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The endemic Pleistocene deer of Crete

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CONTENTS

Abstract

On the island of Creta there are numerous localities with remains of endemic Pleistocene deer. These fossils show a remarkably broad morphological variation, which cannot be ascribed to one or two species, as is done in previous studies.

Only in a few localities the material is sufficient for a biometrical study. Differences of a more typological nature can be established on the basis of skull and antler morphology and certain characteristics of the P^2 and the wear pattern of the teeth.

Skeletal material of limbs lets us recognize six different size categories; together with other characters, as skull morphology, it was possible to recognize eight morphotypes, which might be considered as species.

Only for the smallest species, *Candiacervus ropalophorus* n. sp. do we have sufficient material from one locality – Gerani 4 – for a fairly complete variation range to be established for the correct combination of skull, dentition, antlers and post-cranial elements. The two existing species, *C. cretensis* and *C. rethymnensis*, can be linked to two other morphogroups of the post-cranial elements by means of their lectotype and holotype, respectively. The material of the other morphotypes are too poor, that for the time being we will use an open nomenclature: *Candiacervus* IIa, b, c, V and VI.

Nearly all taxa of the Cretan Pleistocene faunas are strongly endemic, but by accepting the models of phylogeny of Mayhew, 1977 on the mice, Kuss, 1975a on hippos and elephants (Kuss, 1973) we can compose a tentative range chart for a fair number of localities and their faunal associations.

It follows that the evolution of the deer cannot be fitted into a simple lineage. We suppose that there were at least two successive invasions by mainland deer, the second of which was followed by a radiation to different species, which probably occupied different biotopes on the island.

No particular mainland ancestor can be indicated, but probably *C. rethymnensis* was morphologically closest to the ancestral stock(s). The radiation led to smaller species with more massive limb bones (*C. cretensis*, *C.* II, *C. ropalophorus*) as well as to larger forms with very slender extremities (*C.* V and VI). It is remarkable that at certain times many of these species lived together; for instance in the deposits of the locality Liko we found remains of six different species.

After the number of species had declined, the last Cretan deer, *C. ropalophorus*, probably became extinct through competition with domestic animals introduced to the island by early Man. Shortly afterwards the last endemic Cretan mouse, *Mus minotaurus* disappeared as well.

I. Introduction

This is the second part of the author's study of the endemic Pleistocene deer of Crete. In Part I the size variation and morphology of the post-cranial skeleton were treated (De Vos, 1979).

The present paper consists of two parts, originally planned (De Vos, 1979, p. 60) as Part II (Cranial morphology) and Part III (Systematics, evolution and general conclusions).

Pleistocene mammals from Crete have been described by Bate (1905, 1907), Simonelli (1907, 1908), Kuss (1965, 1966, 1970, 1973, 1975a and b), Accordi (1972), Kotsakis *et al.* (1976, 1979), Mayhew (1977) and Malatesta (1980). It was Sondaar (1971, 1977) who drew attention to the unbalanced character of this endemic island fauna: in other words particular groups of animals such as deer, hippos, elephants and murids are present, whereas other groups, such as carnivores are absent. Generally one finds extreme radiation in a limited number of genera in island faunas. "Darwin's finches" from the Galapagos Archipelago are a classic example. Crete was not the only island with an unbalanced Pleistocene fauna. A survey of unbalanced island faunas has been given by Sondaar (1977).

Mainland faunas, which are balanced, contain species belonging to different orders, families and genera, and therefore the fossils from a single locality are not difficult to distinguish. Even when there are more species of one genus, it is usually possible to separate them easily by size and morphology.

Unbalanced faunas on the other hand consist of several species belonging to a limited number of genera and it is often difficult to separate the various species of a single genus. Material collected from one level in a locality on an island sometimes shows a large variation in size and morphology, which far exceeds the variation of mainland species. In such cases it is often impossible to delimit separate groups. A good example of this phenomenon is *Myotragus balearicus* Bate, 1909, a Pleistocene bovid from the Son Muleta cave, Mallorca. With regard to its great variability Sondaar (1977, p. 692) stated: "It is not clear whether we can explain this variation as an example of an extremely variable species or whether we are simply unable to recognize different forms in that material".

Similar wide variation in size and morphology is found in the deer material from one locality and from one level at several localities on Crete. De Vos (1979) concluded that as far as the post-cranial skeletal elements are concerned, there are at least six size groups. Up to four size groups have been found together (Liko). But as the adjoining size groups show overlap, it is not always possible to classify individual specimens. We encounter the same problem in the dental elements, skulls and antlers. With reference to the method of grouping, Sondaar (1977, p. 694) already stated that the classical method used to distinguish the mainland species, which is generally based on size, will not be particularly useful for classifying the island forms. For our Cretan deer we shall therefore adopt the following approach.

Firstly, in Chapter III, the variation in the various elements will be described and a number of morphotypes will be distinguished in our skull, antler and dental material. The combination of some of the morphotypes is immediately evident from more or less complete skulls with dentition and/or antlers. In order to make a logical combination of the morphotypes on the basis of isolated cranial parts and the size groups of the post-cranial elements (De Vos, 1979), we shall use the relative abundances of the different morphotypes per locality (Chapter IV). In this way we can assess the taxonomic value of our morphological and size criteria (Chapter V). The resulting combinations are the basis for the distinction of the different species (Chapter VI). In Chapter VII we discuss the biostratigraphy and in Chapter VIII-1 we give a successive faunal picture. In Chapter VIII-2 we discuss the origin of the Cretan deer and in Chapter VIII-3 the speciation.

II. Localities, material, terminology and measurement

II-1. Localities and material

In this paper the cranial parts from the following localities will be described: Gerani (Ge) 2, 4, 5 and 6, Sourida (SO), Mavro Mouri 4c (MV4c), Liko (li), Rethymon fissure (RES) and Gumbes lb: see table 1. Data concerning the material from Sphinari, Kutri, Ravduka, Tripiti, Gonia, Caves between Chania and Souda, Stavros localities, Katholiko, Cape Maleka 1, 2 and 3, Marathi, Melidoni, Exopolis, Gerani 1, 3, Bate cave, Mavro Mouri 1, 2, 3, 5, 6, 7, 8, Simonelli cave, Gumbes 2 (= Grida Avlaki), 3, Panajia 1, 2, Skaleta, Peristeri, Bali 1 and 2, Kalo Chorafi, Milatos 1, 2, 3 and 4, Katharo, Sitia, Kharoumes 1, 2, 3, 4, 5, 7, Kato Zakros and Xeros are taken from the literature.

All localities mentioned above have already been described by earlier authors (Bate, 1905; Kuss, 1965, 1970, 1973; Mayhew, 1977; Kotsakis *et al.*, 1979). For detailed information the reader is referred to these publications. The location of the sites mentioned in this paper is given in fig. 1.

In the course of our investigation it became apparent that different size-groups and morphotypes can be distinguished. Not all groups are present at each locality. The relative abundance of the individual groups differs from one locality to the other. The different groups will be described in most cases only from those localities at which they are abundant. Measurements for localities from which there is little material can be obtained from the author on request.

II-2. Terminology and measurements

The presence of decidious teeth indicates that much of the cranial material we collected originates from juvenile animals. Only specimens of recognizably full-grown animals will be dealt with. An exception will be made for the spikes.

Dentition

The terminology for the dental elements, the parameters and the way these were measured are from Heintz (1970). The results of the measurements are given in tables 2–6. Some parameter combinations are given in scatter diagrams (figs. 2–4).

Three age groups are distinguished on the basis of the wear patterns of the molars (Bemmel, 1949):

– early adult (young) animals; to this group belong teeth which show no or little wear. The dentine pattern in such unworn molars consists of four crescents, surrounded by enamel. With a little wear the dentine of the paracone makes contact with that of the metacone, while at the anterior side the dentine of the protocone is connected to that of the paracone. At the posterior side the dentine of the hypocone is connected with that of the metacone;

- middle-aged animals; in this group the dentine of the protocone is connected to that of the hypocone;
- old animals; this group includes teeth in which the enamel islets of the molars have almost or entirely disappeared.

The age-groups described above refer to the upper molars. The lower molars undergo similar age-related changes, involving the protoconid, entoconid, metaconid and hypoconid. Determination of the relative age was based primarily on the wear pattern of the M2.

Antlers

The terminology and method of measuring the antlers are given in fig. 5. The terminology is a combination of that used by Pocock (1933) and Heintz (1970). The following terms are used:

pedicle; the bony process of the skull, supporting the antler.
a1; proximal, or first anterior branch (= brow-tine).
p1; proximal, or first posterior branch.
a2; anterior branch of the p1.
p2; posterior branch of the p1.
a3; anterior branche of the p2.
and so on.
base; piece of the antler between the pedicle and the place of origin of the first tine (a1).
beam; part of the antler from which the tines grow (base + p1 + p2 + p3).
burr; ring of pearls at the proximal end of the beam.
first segment; the shortest distance between the upper edge of the burr and the upper edge of the a1.
second segment; the distance between the al and the a2.
spike; undivided snag.

The measurements of the antlers are given in the figures 5–36. Parameters of the burr (DAP = anterior posterior diameter, DT = transverse diameter) are shown in scatter diagrams figs. 6 and 7.

