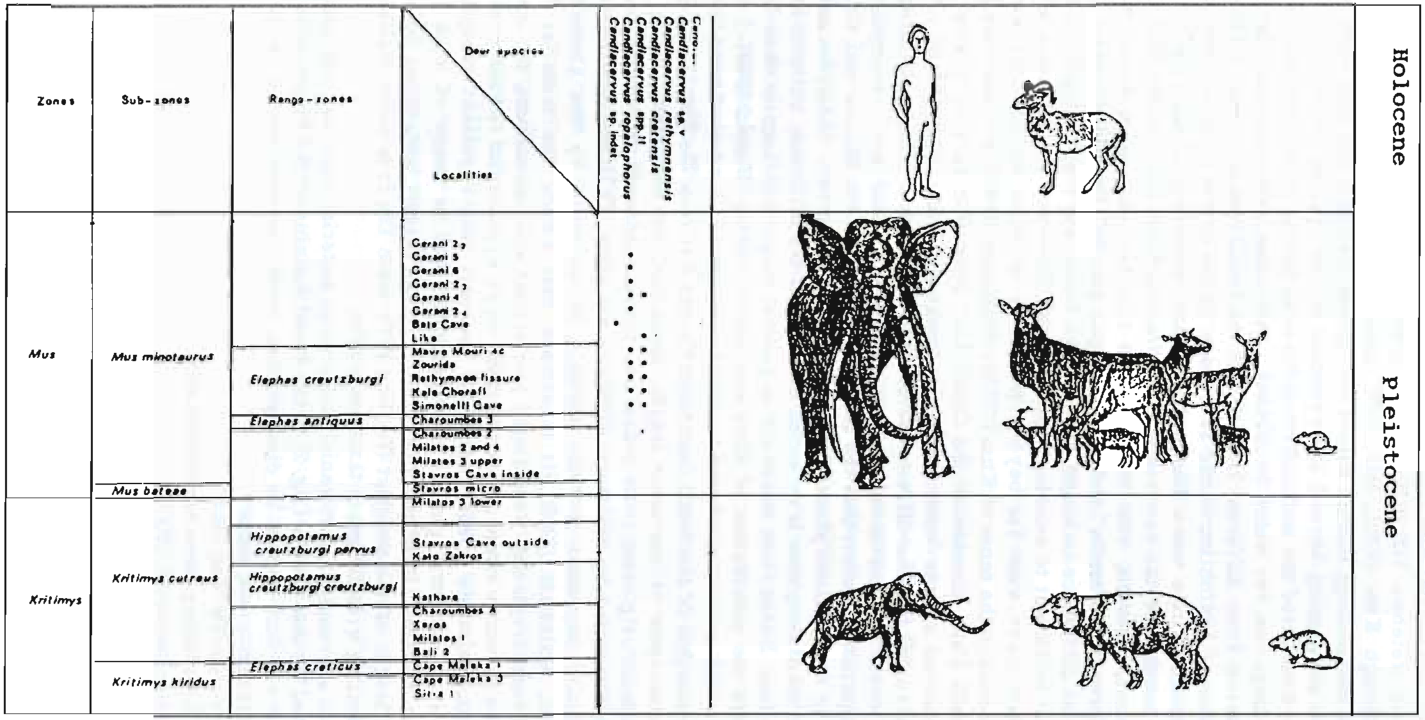

Fig. 1. The biostratigraphy of Crete (after De Vos, 1979)