Skulls

The measurements of the skulls have been taken according to the method of Dornesco and Marcosi (1961). The four basic craniometrical points are defined as follows:

- basion: the medial point of the ventral edge of the foramen magnum;
- othion: the most lateral point of the occipital at the level of the temporal;
- prosthion: the rostal-ventral corner of the intermaxillary;
- zygion: the most lateral point of the zygomatic arch.

The measurements used are:

- basilar length: lenght from prosthion to the basion;
- the distance between left and right zygion;

- the height from the linea-nuchalis superior to the basion;
- anterior-posterior diameter of the orbit;
- heigth of the orbit.

From the measurements the following indices were calculated:

- index 1: basilar length/width zygomatic arch;
- index 2: height of the orbit/anterior-posterior diameter of the orbit;
- index 3: width of the occipital/height from the linea-nuchalis superior to the basion.

The measurements and indices are given in table 7 and some statistical values are shown in table 8.

All measurements were taken with Vernier callipers. In the case of the antlers the measurements of the length were taken with a measuring tape. All measurements are given in mm units, unless indicated otherwise.

Statistics

The statistical method is the same as that used by De Vos (1979). A number of symbols are the same throughout the discussion and in the tables: N = the total number of observations for some parameter or ratio; M = mean of the measurements; max. = maximum; min. = minimum; SD = standard deviation; V = coefficient of variability.

III. Morphology and biometry

III-1. Size groups and morphotypes of the teeth

III-1-a. Size groups

Tables 2–6 and scatter diagrams figs. 2–4 show the measurements of the teeth material from Liko and Gerani 4. A comparison of the measurements of the teeth from Gerani 4 with the data for the material from Liko shows that the material from Liko is significantly larger, although there is an overlap. It is apparent that:

a. in 28 out of 30 cases the minimum values of various parameters of the Liko material are higher than those from Gerani 4. They are equal for one parameter and lower for one other (tables 2–6);

b. the maximum values from Liko are greater than those from Gerani 4 for all parameters (tables 2–6);

c. the mean values of the Liko data are distinctly higher than the comparable ones for Gerani 4 in all cases (tables 2–6, 9).

The differences mentioned above, justify the recognition of different groups for Gerani 4 and Liko, on the basis of the size of the dental elements. The size group of Gerani 4 will be indicated as size group A. However, the data on the Liko material do not always form homogeneous clusters. In fig. 2 we see that four specimens clearly have a larger upper dentition than the bulk of the material. The upper dentition of the majority of the material from Liko will be indicated as size group B, while the four larger specimens are attributed to size group C. Two different size groups cannot be clearly distinguished in the lower dentition from Liko (fig. 3).

From the comparison of the upper dentition from Liko and Gerani 4 we conclude that there are three size groups for the tooth-rows, viz., A, B and C, the ranges and means of which are given in table 10.

III-1-b. Morphotypes in the P^2

Three different morphotypes can be distinguished on the basis of the shape of the protocone and hypocone:

morphotype–1: this morphotype shows a regularly rounded protocone, which is roughly the same size as the hypocone (Plate I, a);

morphotype–2: this morphotype shows a regularly rounded protocone, which is smaller than the hypocone (Plate I, b);

morphotype–3: this morphotype shows a bilobate protocone, which is similar in size to the hypocone (Plate I, c).

III-1-c. Wear pattern of the teeth

Two types of wear pattern are distinguished in the mandibles of middle-aged animals:

1) a wear pattern which results in a flat occlusal surface (Plate II), indicated as the "flat wear pattern";
2) a wear pattern which emphasizes a distinct relief, formed by two transverse ridges running over the main conids on the occlusal surface (Plate III). This will be indicated as the "lophodont wear pattern".

III-1-d. Cingulum

Some specimens have a weak cingulum (Plate IV, a), while others have a strong one (Plate IV, b).

III-2. Morphological types of antlers

Five types of fully grown antlers can be distinguished:

antler type 1 (Plate V; fig. 8)

This antler type is characterized by a bludgeon-shaped beam which bears only the sub-basilar brow-tine (al).

antler type 2 (Plate VI; fig. 9)

This type resembles antler type 1, but it has no bludgeon-shaped distal end of the beam. (The figured specimen is broken at the distal end, but broken specimens from Liko cannot have possessed a bludgeon-shaped distal end, because such ends have not been found at this locality).

antler type 3 (Plate VII; fig. 10)

This type of antler is characterized by two tines next to each other, at the position of the brow-tine.

antler type 4 (Plate VIII; fig. 11)

This type of antler is characterized by having a beam with more tines.

antler type 5 (Plate IX)

This type of antler is characterized by a supplementary tine just above the burr. This supplementary tine always arises at the frontal side. (The figured specimen comes from a layer from Liko, deeper than the layer of 75 cm. This is why this specimen is not discussed in this paper. No specimens of this type are available in our collection from the layer of 75 cm in Liko and other localities excavated by us.

III-3. Size and morphotypes of the skulls

Four types of skulls can be distinguished.

Skull type a (Plates X and XI).

All thirty-nine skulls from Gerani 4 belong to this type. The male skulls can be distinguished from the female skulls by the presence of antlers or pedicles. There are 17 more or less complete male skulls and 22 of females. In 16 of the male skulls the antlers have been shed, in one specimen (Ge4–15) the proximal part of the antlers are still attached to the pedicles. Most of the skulls, male as well as female, lack the pre-maxillaries and the jugals.

The measurements of the distance from linea-nuchalis superior to the basion in male skulls are given in tables 7 and 8. Furthermore, the male skulls are characterized by the thick dorsal rim of the orbit. The orbit of skull type a is more or less rounded.

The male skulls show some remarkable characters when compared to the skulls of recent and fossil cervids from the mainland:

- the strong convexity of the frontals between the orbits;
- the rapid narrowing of the snout between the orbits and infra-orbital foramina;
- the small size of the pre-orbital vacuities;
- the small size of the gland pits;
- the cruciform nasals;
- the large supra-orbital foramina;
- the thick rim of the dorsal orbital wall;
- the absence of canines;
- the round orbitae.

These characters are also shown in the material described by Simonelli (1908), Kuss (1965, 1975b) and Malatesta (1980). Kuss (1975b) considered these characters to be general features of all Cretan deer, probably because his descriptions were based mainly on skull material from Gerani 4. However, as will be shown below, other skull types are present in the Cretan deer as well.

The uniformity in morphology and measurements (table 7) of the material from Gerani 4 is striking. Skull parameters and measurements are given in tables 7 and 8. The value of index 1 indicates that the female skull is more slender than the male skull, which is a common feature in cervids.

The following three types could only be distinguished in male skulls. They all differ from type a skulls by their larger size (table 7), but types b, c and d are of the same size. However, these types differ in their morphology on some points.

Skull type b (Plate XII)

Of this type there is only one specimen present (Li-757), originating from Liko. It has the same morphology as skull type a, but it is a little larger.

Skull type c (Plate XIII)

Of this type there is only one specimen (Li-758), again originating from Liko. It is characterized by the dorsal rim of the orbital wall, which is intermediate in thickness between the previous type (b) and the following type (d).

Skull type d (Plate XIV)

Of this type there is again only one specimen from Liko (Li-759). It is characterized by the dorsal rim of the orbital wall, which is not pronounced. Furthermore the orbit is oval in shape with the longer diameter in anterior-posterior direction.

IV. The material and relative abundance of the different morphotypes in the localities

IV-1. Gerani 4

The material from the upper 40 cm of this locality (De Vos, 1979, p. 61) has been used for our investigation.

The following size-groups and morphological groups are present (Table 11).

- one type of skull; type a (100%, N = 17);
- two sizes of teeth; size group A (98%, N = 69) and size group B (2%, N = 1);
- two morphotypes of P^2; type 1 (98%, N = 58) and type 2 (2%, N = 1)
- two types of antlers, type 1 (98%, N = 56) and type 2 (2%, N = 1).

IV-1-a. Skulls

All the male skulls belong to type a. The special characteristics of the skulls have been given in Chapter III-3.

IV-1-b. Dentition

The bulk of the dental material (98%) belongs to size A. The tooth-rows attributed to size A have a P^2 of morphotype-1. The measurements of the upper tooth-row are given in table 2 and in the scatter diagram of fig. 2. The measurements of the isolated upper molars are given in table 4. The molars become larger towards the rear.

The occlusal surface is flat in middle-aged animals. The styles and pillars are weakly developed. A weak cingulum is present at the base of the crown of the molars at the lingual side, visible at the antero-lingual side (= protostyle); sometimes it disappears at the level of the protocone, but appears again in the valley between the protocone and the hypocone, forming an entostyle. The cingulum is sometimes absent below the hypocone, but, if present, it appears at the posterior lingual side. When there is a cingulum, it is usually most strongly developed on the M^1. At the occlusal surface there is no pli-prefossette. The pli- postfossette of the hypocone is always present in unworn molars, but varies in size.

The measurements of the premolars are given in table 3 and the scatter diagram of fig. 4a shows them for the P^2. Between the protocone and hypocone of the P^2 there is generally a valley extending from the wear surface to about 2 mm above the root.

The morphology of the labial wall of the P^3 is not symmetrical, because the paracone runs downwards oblique to the anterior side. The lingual wall consists either of two cusps (protocone and hypocone) or of one (the protocone). The hypocone, if present, is always weaker than the protocone. Sometimes a weak and crenulated cingulum is present at the antero-lingual side of the crown.

Contrary to the morphology of the labial wall of the P^3, the labial wall of the P^4 is symmetrical, because the pillar of the paracone runs straight downwards. The lingual side always consists of one cusp, the protocone. At the base of the crown a very weak and crenulated cingulum is sometimes present at the lingual side.

The measurements of the lower rows are given in table 2 and in scatter diagram fig. 3. The measurements of the isolated lower molars are given in table 6. The occlusal surface of middle-aged animals is flat. In old and very old animals we notice a relief on the occlusal surface. The ectostylid is developed at the lingual side of the molars. There is no tubercle between the hypoconid and the third lobe of the M_3, and no cingulum at the base of the crown.

The measurements of the isolated lower premolars are given in table 5. The P_2 is triangular and can easily be distinguished from the P_3 and the P_4. The P_2 is slightly smaller. Its paraconid and parastylid are fused to form one cusp. The hypoconid is separated from the protoconid by a very weak groove. The P_3 is not molarized. Different stages of molarization were observed in the P_4. An unmolarized P_4 can be distinguished from the P_3 by the more strongly developed metaconid. In some P_4 the second valley is open, just above the base of the crown, but in others it is totally closed, due to the expansion of the metaconid. In such teeth, the anterior part is molarized. Also the third valley may be open from the top of the P_4 to half-way down the crown; in other teeth the third valley is closed due to the expansion of the metaconid. In such cases the posterior part of the P_4 is molarized. When both the second and the third valley are closed, the P_4 is considered to be completely molarized. The anterior part of the P_4 is rather frequently molarized. The entoconid and the ectostylid are fused at the lingual side at the top of the P_4, so that the position of the fourth valley is recognizable as an islet.

The Gerani 4 material of dentition size A is very uniform in morphology and belongs to one natural group. This is supported by the fact that in 25 out of the 30 variation ranges the value of the coefficient of variability lies between 2 and 8 (see tables 2–6). According to Simpson *et al.* (1960) such values may safely be accepted as indicating material derived from a single population.

Dental material attributed to size B

Two partial tooth-rows are attributable to size B, viz., Ge4-3015 and Ge4-193.

Specimen Ge4-3015 is a maxillary fragment with only premolars retained. This specimen differs also from the rest of the dental material in its type of fossilization; it is somewhat darker in colour. The P^4 is damaged. The size of the premolars, in particular their width, is larger than in the premolars of size group A and the cingulum is better developed. The measurements of the dental elements are given in table 12 and of the P^2 again in the scatter diagram of fig. 4a. Table 13 shows that this P^2 differs significantly in both size parameters from the P^2 of size group A. The P^2 has a reduced protocone (morphotype-2). For the P^3 the 95% level of significance (table 13) is only reached for the width.

Specimen Ge4-193 is a mandible ramus, in which the P_2 is missing. According to the degree of wear of the teeth, it is from a middle-aged animal. The measurements of the dental elements are given in table 12. The teeth differ significantly in size from those of size A (table 13), except for the length of the P_3. While the wear surface of the teeth from mandibles of comparable relative age in size group A are flat, the teeth of specimen Ge4-193 show a lophodont wear pattern.

IV-1-c. Antlers

– Spikes

There is one complete spike with a length of 59.6 (Ge4-3515), which is still attached to the pedicle, broken off from the frontal. There is no burr, but instead there are ridges running parallel to the axis of the spike. At this level the cross section is oval, with the longer diameter in antero-posterior direction (DAP = 14.4; DT = 11.8). Towards the distal end the spike becomes more flattened in medial-lateral direction.

Two proximal spike fragments are present. One, Ge4-3514, has a length of 1 cm, the other, Ge4-3517, a length of about 2 cm. Both are still attached to the pedicle and have no burr, but instead have ridges running parallel to the axis of the spike, like specimen Ge4-3515. The cross section is again oval, with the longer diameter in antero-posterior direction.

Six spikes (Ge4-3504, 3507 and 3510-3513) have the same morphology as the preceding ones, but have been shed. In most cases the distal ends of these spikes are broken or chewed off some 4-20 cm above the ridges. The cross section of the proximal ends of these spikes is oval, with the longer diameter directed anterior-posteriorly. The diameters of the smallest spike (Ge4-3507) are: DAP = 13.6; DT = 12.4. The same dimensions of the proximal end of the largest spike (Ge4-3512) are: DAP = 17.2 and DT = 16.4.

Three proximal spike fragments, which are shed, possess a real burr. These spike fragments are: Ge4-3506, with a length of 52.1, Ge4-3508 with a length of 72.6 and Ge4-3509, with a length of 98.4. In all three specimens the burr is damaged, so it is not possible to give reliable measurements.

– Antlers and antler fragments attributed to antler type 1

This type is best represented in Gerani 4 by specimen Ge4-2870 (Plate V and fig. 8). It is an antler with a long beam (77 cm). The brow tine arises from the beam at a distance of about 9 cm from the burr. The burr is oval in cross section, with the longer diameter in anterior-posterior direction. The cross section of the first segment is oval with the larger dimension in a medial-lateral direction. The a1 is broken off at about one cm from its base; it forms an angle of about 90° with the base of the beam. Above the a1 the p1 bends backwards and immediately forwards again. The distal part of the p1 therefore is parallel to the base of the antler, which gives the antler a straight appearance. Just above the al the p1 is fairly round. The p1 becomes more flattened towards the distal end, and the last 20 cm part of the p1 is bludgeon-shaped.

There is only one specimen (Ge4-2886) with a complete brow-tine. However, its p1 is broken off at about two cm above the a1. The burr has an oval shape. The angle between the brow-tine and the base of the beam is 108°. The brow-tine first bends outwards and then inwards; it points a little upwards. The brow-tine is rounded in cross section.

The antler fragments Ge4-2872 through 2906 consist of a burr, part of the brow-tine (a1) and part of p1. The burr is in all cases oval, with the longer diameter in anterior-posterior direction. The smallest burr occurs in specimen Ge4- 2891 (DAP = 30.7; DT = 30.5); the largest in specimen Ge4-2892 (DAP = 47.0; DT = 43.2). The length of the first segment varies between 68.8 (Ge4-2874) and 111.8 (Ge4-2906) and has a mean of 87.9 (N = 35). The diameter of the basal part of the a1 in medial-lateral direction is the same as the diameter of the beam in medial-lateral direction. In most cases the p1 is broken off at a short distance from the a1, with the exception of the specimens Ge4-2871, 2872 and 2904, in which the lengths are 40, 25 and 16 cm, respectively. About half of the antlers show ridges perpendicular to the longer axis at the tips of the a1 and p1.

In addition to proximal antler fragments, we also found distal, bludgeon-shaped fragments. Most of them are very small, with the exception of a few large and remarkable ones. These are:

Ge4-3519: This fragment 32 cm long is oval at the proximal end and strongly flattened medially-laterally at the distal end. DAP distal = 46.4; DT distal = 22.4; DAP proximal = 31.7; DT proximal = 20.0.

Ge4-3521: length = 28 cm; DAP distal = 18.4; DT distal = 23.9; DAP proximal = 36.2; DT proximal = 24.0.

A few distal fragments show the bludgeon shape as well as a wavy appearance. Such waves have possibly been caused by the lack of some micronutrient. Examples of such specimens are:

Ge4-3522 (fig. 12; the measurements are given in the figure) and specimen Ge4-3518. The length of the latter specimen in straight line is 38 cm. The undulating part is flattened medially-laterally. The distal DT of the bludgeon-shaped end is 50.2; DAP distal is 29.8. The proximal end has a DAP of 26.6 and a DT of 21.4.

Finally we mention a part of a beam with a length of 52 cm, from which both proximal and distal ends are missing. The beginnings of a bludgeon shape are faintly present at the broken distal end.

– Antler attributed to antler type 4

The antler Ge4-2909 (fig. 13) differs from all the other specimens from Gerani 4 by the presence of an a2 and by its type of preservation: it is somewhat darker in colour. The burr is damaged. The brow-tine is broken off or chewed off at about two cm from its lower end. The diameter of the base of the p2 is a little smaller than that of the a2. Both p2 and a2 are broken off or chewed off at about one cm from their base. The p1 is flattened in lateral-medial direction.

– Burrs

The scatter diagram of fig. 6 gives the measurements of the burrs. The shape of the burrs is generally oval with the larger dimension in anterior-posterior direction.

– Material from Gerani 4, mentioned by Kuss

Kuss (1973) mentioned that he had collected material from Gerani 4. In 1975 he described and figured some of his specimens. The basis for his description of the skulls were three male and two female specimens. From description and figures we may conclude that the skulls belong to our skull type a. Of the antlers he figured only one specimen (p.77, fig. d) the morphology of which consists of a beam with only a brow-tine. The distal end of the beam is missing. The morphology of this antler is similar to that of our antler type 1 (or 2).

IV-1-d. Combinations

The majority of our Gerani 4 material permits us to make the following combination of types. This combination gives a fair estimate of the nature of one of our species.

Skull type a possesses antlers of type 1 and upper tooth-rows of size A with a P^2 of morphotype-1. The wear pattern of the teeth is flat and the cingula are weak.

IV-2. *Liko*

The material from the uppermost 75 cm of the locality Liko has been used for our investigation.

The following size-groups and morphological groups are present (table 11).