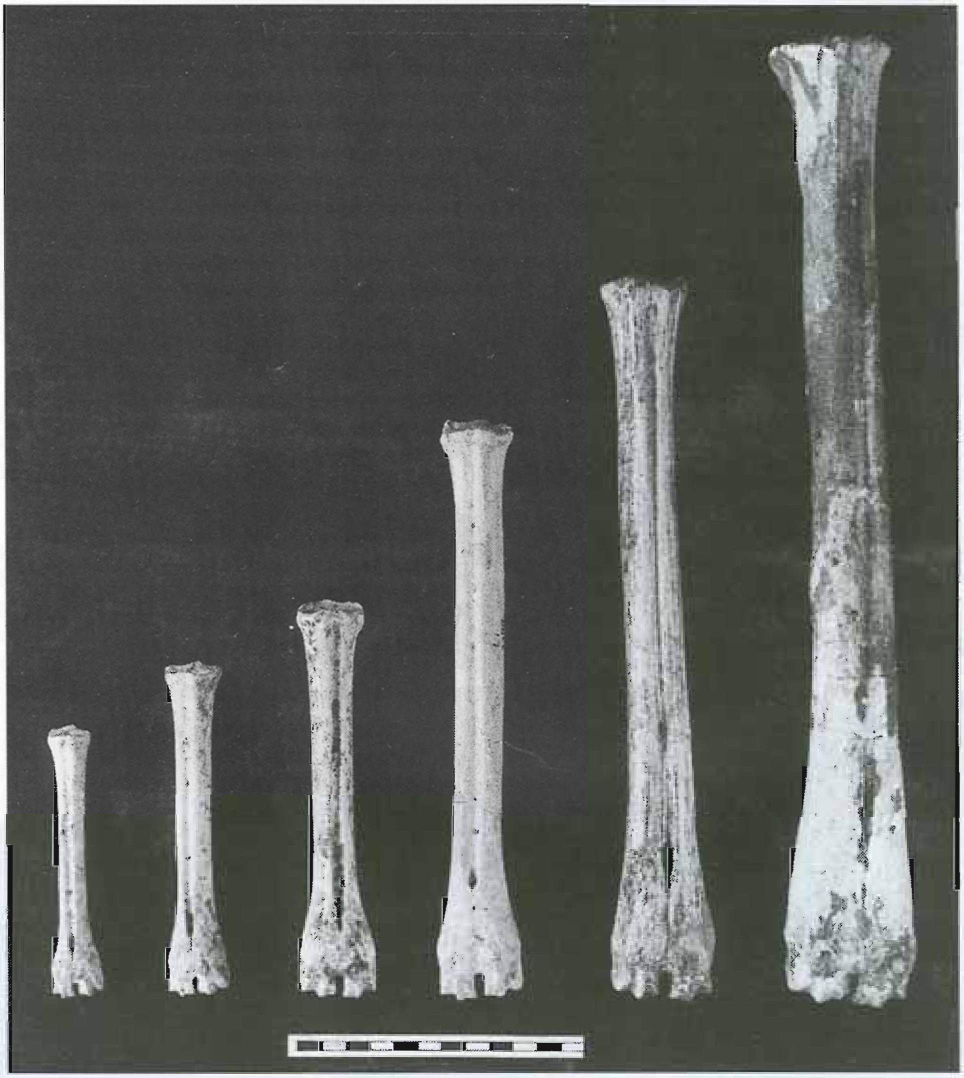

Fig. 2: The six size-groups in the metatarsals of the Cretan cervids.

Fig. 3: Scatterdigram showing that the cernid of Gerani is smaller than the one of Liko.