- three types of skulls; b, c and d;
- two sizes of teeth; B and C. For size B the P^2 belongs to morphotype-1; in size group C we found morphotypes 1 and 3;
- three types of antlers; 2, 3 and 4.

IV-2-a. Skulls

Three male skulls (Li-757, 758 and 759) and two female skulls (Li-756 and 760) are available. The males are distinguished from the females by the presence of antlers or pedicles. All three male skulls from Liko are of similar size, but they are slightly larger than those from Gerani 4 (table 7). The two female skulls fall within the range of variation of the ones from Gerani 4 (table 7) and are similar in morphology. However, the male skulls differ in certain characters from the Gerani 4 specimens as well as from each other, so that the three specimens are thought to belong to three types (b, c and d) (see pp. 13 and 14).

Specimen Li-757 (skull type b; Plate XII)

This specimen represents a middle-aged animal and is complete, except for the tip of the left premaxillary, the jugal and the rim of the left orbit. The distance from the linea-nuchalis superior to the basion is 60 in this Liko specimen, while in the Gerani 4 material the range of this dimension is 50.0-57.8

(N = 13). Furthermore, the Liko skull can be distinguished by the thickness of the orbital wall, which is 14.8 (which is 24% of the linea-nuchalis to the basion distance, as against 11% as an average for the Gerani 4 specimens). In this character it is also different from both other Liko types. The orbit is more or less circular (index 2 = 0.94).

The tooth-rows of size B are preserved. The length of the left P^2–M^3 is 67.4 and of the right P^2–M^3 67.8. The wear pattern of the teeth is flat. The protocone and the hypocone of the P^2 are of similar size (morphotype-1). The cingulum is weak.

Antler fragments are preserved on the pedicles. Of the left antler it is only a part of the base that is preserved. The right antler consists of a burr, which is damaged; a base with a length of 82; an a1 and p1, which are both broken off at about 2 cm from their base. The antlers are thought to belong to antler type 2, because no bludgeon-shaped distal ends have been found at Liko.

Specimen Li-758 (skull type c; Plate XIII)

This specimen is from a middle-aged animal. Part of the posterior edge of the palate, the dorsal and posterior parts of the left orbit wall and the anterior part of the snout are missing. The distance from the linea- nuchalis superior to the basion is 64.3. The rim of the dorsal orbit wall is thicker (6.0, which is 9% of the distance from the linea-nuchalis superior to the basion) than it is in the next skull, but thinner than the previously discussed skull. The thickness of the rim falls within the range of variation of the thickness found in the specimens from Gerani 4. The orbit is nearly circular (index 2 = 0.97).

Only the right M^2 and M^3 are present; they are of size B. Of the premolars and other molars only the alveoli can be observed. The length of the M^2 is 13.4; the length of the M^3 is 15.2. These two teeth are more or less lophodont, the paracone and the protocone as well as the metacone and the hypocone form transverse ridges. The cingula are weak.

The left antler is still attached to the pedicle, the right antler is missing. The left antler has two tines lying in a horizontal plane at the normal position of an a1. The anterior-posterior diameter of the burr is 49.0; the transverse diameter is 51.0; the length of the first segment is 62. The outermost of the two sub-basilar tines bends medially and is broken off at about 3 cm from its base. The inner tine bends medially and dorsally. The tip of this tine, which has a length of about 9 cm, has been chewed. The p1 bends caudally and is broken off at about 10 cm above the sub-basilar tines. This antler is referred to our antler type 3.

Specimen Li-759 (skull type d; Plate XIV)

This specimen is from an old animal and is fairly complete. It lacks the anterior part of the snout, the right jugal, the dorsal part of the left orbital wall and there is a hole in the right maxilla. The distance from the linea-nuchalis superior to the basion is 63.6. The rim of the dorsal orbital wall is very thin, 3.4 (this is 5% of the distance from the linea-nuchalis superior to the basion). The shape of the orbit is more or less oval, with the longer diameter in anterior-posterior direction (index 2 = 0.85).

Of the dentition only the right series P^2–M^1 is preserved, but the teeth are so worn that it is impossible to see their grinding type or to which morphotype the P^2 belongs. The teeth belong to size B; cingula are not visible.

Antler fragments are present on both pedicles. The right antler fragment consists of a burr with pearls, a base, a1, p1, a2 and p2. The a1 and a2 point anteriorly and lie in the same plane. The antero-posterior diameter of the burr is 37.6; the transverse diameter is 40.9. The length of the first segment is 81.4. The a1, which is sub-basilar makes an angle of 90° with the beam. The base of the a1 is slightly oval with the longer dimension in anterior-posterior direction. The a1 bends slightly medially. The end of the a1 is missing. The length of the second segment is 80. The a2 is broken off at a distance of 20 from its base. The p2 is broken off at its base. The first segment is oval in cross section with the larger dimension in medio-lateral direction. The total length of the right antler fragment is 170.0. The left antler fragment is similar in morphology. The antero-posterior diameter of the burr is 40; the transverse diameter is also 40; the length of the first segment is 88.2; the length of the second segment is 73.9; the total length is 170.0. The a1 (length 50) is chewed at the end; the a2 and p2 are broken off at about 2 cm from their base. These antlers are referred to antler type 4.

IV-2-b. Dentition

All the dental material is attributed to size B, with the exception of the tooth-rows of four maxillaries, which are attributed to size C. The P^2 of size B have morphotype-1.

The four deviating maxillaries are:

– The tooth-rows P^2–M^3 sin. and dex. (Li-763 and 764), originating from one individual. They are relatively large (length P^2–M^3 of specimen Li-763 is 85.2; that of specimen Li-764 is 88.8; see scatter diagram of fig. 2 and table 10). The wear surface is not flat, but more or less lophodont. The protocone of both P^2 is bilobated; the hypocone is well developed (morphotype-3). The cingulum of the premolars and molars is very weak.

– The tooth-rows P^2–M^3 sin. and dex. (Li-2046 and 2047), again belonging to one individual. They are relatively large (length P^2–M^3 of Li-2046 is 90.0; that of Li-2047 is 89.0; see fig. 2). The premolars and molars possess well-developed cingula. There is a well-developed protostyle on the M^3. The P^2 are bilobate, in this case the protocone and hypocone are of similar size (morphotype-1).

The measurements of the lower tooth-rows of Liko are given in table 2 and in scatter diagram of fig. 3. Although the coefficient of variability is higher than 8 for the lower dentition in 12 out of 15 cases, it is not possible to distinguish two distinct groups. There is however a tendency towards a flat wear surface in small tooth-rows, whereas in the larger forms the surface is more or less lophodont.

IV-2-c. Antlers

– Spikes

Specimens Li-2610 through 2614 (fig. 14) and Li-2617 are six proximal spike fragments, which are still attached to their pedicles. The distal parts of the spikes show ridges perpendicular to the axis of the spike. At the position where normally a burr can be expected, ridges of pearls occur parallel to the axis of the spike; the cross section of the spikes just above the pedicle is oval, with the longer diameter in antero-posterior direction. The dimensions of the largest spike (Li-2617), measured just above the pedicle, are 20.4 for the anterior-posterior diameter and 20.2 for the transverse diameter.

17 specimens (Li-2615-2616, Li-2618-2629, Li-680, Li-681 and Li-683; Li-2627 is shown in figure 15) have the same morphology as the preceding ones, but have been shed. The distal parts of these spikes are in most cases broken off or chewed off a few cm (3–13) above the ridges. The dimensions of the smallest spike Li-2620 are: DAP = 12.6; DT = 9.8. For the largest spike (Li-681) these measurements are DAP = 24.6; DT = 20.6.

Spikes Li-2630 through 2636 and Li-682 have a real burr. In most of these spikes the distal ends are broken off or chewed of a few cm (5-12) above the burr. The dimensions of the burr of the smallest spike (Li-2632) are: DAP = 24.8 and DT = 23.4. Spike Li-2636 (fig. 16) is exceptionally large with a length of 160, measured in straight line. Towards the distal end this spike is flattened in medial-lateral direction.

Specimen Li-670 is a spike provided with an accessory front tine. The beam has a length of 160. At a distance of 125 from the burr there is an accessory bud at the anterior side (DAP of the burr is 37.1; DT is 31.6).

– Proximal antler fragments Li-637 through 640, 642 through 679 (without Li-643, 657, 670, 677) and 2518 through 2583 (total 104 specimens) consist of base, a1 and p1. The diameter of the base of the a1 is about the same as the diameter of the basal part of the p1. The distal end of the p1 is mostly broken off or chewed off a few cm above the a1. The p1 bends caudally. As an example of the morphology Li-638 is figured (fig. 17). All other specimens are morphologically identical to Li-638, but they vary in size. The specimen with the smallest burr is Li- 2554 (DAP = 27.8; DT = 25.2), that with the largest burr Li-2569 (DAP = 53.6; DT = 47.1). The length of the first segment varies from 62.3 (Li- 652) to 124.2 (Li-673). The p1 is extremely long in specimen Li-2581, namely 27 cm. The angle which the a1 makes with the base of the beam varies between 90° and 125°.

There are 12 specimens (Li-2584 through 2597, without Li-2593 and 2595) in which the a1 has a lateral position on the base of the antler. In these specimens the diameter of the a1 is half the diameter of the base of the antler. As an example of the morphology Li-2585 is figured (fig. 18). The eleven other specimens show the same morphology, but vary in size. The specimen with the smallest burr is Li-2584 (DAP = 34.4; DT = 30.9), the one with the largest burr is Li-2588 (DAP = 47.6; DT = 40.4). The length of the first segment varies from 69.5 (Li-2584) to 100.0 (Li-2588).