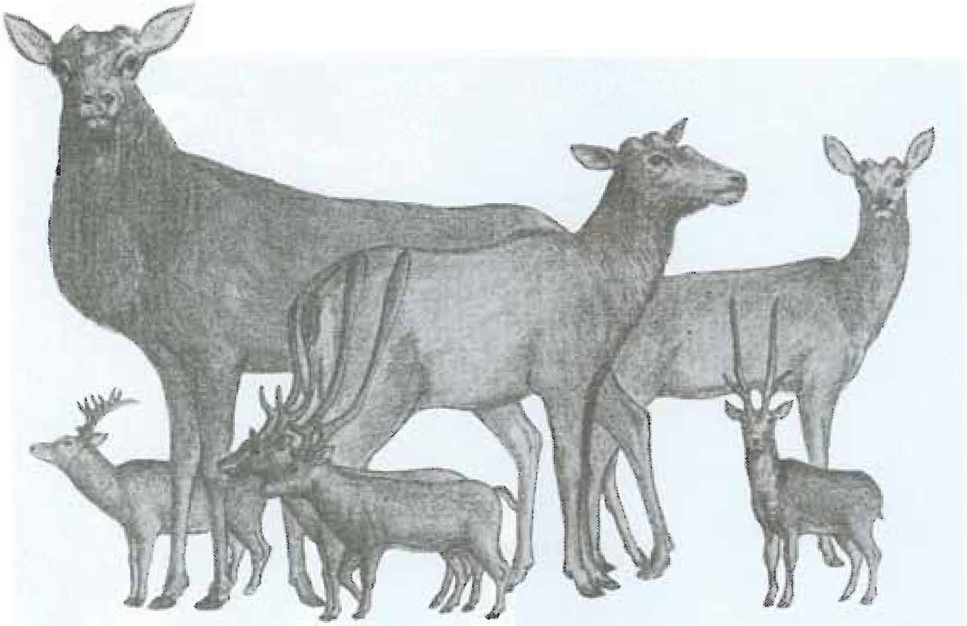

Fig. 4: Seven of the eight Cretan species

Fig. 5: Three morphotypes of P2; the left one is the morphotype of *Candiacervus ropalophorus.*

Fig. 6: The flat occlusal surface in the mandible of *Candiacervus ropalophorus*

Fig. 7: A mandible of a large species with a lophodo occlusal surface.

Candiacervus rethymnensis Kuss, 1975
Candiacervus sp. V (= "Cervo taglia media" of Kotsakis et al. 1976), and
Candiacervus sp. VI (= "Cervo taglia grande" of Kotsakis et al. 1976).

In 1986 Capasso Barbato and Petronio attributed the material from *Candiacervus sp.* VI to the genus *Cervus* and erected a new species: *Cervus major*.

In her unpublished thesis of 1989 Capasso Barbato attributed without giving arguments the material of *Candiacervus* species IIa, b and c of De Vos, 1984, to the species *Candiacervus ropalophorus*, although De Vos (1979) clearly proved statistically that the populations of the site Gerani 4 (with *Candiacervus ropalophorus*) and Liko (with *Candiacervus* II taxonomical units) are significant different in size (fig. 3).

Further Capasso Barbato (1989) ignored the distinction in antler morphology in the species IIa, b, c, without discussing it. From *Candiacervus* species V of De Vos (1984) Capasso Barbato (1989) made a new species: *dorothensis*. These data of the unpublished thesis were published in 1990 and 1992a and b (Capasso Barbato 1990, 1992 a and b).

The speciation

In the past different hypotheses concerning the speciation have been postulated. De Vos (1984) and De Vos & Dermitzakis (1986) discussed these hypotheses and added a few more. They speculated on the possible mode of development of the different taxa of the Cretan deer. They discussed five models

-1. One invasion-Single lineage model

De Vos (1984) and De Vos & Dermitzakis (1986) rejected this model, because it implies that one has to find the largest forms in the older deposits and the smallest in the younger sites and furthermore, one cannot find more than one taxon per horizon per site. These conditions are contradicted by the fact that the largest form have been found in localities of relatively young age and different taxa were frequently found in the same horizon.

-2. Two Invasion-Two lineages model

This model does not explain the presence of three or more species in the same horizon.

-3. More invasions model

The most extreme number of invasions could be six, based on the size groups. This model was rejected for paleontological and on morphological reasons.

-4. One Invasion-Radiation Model

In this model is supposed that the cervids originated from one ancestral stock, in which some kind of radiation had taken place. This is based on the fact that in several stratigraphic horizons several taxa were found, so that one has to accept that the different taxa actually lived at the same time.

-5. Two invasions- Two radiations model

In this last model it is suggested that there were two invasions followed by two radiations

Based on the suggestion that the cervids are only in the Mus- zone, model 4, the One Invasions-Radiation Model is considered here as the most likely one.

In which way the speciation took place is not clear. Gradual genetic changes may have played a role. Although we can not exclude allopatric speciation, it is more realistic to suppose that the speciation took place in Crete itself. So what is left are parapatric speciation and sympatric speciation. As there are no great differences in habitat, parapatric speciation seems not very likely, but cannot be excluded either. Sympatric speciation makes the best chance, but cannot be proven yet.