There is one specimen (Li-2595, fig. 19) in which the end of the a1 bifurcates into two small tips, which are situated in a horizontal plane relative to the beam. The p1 bends backwards and medially. The diameter of the a1 is the same as that of the base of the antler.

There is one more specimen Li-669 (fig. 20) of which the a1 shows a bifurcation at its tip; here the points are situated in a vertical plane relative to the beam. The distal end of the p1 bends backwards.

– More complete antlers consisting of a beam provided with a sub-basilar brow-tine (a1), which can be attributed to antler type 2.

Antler type 2 is best represented by specimen Li-2593 (fig. 9, Plate VI). This antler is one of the largest in the collection from Liko. The beam is lyre-shaped. It is oval in cross section over its entire length; its proximal part has the larger diameter in medial-lateral direction, while at the level of attachment of the a1, the larger diameter is antero-posterior. The brow-tine points upwards and inwards; it arises from the outside of the beam; its tip is chewed off. The p1 bends backwards and then immediately forwards.

Specimen Li-657 (fig. 21) is a simple fork. It shows a beam, which is lyre-shaped. At 90 above the burr a brow-tine (a1) is present. Just above the brow-tine the p1 curves backwards and then forwards again. The p1 is round in cross section over its entire length. The burr is damaged, so no measurements could be taken.

Specimen Li-641 is a right simple fork. The burr is damaged. The morphology is similar to that of specimen Li-657.

Specimens Li-635 and 636 originate from the same individual. Both antlers are attached to the pedicles with parts of the frontalia preserved. The left antler Li-635 consists of a beam, which is rather straight. At the level of 109.5 above the burr there is a brow-tine, which points upwards. The p1 curves slightly backwards and forwards at the level of the brow-tine.

The right antler Li-636 is similar in morphology. The angle made by both beams is 100°.

There are two straight pieces of beams, Li-2597 and 2596, with a length of 42 and 47 cm, respectively.

– Antlers with the a1 sub-divided into two tines, lying in a horizontal plane, attributed to antler type 3.

This type of antler is best represented by specimen Li-686 (fig. 10, Plate VII). This specimen is one of the larger antlers in the material. The outer tine of the a1 bends upwards and then inwards. The inner tine of the a1 is broken off at about 10 cm from its base. The outline of the cross section at the base of the beam is convex at the caudal side and concave at the anterior side. The p1 bends slightly backwards. The p2 is accessory. The distal part of the p1 is flattened in medial-lateral direction. The a2 makes an angle of 136° with the p1. Towards the distal end the a2 is flattened in medial-lateral direction, and it ends in a point.

Specimen Li-688 (fig. 22). This antler is of a young animal, inferred from the measurements of the burr. Both tines of the a1 are broken off at 10 from their base. The p1 bends backwards and medially. The p1 is chewed off at 50 above the a1.

Specimen Li-687 (fig. 23). The outer tine points upwards, the inner tine forwards. The p1 bends backwards and is broken off at about 70 above the a1.

Specimen Li-2607 (fig. 24). This antler fragment consists only of the double a1 and a part of the p1. Both tines point upwards, the innermost tine is slightly damaged. The p1 is broken at 90 above the a1. The p1 is laterally flattened.

Specimen Li-2608 (fig. 25). The outline of the cross section of the base is convex posteriorly and concave at the frontal side. The outer tine of the a1 makes an angle of 90° with the base of the beam; the distal end is chewed off at the tip. The inner tine of the a1 is very small. The p1 is broken off just above the a1.

Specimen Li-2609 (fig. 26) consists only of a small part of the beam and the sub-divided a1. Both tines curve laterally and then medially.

– Antlers, consisting of at least a1, p1, a2 and p2, attributed to antler type 4.

This type is represented best by specimen Li-684 (fig. 11 and Plate IX). It is a rather small antler. The beam curves slightly caudally. The a1, which is placed laterally on the beam, is pointing upwards and medially. The a2 and a3 are broken off at their bases. The p3, which is in line with the p2, bends slightly caudally.

Specimen Li-643 (fig. 27). The beam is lyre-shaped. The burr is damaged. The brow-tine makes an angle of 90° with the base of the beam. It points a little inwards and is broken off at 60 from its base. The p2 is accessory. The a2 is chewed off at the tip. The a2 seems to be a continuation of the p1. Above the burr the beam is oval, with the larger diameter in medial-lateral direction; above the a1 the beam remains oval in cross section, but with the larger dimension antero-posteriorly.

Specimen Li-2603 (fig. 28). The beam is rather straight. The burr is damaged. The brow-tine points upwards and makes an angle of 120° with the base of the beam. The a2 is broken off at its base. The p2, which is in line with the p1, has a length of 30 only. The diameter of the base of the p2 is smaller than the diameter of the bases of the a2, 11 and 30, respectively.

Specimen Li-2601 (fig. 29). The beam curves backwards. The burr is damaged. The a1 makes an angle of 120° with the base of the beam and points both upwards and inwards. The distal end of the a1 is broken off at 30 from its base. The distal ends of the a2 and p2 are both broken off at about 20 mm above the diverging point. Above the burr the beam is oval in cross section along the entire length, with the longer diameter in anterior-posterior direction.

Specimen Li-677 (fig. 30). The beam curves backwards. The burr is damaged. The a1 makes an angle of 110° with the base of the beam and is oval in cross section, with the longer diameter in anterior-posterior direction. The distal end of the a1 is broken off at 20 mm. The p1 bends backwards. The p1 bifurcates into the a2 and p2. The a2 is slightly stouter than the p2. The p2 appears as a continuation of the p1. The a2 and p2 are both chewed off at their tips. The length of the remains of the a2 and p2 is about 20 mm. The base of the beam is oval with the longer diameter in medial-lateral direction. Above the a1 the beam is flattened medially-laterally.

Specimen Li-2604 (fig. 31). The beam curves backwards. The burr is damaged. The a1 makes an angle of 95° with the base of the beam. The a1 is placed laterally on the beam and points medially. The a1 is chewed off at 70 mm from its base. The p1 bends caudally and medially. It bifurcates at the distal end into an a2 and p2. The p2 is a continuation of the p1 and the a2 is pointing towards the front. The a2 is chewed off at 20 mm from its base. The beam is oval with the longer diameter in the medial-lateral direction.

Specimen Li-2600 (fig. 32). This is the distal fragment of an antler consisting of the a1, a2, p1 and p2. The distal end of the a1 is broken off at 40 mm from its base. The a1 is oval with the larger diameter in anterior-posterior direction. The p2 bends slightly caudally and is chewed off at 20 mm from its base. The a2, which is stouter than the p2, points towards the front and is chewed off at 20 mm. The p1 is flattened antero-posteriorly.

Specimen Li-2605 (fig. 33). The a1 is broken off at the base and lost. The p1 bends caudally and diverges into an accessory p2 with a length of 40 mm and an a2, the distal end of which is broken off at about 40 mm from the segregation point. The base of the beam is oval with the longer diameter in medial-lateral direction. The beam is flattened above the p1. The a1, a2, p1 and p2 are situated in the same plane.

Specimen Li-2598 (fig. 34). The beam is very straight. The burr is damaged. The a1 is broken off at the base. The p1 bends medially above the a1 and diverges into the a2 and the p2. The distal end of the a2 is broken off at 20 mm from the diverging point. The base of the a2 is much smaller than the base of the p2. The p2 diverges into the a3 and the p3. The p3 is accessory. The a3 bends towards the front. The base of the beam is oval with the larger dimension in medial-lateral direction. The p1 is flattened just below the a2, with the greater diameter in antero-posterior direction.

Specimen Li-2602 (fig. 35). The beam is very straight. The burr is damaged. The a1, broken off at its base, was situated laterally on the beam. The p1 is a continuation of the base and bends slightly medially. The p1 bifurcates into a p2 and an a2. The p2 is accessory. The a2 bends anteriorly. The diameter of the base of the a1 is about half the diameter of the basal part of the beam; the a1 arises laterally on the outside. The a2 is oval with the longer diameter in antero-posterior direction.

Specimen Li-2599 (fig. 36). The beam is rather straight. The burr is damaged. The a1 is broken off at about 20 mm from its base. The a1 is placed laterally on the beam, the diameter of the base of the a1 is about half the diameter of the basal part of the beam. The p1, which is in line with the base of the beam, diverges into an a2 and p2. The a2 is broken off at its base.

– Burrs

Six proximal antler fragments (Li-2444 through 2449) consist only of the burr with part of the base. They are still attached to the pedicle. However, these specimens are damaged in such a way that no reliable measurements could be taken.

Twenty-eight antler fragments (Li-2416 through 2443) also consist of only the burr with a part of the base. These specimens however have been shed. They are also too damaged to yield reliable measurements.

Specimens Li-689 through 713 and Li-2450 through 2517, (N = 93) are measurable. The measurements are given in the scatter diagram of fig. 7. The shape of the burrs is oval, with the longer dimension in antero-posterior direction. The specimen with the smallest burr is Li-2450 (DAP = 29.4; DT = 28.6); the specimen with the largest burr is Li-702 (DAP = 55.7; DT = 47.4).