Adaptive radiation of the Cretan cervids

In this paper the opinion of De Vos (1984) is followed that there are 8 taxonomic units (fig. 4) attributed to one genus: *Candiacervus.*

Candiacervus ropalophorus De Vos, 1984

This is the smallest deer found so far in Crete. It had a withers height of about 40 cm. Characteristic of this species is, that it has relative shortened metacarpal and the limb-bones are relatively more massive than in *Cervus elaphus*. Some metatarsals (6%) are fused with the naviculo-cuboid; 68 % of the naviculo-cuboids are fused with the central cuneiform (De Vos, 1979). The shortening of the metapodials and the frequent fusion of the metatarsus with the navico-cuboid are interpreted by Leinders and Sondaar (1974) as an adaptation of the locomotory system to island environments. Speed and zig-zag movements lost their significance of the absence of carnivores. Through the shortening of the legs the centre of gravity was lowered, resulting in a greater stability. Through the fusion of the tarsals the foot became less vulnerable, This low-gear locomotion was advantageous in the mountainious and carnivore lacking environments (Leinders, 1979).

The P^2 is characterized by a protocone that is similar in size to the hypocone (fig. 5).

The antlers are very peculiar; they are long (up to 77 cm) for such small animals. The antler has only a browtine, which is placed about 10 cm from the burr; this is called sub-basilar. The occlusal surface of the teeth-rows in middle-aged animals is flat and the teeth are rather hypsodont (fig. 6).

Candiacervus spp. II

In size following Candiacervus ropalophorus are three species with the same size (withers height about 50 cm), but different in skull morphology and antlers. These three species are indicated as *Candiacervus* sp. IIa, IIb and IIc. They also had shortened and more massive legs. This shortening is of the same degree as in *Candiacervus ropalophorus*. Also here the occlusal surface of the teeth is more flat and the teeth are rather hypsodont, which suggests that they have eaten more grasses.

These short-legged, small, heavily-built cannot be considered as being due to ontogenetic scaling or paedomorphic changes . The relative shortening of the legs is not directly connected with dwarfism, but must have a special adaptational meaning (Sondaar, 1977). Sondaar (1977) pointed out, that shortening of the leg reduces locomotion speed. The faunas, to which the dwarfish and short legged forms belong, are so-called unbalanced faunas (Sondaar, 1977). These faunas lack carnivores. For these short-legged species there was no need to be able to move at high speed, since there were no predators to escape from. On the other hand, short distal parts of the legs might be advantageous in fouraging in the mountainous environment of islands (Sondaar, 1977).

Candiacervus cretensis (Simonelli, 1907)

This species had a withers height of about 65 cm. The legs were also shortened, but in a lesser degree than the previous species.

Candiacervus rethymnensis Kuss, 1975

A species, which, qua length of its legs, is comparable with the mainland species Cervus elaphus. It had a withers height of about 90 cm. This species and the following two species are only known from their post-cranial skeletal elements.

Candiacervus sp. V (Cervus dorothensis), and
Candiacervus sp. VI (Cervus major)

These two species are characterized by the fact that their leg bones are more slender than any species on the continent. *Candiacervus* sp. V possessed a withers height of about 120 cm, while *Candiacervus* sp. VI had a withers height of about 165 cm. In these last two species the occlusal surface of the teeth is lophodont (fig. 7), which suggests that they have eaten more branches and leaf-like food.

DISCUSSION AND CONCLUSIONS

Although there are different opinions concerning the number of cervid species in Crete, it is clear that the species differ in dental, cranial and postcranial morphology, which point to the fact that they must be adapted to different habitats and occupy different niches. There was only one invasion and the species originate from an untill now unknown ancestor of the continent. The speciation of the Cretan cervids is clearly a case of adaptive radiation, which can be compared to the speciation and adaptive radiation of the Darwin's Finches of the Galαpagos islands.

REFERENCES

Accordi, B. 1972. Lo scavo della " Grotto Simonelli", con cervi nani del Quaternario, effettuato a Creta nel 1971 dall'Istituto di Geologia e Paleontologia dell'Universitŏ di Roma, con il finanziamento dell'Accademia Nazionale dei Lincei. Quaderno Accademia Nazionale dei Lincei 167: 1-17, Roma.