IV-2-d. Combinations

The following combinations of types are found:

- skull type b, with antler type 2, with teeth of size B and P^2 of morphotype-1;
- skull type c, with antler type 3, with teeth of size B, morphotype of the P^2 unknown, as these teeth are missing;
- skull type d, with antler type 4, with teeth of size B.

Each of these combinations is based on a single individual.

IV-3. *Other localities*

IV-3-a. Localities represented in the collection combined with a few literature data

Mavro Mouri 4c

No skull material is available. There are 22 P^2. The scatter diagram fig. 4b shows the measurements for their length and width. There are two clusters, representing two different size classes. The existence of two size classes is supported by the values of the coefficient of variability, which exceed 8 for 15 out of 27 parameters (see tables 2-6).

In figure 4b 10 of the 22 specimens form the cluster with the smallest dimensions. These dimensions are similar to those of size group A from Gerani 4. This is in agreement with the morphology of the P^2, which is of type-1.

Twelve specimens form the cluster with the larger dimensions; they would fit in with size group B. The teeth of this cluster are not uniform in morphology. In most (8 out of 12) the morphology is of type 2. The other four (MV4c-509, 511, 512 and 546) are of morphotype-1.

There is one burr (MV4c-670), which is the largest burr discovered on Crete so far (DAP = 56.4; DT = 58.6).

Kuss (1975, p. 44) mentioned from this locality a large mandible (length of the P_2–M_3 = 86.5). Only one antler is figured by Kuss (1969, p. 146, fig. d). This antler consists of a beam with an a1, p1, a2 and p2, and corresponds to our antler type 4.

Rethymnon Fissure

No antler or cranial material is available from this locality.

Two size groups can be distinguished in the dental material. This division into two groupings is supported by the values of the coefficient of variability, which exceed 8 for 10 of the 16 parameters (tables 3-6). The scatter diagram of fig. 4b shows the dimensions of the P^2 from this locality. There are eight P^2 and one can easily distinguish two groups, each consisting of four P^2. The four smaller ones (RES-454, 455, 461 and 560) fit in with size A; they are uniform in morphology and their protocone and hypocone are of equal size (morphotype-1).

The four larger ones, of size B, are less uniform in morphololgy. In three P^2 of this cluster (RES-456, 457 and 458) the hypocone is larger than the protocone (morphotype-2) and in one (RES-459) the protocone is of the same size as the hypocone (morphotype-1).

Gumbes 1b

The material is limited to a few teeth and mandibles of size A and one mandible (Gulb-13, Plate III), which is of remarkable size and morphology. It is one of the largest mandibles in our collection. It is fairly complete, but it lacks the anterior part in front of the P_2, the dorsal part of the processus coronoideus, and also the P_2 and P_3 are missing. Of the P_4 only the posterior root is present. The length of M_1-M_3 is 54.3; this value is similar to that of the largest mandibles from Liko (table 2) and Gerani 4 (Ge4-193) (table 9). The wear pattern of the teeth is lophodont, and the horizontal ramus is high (35.1) at the level of the M_2.

Sourida

On the basis of the P^2 it is supposed that two size groups (A and B) are present (fig. 4b). There are four P^2. One is of size A and has morphotype-1; the other three are of size B and morphotype-2.

No skull or antler material is present.

Gerani 2

Teeth material of size A was found in which the P^2 are of morphotype-1. No cranial material is available. There is one antler fragment consisting of a beam with a sub-basilar brow-tine, probably corresponding to our antler type 1.

Gerani 5 and 6

In the small collections of these localities all the dental material is of size A. The P^2 are of morphotype-1. There is no skull or antler material.

IV-3-b. Localities for which the data are taken from the literature

Simonelli Cave

Accordi (1972) gave no measurements of the deer remains, but his fig. of Plate II shows illustrations of eleven antlers, including spikes, antlers with an a1, a2, p1 and p2 (corresponding to our antler type 4) and antlers consisting of a beam with only one brow-tine (corresponding to our antler types 1 or 2).

Kuss (1975b, p. 77, fig. b) figured an antler from this locality consisting of a base, a1, a2, p1 and p2, corresponding to our antler type 4. In this specimen however, the al and a2 bifurcate at their tips into two small tines, lying in a vertical plane.

Malatesta (1980) gave a more detailed description of cervid material from this cave. Concerning the skulls he remarked that all 77 frontals found have pedicles. He further mentioned two kinds of wear of the teeth. In about 85% the wear affects the whole molar arch rather evenly. In about 15% of the mandibles some consecutive teeth are said to be more worn than others.

Malatesta (1980, p. 32) furthermore mentioned that over 500 beams have been found. These antlers have been shed and no skull with antlers has been found. Apart from some simple beams with no trace of a burr the vast majority of the antlers only have a brow-tine. The beam of these specimens bends inwards and ends in a point, or sometimes it flattens to form some kind of palmation. The latter type of antler would correspond to our antler type 1. Malatesta (1980) also described antlers with more tines than only the brow-tine, corresponding to our antler type 4. On p. 34 he mentioned another type of antler, for which he gave the following description: "In some cases a supplementary tine grows out just above the burr. Generally it is a small protuberance, but sometimes a little tine develops, as in the specimen illustrated by Kuss (l.c., fig. 3c). This supplementary tine nearly always grows on the front of the burr, but in one specimen it is set upon the external side of it. The six specimens of Simonelli cave, which carry supernumerary tines correspond in two cases to very big antlers, in two cases to middle-size antlers, in one case to a very young antler (about two years old) and in the last one to a slender antler, where the burr is faintly marked by a coronet of few spaced pearls". This type of antler would correspond to our antler type 5.

The data concerning the postcranial skeletal elements given by Malatesta (1980) correspond to our size groups 1 and 2; a few specimens possibly correspond to our size 4.

Kalo Chorafi

Kuss (1965) described material from this locality. From Kuss' description of the skulls no conclusions can be drawn concerning the types distinguished in this paper.

Kuss (p. 315) mentioned that 100 antlers were found, most of them fragmentary and almost all beams having only one brow-tine. The distal ends of the beams of these specimens are relatively long and always strongly curved, in most cases they possess an oval cross section. It is possible that they are bludgeon-shaped. Some bludgeon-shaped distal ends are present. This type of antler corresponds to our antler type 1.

Specimen no. 61/1964, figured by Kuss (p. 321, fig. 4b) has a second tine in addition to the brow-tine. This specimen corresponds to our antler type 4.

The second specimen (no. 17/1963) figured by Kuss (p. 317, pl. 3c) has a tine growing just above the burr in addition to the brow-tine.

Apart from the teeth of small deer Kuss (p. 325, fig. h) figured and mentioned a large I_1, which however is fragmentary.

From the descriptions given by Kuss (1965) we can draw the following conclusions:

1) three types of antlers are present, corresponding to our types 1, 4 and 5;
2) at least two sizes of teeth are present.

Stavros

Kuss (1967, p. 211, fig. 2) figured a mandible with the tooth-series P_4–M_2 and the first lobe of the M_3. He stated (1975b, p. 46) that this is a fragment of the largest mandible of his collection. His measurements (1975b, p. 46) indicate that it is also larger than any mandible stored in our own collection.

Gerani 1

Kuss (1975b, p. 44) described and figured (p. 75, table II, fig. c-d) a large I_1. In contrast to his other incisor material it is of larger dimensions, has no lingual cingulum and is very hypsodont.

An antler consisting of a beam with more than one tine (our antler type 4) is figured (p. 77, fig. a).

Bate Cave

Three sizes of deer were recognized by Kotsakis *et al.* (1976) on the basis of post-cranial skeletal elements. Two belong to size 5 and 6. We cannot determine to which size (1 or 2) their *Megaceros cretensis* belongs.

Descriptions of the antler and skull material are not given, only figures of a male skull with pedicles and a female skull without (Plate III, fig. 1 and 2). It is not possible to determine any of our morphotypes from these figures.

Mavro Mouri 3

Kuss (1969, p. 146, fig. a) illustrated an antler consisting of a beam with more than one tine (our antler type 4). In his fig. 2, on the same page, a drawing is given of an antler consisting of a beam with only the brow-tine. However, since the distal end of the beam is missing, it is not possible to tell whether this antler belongs to our antler type 1, 2 or 4.

Gumbes II (= Grida Avlaki)

Kuss (1969, plate 2, fig. b, p. 146) figured an antler consisting of a beam with several tines (our antler type 4) and he mentioned that there are antlers with only the brow-tine (corresponding to our antler type 1 or 2).

According to Kuss (1969) the latter antlers differ from the ones from Kalo Chorafi by the relative weakness and the almost circular cross section of the beam. Bludgeon-formed distal ends are not mentioned.

Furthermore Kuss (1975b, p. 44) mentioned a tooth-row (P^2–M^3), which he attributed tentatively to a large species of deer.

IV-3-c. Localities from which the presence of cervid material has been mentioned only

The presence of cervid material is mentioned for the following localities, but without details:

Kutri (= Phalasarna); Kuss (1966, p. 180)

Gerani 3; Kuss (1970, p. 76)
Mavro Mouri 1: Kuss (1970, p. 76)
Kharoumes II, III, IV, V and VII; Kuss (1970, p. 79)
Skaleta; Kuss and Misonne (1968, p. 58) and Kuss (1975b, p. 73, plate I, fig. d).