Azzaroli, A. 1953a. La sistematica dei cervi gigantei e i cervi nani delle isole. Atti della Societa Toscana di Scienze Naturali, Memorie, A, 59 (1952): 119-127.

Azzaroli, A. 1961. Il nanismo dei cervi insulari. Palaeontographia Italalica, Vol. LVI, Paleontologia ed ecologia del Quaternario, vol IV, Memoria nr. 1 Pisa: 1-32.

Azzaroli, A. 1977. Considerazioni sul mammiferi fossili delle isole Mediterranee. Bollettino di Zoologia 44: 201-211, Padova.

Bachmayer, F., J.P. Brinkerink and N. Symeonides. 1975. Pleistozône Schildkrφten aus Hφhlen der Insel Kreta. Annales Gιologiques des Pays Hellιniques, 27: 110-122, Athena.

Bate, D.M.A. 1905. Four and a half Months in Crete in search of Pleistocene Mammalian Remains. Geological Magazine, n.s., Dec., V, vol. II, no. V: 193-202, London.

Bate, D.M.A. 1907. On Elephant Remains from Crete, with Description of Elephas creticus n.sp. Proceedings of the Zoological Society of London: 238-250.

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

Bosold, K., 1986. Geschlechs und Gattungsunterschiede an Metapodien und Phalangen mitteleuropôischer Wildwiederkôuer. Sôugetierkundliche Mitteilungen, 16: 93-153.

Capasso Barbato, L. 1989. Cervidi endemici del pleistocene di Creta. Dottorato in Palaeontologia, Modena-Bologna, Vol. I and II.

Capasso Barbato, L. 1990. Les Cervidιs endιmiques de Crθtes. Quaternaire, 3-4: 265-270.

Capasso Barbato, L. 1992a. Nuova specie di cervide del pleistocene di Creta. Atti della accademia Nazionale dei Lincei, Memorie Lincee, Scienze Fisische e Naturali, serie IX, Vol. 1, Fascicolo 7: 183-220.

Capasso Barbato, L. 1992b. Observations on the biostratigraphy of Cretan Pleistocene vertebrates. Il Quaternario, 5 (1): 67-76.

Capasso Barbato, L.C. and C. Petronio. 1986. Cervus major n. sp. of Bate Cave (Rethymnon, Crete). Atti della Accademia Nazionale dei Lincei, Memorie, classe di Scienze fisischi, matematische e naturali, Serie VIII, vol. XVIII, Sez. IIa (Fisica, chimica, geologia, paleontologia e mineralogia), fascicolo. 2: 59-100. Roma.

Dermitzakis, M.D. and P.Y. Sondaar. 1978. The importance of fossil mammals in reconstruction paleogeography with special reference to the Pleistocene Aegean Archipelago. Annales Gιologiques des Pays Hellιniques, 46: 808-840, Athena.

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

De Vos, J. 1984. The endemic Pleistocene deer of Crete. Verhandeling der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Eerste reeks, Deel 31. North-Holland Publishing Company, Amsterdam, Oxford, New York: 1-100.

De Vos, J. and M.D. Dermitzakis. 1986. Models of the development of Pleistocene deer on Crete (Greece). Modern Geology, 10: 243–248.

Grant, P.R. 1986. Ecology and Evolution of Darwin's Finches Princeton University Press, Princeton, New Jersey: 1–458.

Heintz, E. 1970. Les Cervidıs Villafranchiens de France et d'Espagne, Volume I et II. Mımoires du Musıum National D'Histoire Naturelle Nouvelle Sırie, Sırie C, Sciences de la Terre, Tome XXII, Fascicule Unique, Paris.

Kotsakis, T., J. Melentis, C. Petronio, and G. Sirna. 1976. Seconda spedizione paleontologica Lincea nell'isola di Creta (1975). Academia Nationale dei Lincei, Quaderno, 223: 3–10, Roma.

Kurtın, B. 1968. Pleistocene mammals of Europe, 1-317.

Kuss, S.E. 1965. Eine pleistozône Sδugetierfauna der Insel Kreta. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 55 (2): 271-348.

Kuss, S.E. 1966. Beitrage zur pleistozônen-Fauna der Insel Kreta. I. Die von Bate 1904 gesammelten Elefanten- und Cerviden-Reste. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 56 (2): 169–181.

Kuss, S.E. 1967. Pleistozône Sδugetierfunde auf dem ostmediterranen Inseln Kythera und Karpathos. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 57 (2): 207-216.

Kuss, S.E. 1973. Die pleistozônen Sδugetierfaunen der ostmediterranen Inseln. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 93 (1-2): 49–71.

Kuss, S.E. 1975a. Hippopotamus creutzburgi parvus n. spp., ein pleistozônes Zwergflusspferd von der Insel Kreta. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 65 (1-2): 5–23.

Kuss, S.E. 1975b. Die pleistozônen Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpatos und Rhodos (Griechenland). Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau 65 (1-2): 25–79.

Kuss, S.E. and X. Misonne 1968. Pleistozône Muriden der Insel Kreta. Neues Jahrbuch fór Mineralogie, Geologie und Palδontologie. Abhandlung. 132 (1): 55–69.

Lack, D. 1947. Darwin's Finches, Cambridge University Press, Cambridge: 1-208.

Malatesta, A. 1980. Dwarf Deer and Other Late Pleistocene Fauna of the "Simonelli" Cave in Crete. Quaderno Accademia Nazionale dei Lincei, Roma 249: 1-128.

Mayhew, D.F. 1977. The endemic Pleistocene murids of Crete I-II. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, Volume 80 (3): 182–214.

Patterson, C., 1978. Evolution.-British Museum (Natural History), London: 1-197.

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

Reumer, J.W.F. and S. Payne. 1986. Notes on the Soricidae (Insectivora, Mammalia) from Crete, II. The shrew remains from Minoan and Classical Kommos. Bonner zoologische Beitrδge 37, 3.

Sickenberg, O. 1975. Eine Sδugetierfauna des tieferen Biharium aus dem Becken von Megalopolis (Peloponnes, Griechenland). Annales Gıologiques des Pays Hellıniques, 27: 25–73, Athena.

Simonelli, V. 1907. Mammiferi quaternari dell'isola di Candia I. Memmorie, Accademia delle Scienze. Instituto di Bologna Classe di Scienze Fisiche, ser. VI, 4: 455–471, Bologna.

Simonelli, V. 1908. Mammiferi quaternari dell'isola di Candia II. Memorie, Accademia delle Scienze. Instituto di Bologna Classe di Scienze Fisische ser. VI, 5: 103–111, Bologna.

Sondaar, P.Y. 1971. Palaeozoogeography of the Pleistocene Mammals from the Aegean, In: A. Strid (ed.) Evolution in the Aegean. Opera Botanica, 30: 60–70.

Sondaar, P.Y. 1977. Insularity and its effect on mammal evolution, In: M.N. Hecht, P.C. Goody, and B.M. Hecht, eds., Major patterns in vertebrate evolution, New York: Plenum Publishing Corporation: 671–707.

Sondaar, P.Y. and G.J. Boekschoten. 1967. Quaternary mammals in the south Aegean island arc with notes on other mammals from the coatal regions of the Mediterranean, I/II. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B, (7): 556–576.

Symeonides, N. and P.Y. Sondaar. 1975. A new otter from the Pleistocene of Crete. Annales Gιologiques des Pays Hellιniques, 27: 11–24.

Weesie, P.D.M. 1982. A Pleistocene endemic island form within the genus Athene: Athene cretensis n. sp. (Aves, Strigiformes) from Crete. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam, Series B, Volume 85: 323–336.

Weesie, P.D.M. 1987. The Quaternary avifauna of Greece, Thesis, Utrecht.

Willemsen, G.F. 1980. Comparative study of the functional morphology of some Lutrinae, especially Lutra lutra, Lutrogale perspicillata and the Pleistocene Isolalutra cretensis. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Amsterdam, Series B, Volume 83: 289–326.