Kuss (1975b, p. 43) mentioned an aboral calvarium fragment coming from the vicinity of Gumbes III and on p. 46 a mandible fragment from Gumbes IV. Both specimens would have belonged to large cervids.

V. The meaning of the observed variation

V-1. Historical review

The descriptions of the cranial material of the deer from Crete in this paper and of the post-cranial skeletal elements in the previous study (De Vos, 1979) show that there is a great variation in size and morphology. On the basis of size and morphology at separate localities different groups can be distinguished. This wide variability and the clear presence of different groups have led in the literature to at least two different interpretations.

Most authors, e.g. Malatesta (1980) and Kotsakis *et al.* (1980), consider all material of the fossil Cretan deer to belong to a single species, with a great variability in size and morphology. The name of this species has been connected in the literature with several different generic names. The following combinations have been used:

Anaglochis cretensis – Simonelli, 1907
Cervus (Eucladoceros) cretensis – Vaufrey, 1929
Megaceros cretensis – Azzaroli, 1952, 1961; Kuss, 1965, 1966, 1967; Kuss and Misonne, 1968; Accordi, 1972; Melentis, 1974; Caloi and Malatesta, 1974
Cervus cretensis – Sicogneau, 1960; Kuss, 1969, 1970, 1973
Megaloceros cretensis – Sondaar, 1971
Nesoleipoceros cretensis – Radulesco and Samson, 1967
Praemegaceros cretensis – Kurtén, 1968; Malatesta 1980
Megaceros (Megaceroides) cretensis – Azzaroli, 1971.

In contrast, Kuss (1975b) considered the material of the fossil deer from Crete to have belonged to two different species, each with a great variability in size and morphology. His two species are *Candiacervus cretensis* and *Candiacervus rethymnensis*. The differentation Kuss made is based only on size.

Small-sized elements from various localities he attributed to *C. cretensis*, material of large size from different localities to *C. rethymnensis*. The synonyms for the first species are already mentioned above. Earlier references to the second species are listed by Kuss on his p. 41:

1905 "horns and teeth of a deer". – Bate, p. 196, from Kutri or Phalasarna.
? 1907 "Bovide". – Simonelli
? 1965 "Bovide?". – Kuss, p. 342
1967 "der bisher stärkste kretische Cervide". – Kuss, p. 209, pl. I, fig. 2
1970 *Cervus* sp. – Kuss, p. 74
1973 *Cervus* sp. – Kuss, p. 50.

Several objections can be made to both the single-species-hypothesis and the two-species-hypothesis.

V-2. *The variation in post-cranial skeletal elements*

The size groups and the relative abundance of our post-cranial material from the different localities have been described in an earlier paper (De Vos, 1979).

As stated above, Malatesta (1980) who described the material from the Simonelli Cave, considered the fossil deer from this cave to belong to a single species. He observed broad variation in the thickness of the metapodials of the same length. He stated (p. 53) that the differences between thicker and thinner metacarpals are so large 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 deer the sexual dimorphism is reflected not only in the thickness, but also in the length of the metapodials. Male bones are in general longer and heavier than female bones, although the distribution of the measurements may show overlap (Bosold, 1968). Such a distribution of measurements, which may be attributed to sexual dimorphism, has been found for the thickness and length of the metacarpals of the fossil deer from Gerani 4 (De Vos, 1979, fig. 3).

The thicker and thinner metacarpals of the same length, mentioned by Malatesta, might indicate that the material originates from older and younger animals. For example, the first two metatarsals illustrated by Malatesta on his plate XXII and attributed by him to females actually represent juvenile animals, as is indicated by the absence of epiphyses.

In addition, Malatesta (p. 91) mentioned that among the material from Simonelli Cave some bone fragments were found (metatarsal and calcaneum), the size of which goes beyond the variation range of his *Praemegaceros cretensis*. The fragments approach the size of the bones of the larger species *Praemegaceros cazioti* from Corsica and possibly correspond to our size group 4. As an explanation for the presence of such large elements Malatesta (1980, p. 91) stated that: "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 having about four times the length of the smallest (see table 12, De Vos, 1979), it is more realistic to suppose that we are dealing with at least two different taxonomic units (species).

This is what Kuss (1975b) decided. On the basis of size, he considered the material from Crete to belong to two species, the smaller *Candiacervus cretensis*, and the larger *Candiacervus rethymnensis*. However, in the smaller as well as in the larger species, the variation in size still goes beyond the variation within a species from the mainland.

The large size range in the material of the small species, if different localities are compared, Kuss (1975b) explained as a consequence of diminution in size of the deer in the course of time. So, according to Kuss (1975b, pp. 39-40) his *Candiacervus cretensis* from the older Kalo Chorafi fauna is larger than *C. cretensis* from the younger Grida Avlaki fauna. However, the large variation Kuss (1965) found in the material of the small species from Kalo Chorafi was explained by De Vos (1979) as being due to the presence of two size groups. The population of the fossil deer of Kalo Chorafi is thus thought to be composed of two species (De Vos, 1979).

Also in the larger species, *Candiacervus rethymnensis*, there would be a diminution in size according to Kuss (1975b, p. 46); he based this conclusion on teeth material only.

An argument against the hypothesis that the Cretan deer became smaller in the course of time, is the fact that both in Stavros, which is considered to be relatively old and in Gerani 4, which is considered to be younger, our size 2 is present (De Vos, 1979, table 14, p. 82).

Kotsakis *et al.* (1976) considered the deer remains originating from Bate Cave to belong to one species (*Megaceros 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 is not sufficient to establish a new species. However, the variation within the material from Bate Cave goes far beyond the range of variation of the species *cretensis* and *rethymnensis* in the sense of Kuss (1975b).

In the post-cranial skeletal elements six size groups were distinguished by De Vos (1979), who considered these size groups as taxonomic units.

The species *C. cretensis* in the concept of the original author Simonelli (1907/1908) corresponds to our size groups 1, 2 and 3. *C. cretensis* in the concept of Kuss (1975b) includes only our size groups 1 and 2. The metacarpal described by Simonelli (1907/1908), belonging to our size group 3, has been placed by Kuss (1975b) tentatively in his *C. rethymnensis.*

The post-cranial skeletal elements of the species *C. rethymnensis* correspond to our size group 4, while the very large bones described as Cervo taglia media and Cervo taglia grande by Kotsakis *et al.* (1976) from Bate Cave are used as the basis for our size group 5 and 6.

There is not only a difference in size, but within the variation of the six size groups four groups were distinguished in the massivity, i.e. the length-width ratio (De Vos, 1979). The size groups 1 and 2 have metacarpals which are shorter and limb-bones which are more massive and more heavily built than those of *Cervus elaphus*. Size group 4 is *Cervus elaphus*-like, while size group 3 is intermediate in massivity. According to Kotsakis *et al.* (1979, pp. 31/32) the remains of the large deer corresponding to our size groups 5 and 6, are extremely thin; they belong to a very big deer, which does not look like any known continental form. This statement is confirmed by the data given in table 11 of De Vos (1979). His suggestion (1979, p. 59) that size groups 5 and 6 are *Cervus elaphus*-like, must now be rejected. The differences in massivity are thought to be linked to functional adaptations, but we do not yet understand how this has to be explained.

The hypothesis of De Vos (1979), that the six size groups represent six taxonomic units, is still considered to be the most realistic one.

V-3. *The variation in the morphology of the antlers*

Five types of antlers have been recognized. Furthermore there is one burr from Mavro Mouri 4c that is larger than all the other burrs found on Crete; it must have belonged to a very large deer. The question is whether these different types of antlers belonged to one large intraspecific variation or to different taxonomic units.

The morphology of the antlers within a species is known to be rather variable. Heintz (1970) mentioned several factors contributing to antler variation within a species. These are:

– Intraspecific variation

The intraspecific variation of the antlers is much greater than that of various skeletal elements and of the teeth. This exceptional variability may be caused by the fact that the antlers are peripherally placed structures; their growth would be under hormonal control and antlers are thought to be less dependent on the size of other skeletal structures.

– Age

The antlers of young animals are generally simpler than those of older animals; however, in very old animals the antlers are again simple in structure, and may show malformations; it is said that such antlers are "put back".

– The environment

Adequate nutrition is necessary for good antler development. Development may however vary from year to year with varying food supply.

– Seasonal influence

The morphology of the antlers changes during the growth season.

Let us consider these factors one by one.

– Intraspecific variation

The Dubois Collection of fossil vertebrates from Trinil, Java, collected by Eugène Dubois during 1890-1900, and now stored in the Rijksmuseum van Natuurlijke Historie, Leyden, the Netherlands, contains an abundance (±60) of well-preserved complete antlers of the Pleistocene deer *Axis lydekkeri* (Martin). This collection of antlers provides a good reference sample for assessment of intraspecific variation. The antlers show a very uniform morphology (De Vos, in prep.) and there are no aberrant forms. Similarly, the collection of antlers from Gerani 4 is very uniform in morphology.

By contrast, the antlers from Liko (about 266 specimens) are so multiform that it is hard to believe that they could have derived from one single taxonomic unit. Such multiform morphology at one locality was already noticed by Kuss (1965) for material from Kalo Chorafi and by Malatesta (1980) for material from Simonelli Cave. With regard to the material from Kalo Chorafi Kuss (1965, p. 316) stated: "Grössenmässig variieren die Geweih-Reste ganz ausserordentlich. In Betracht der sehr viel einheitlicheren Skelett-Reste kann man sich zunächst gar nicht vorstellen, dass alle zu einer Art gehören".

Although Kuss (1965) described three types of antlers, corresponding to our antler types 1, 4 and 5, he (1975b) only distinguished two species from Kalo Chorafi on the basis of the size of the antlers. Large antlers of our type 1, like the antler figured by Kuss (1975b, fig. c, Plate III), he attributed to his large species *Candiacervus rethymnensis*, while the smaller antlers of our types 4 and 5 he attributed to his small species *Candiacervus cretensis*.

For the material from Simonelli Cave, Malatesta (1980, p. 32) stated: "Although the range of length of antlers is very narrow (the largest specimen is 24 cm long), the range of variability in size and shape of the beam and tines is wide". For the material from Simonelli Cave Malatesta (1980) distinguished the antlers corresponding to our types 1, 4 and 5. However, he considered all these types to belong to a single species: *Praemegaceros cretensis*.

Concluding we can say that the variation in antler morphology is much greater than one would expect in a single species.

– The variation as a function of ontogeny

Malatesta (1980) considered the abundant material from Simonelli Cave to belong to a single species. He considered only the antlers corresponding to our antler type 4 to be full-grown. At variance with this hypothesis is the fact that this type is represented by only ± 1% of the 500 specimens, while most of the bone material is from adult animals. We consider all the antlers with the exception of the spikes, as full-grown.

Kuss (1975b) distinguished two deer "faunas", an older and a younger one. Both "faunas" contain his species *Candiacervus cretensis*. Its antlers would be simple in the older "fauna", consisting only of a beam with a sub-basilar brow-tine. In the younger "fauna" the antlers of *C. cretensis* would be much more complicated. Kuss suggested the following growth series for the antlers of *C. cretensis* of the Grida Avlaki fauna: first spikes, then simple antlers, consisting of a beam with only a sub-basilar brow-tine, and finally much more complicated antlers. However, Kuss (1975b, p. 38) was unable to put all his specimens in age order. Some spikes are so large that he doubted whether all spikes could have belonged to animals of the same age. For this reason he suggested that two or three years of spike production would have preceded the second phase in the antler development.

In the material from Liko, spike Li-2636 is exceptionally large. It appears from the scatter diagram of fig. 7 (DAP and DT of burrs of antlers from Liko) that this spike falls in the size range of individuals of middle age. If such an age is accepted for this spike, then more than three years of spike production should have occurred. This seems unlikely, however, in view of the relationship between antler complexity and life-span in extant deer. It is more reasonable to suppose that this large spike belonged to a different and larger deer taxon than the rest of the spike material. This implies that at least two different taxonomic units of deer are present at Liko. If one assumes that the different kinds of antlers are from different systematic groups of deer, then it is easier to arrange the antlers in order of age. As an example we can consider the antlers in which the a1 is divided. In our concept Li-688 (fig. 22) is an antler of a young animal (DAP of the burr is 30.4; DT is 26.9), Li-686 (fig. 10) an antler of a middle-aged individual (DAP of the burr is 45.0; DT is 42.0), Li-687 (fig. 23) an antler of an old animal (DAP of the burr is 51.0; DT is 49.0) (see scatter diagram of fig. 7). Similar consistent series can be produced for the other types of antlers.

– Environmental influences

In recent deer, such factors influence the size, but not the morphology; i.e. the basic scheme of the shape of the antlers does not change. As a consequence it is not very likely that the different antler types result from differences in environmental factors acting on the individuals of a single species.

– Seasonal influences

Seasonal variation cannot play an important role, because most of the material from Liko consists of shed, mature antlers.

– Pathological aberrations

Kuss (1965, p. 318) described an antler of type 5 (no. 71/1963) with a supplementary tine growing just above the burr. Kuss considered this configuration to be a senile anomaly, but this hypothesis, based on a single specimen, is not confirmed by Malatesta (1980, p. 34). In Simonelli Cave Malatesta found six of such specimens, which in chapter II were shown to belong to different age groups. In general, pathological variation is of little importance, as it does not modify the fundamental shape of the antlers in a species.

According to Beninde (1937) taxonomic interpretations based on antlers are likely to be valid only if based on specimens which are fully grown, reasonably complete and show a constant morphology in at least four or five specimens coming from one locality.

We noted already that the total material of antlers from the localities of Crete shows a variation in morphology, which is larger than one would expect in a single species. From the criteria given above we conclude that this variation in morphology is not caused by differences in ontogenetic age or by environmental influences, seasonal influences or pathological aberrations. Furthermore, we wish to stress that we are dealing with antlers that are full-grown and reasonably complete.

We find at least four or five specimens with similar morphology at one locality. For these reasons we consider the variation in the morphology of the antlers to be an indication that we are dealing with different taxonomic units. As we could distinguish at least five types of morphologically different antlers, we conclude that there are at least five taxonomic units.

V-4. *The variation in the size and morphology of the teeth*

In addition to the teeth of a small deer, attributed to the species *Candiacervus cretensis*, Kuss (1975b, p. 44) mentioned and figured a left I_1 from Gerani 1, which is very hypsodont and has no lingual cingulum. Kuss (1975, p. 44) attributed this specimen to the larger species *Candiacervus rethymnensis*. From the locality Kalo Chorafi Kuss (1975b, p. 44) mentioned a right I_1. This specimen is smaller than the one of *C. rethymnensis* from Gerani 1 and that is why Kuss (1975b, p. 44) wondered whether it could belong to this species.

In the same publication Kuss (1975b, p. 46) mentioned two large mandible fragments, one from Stavros and the other from Gumbes 4, both of which he attributed to his species *Candiacervus rethymnensis*. However, the mandible from Stavros is larger than that from Gumbes 4. Kuss explained this difference by assuming a decrease in size in the species *C. rethymnensis* in the course of time. Therefore Kuss (1975) assumed that the material from Stavros is older than that from Gumbes 4. However, in Bate Cave, which must be considered to be of the same age as Gumbes 4 in the concept of Kuss (1970), the remains of the largest deer, larger than the one from Stavros, are found together with the small species (Kotsakis *et al.*, 1976).

From the description of our dental material it becomes clear that there are at least three size groups of the teeth, viz.: the sizes A, B and C.

Not only differences in size can be distinguished, but also differences in morphology.

Firstly, we noticed that the wear pattern is flat in the mandibles of middle-aged animals of size A, whereas the wear pattern of the teeth of the larger mandibles of size B or C is sometimes lophodont. This difference in wear pattern suggests a difference in diet; we can interpret this difference in morphology as a functional adaptation.

Secondly, all P^2 from Gerani 4 attributed to size A belong to morphotype-1. This could indicate that the P^2 morphotypes may have systematic value too.

Thirdly, we noticed the presence or absence of a cingulum. Whether this difference has a systematic value is not yet clear.

Summarizing, we come to the conclusion that the differences in the morphology and size of the teeth can be of systematic value. At least three taxonomic units can be distinguished on the basis of the size of the dentition.

V-5. *The variation in the size and morphology of the skulls*

Considering the three skull types (b, c and d) from Liko, it seems possible to assign the three specimens to three different species. However, it is equally possible that we misunderstand the range of variation within single species. For a better appreciation we will discuss some other possibilities:

1. Suppose that only one species of deer is present.

Our distinct types thus are merely morphological variants within that taxon. If this "single species hypothesis" is correct, it involves accepting the fact that there is an enormous amount of intraspecific variation.

Such a wide range is contradicted in species of recent and fossil deer. For example, Pocock (1942, 1943) described the skull characters of some recent subspecies of the Sambar deer (genus *Rusa*), occurring East of the Bay of Bengal. He described the skull characters of the species *unicolor*, represented by the subspecies *unicolor* from Ceylon, *equina* on the island of Sumatra, *swinhoii* on the island of Formosa, *brookei* on the island of Borneo, *marianna* in the Northern and Central Philippines and *basilanensis* from the islands of Mindanao and Basilan (Southern Philippines). Van Bemmel (1973) united the subspecies *equina*, *swinhoii* and *brookei* to the species *equina*, and the two subspecies *marianna* and *basilanensis* in the species *marianna*. The skulls of these species or subspecies from different islands differ only in size and in the morphology of the nasals. The smaller forms *marianna* and *basilanensis* are distinguished by cruciform nasals. Such uniformity in skull morphology in one species or systematic group can be seen not only in recent deer but also in the fossil population from Gerani 4.

2. On the basis of the resemblance of the flat wear pattern of the teeth we can assume that the skulls Li-757 and Li-759 represent the same species; the third skull (Li-758) represents another species, because it has a lophodont wear pattern. The probability that this hypothesis is correct is very low, because the two skulls differ in the thickness of the dorsal rim of the orbit (Li-757 very thick; Li-759 very thin), the shape of the orbit (Li-757 round; Li-759 oval) and the morphology of the antlers (Li-757 antler type 2; Li-759 antler type 4).

3. Li-758 and Li-759 may belong to one species, because of the less thick dorsal rim of the orbital wall; the third skull (Li-757) would represent another species, because of the very thick rim of the dorsal orbital wall. However, the two skulls differ in antler morphology (Li-759 has an antler type with only one sub-basilar brow-tine; Li-758 has an antler type the brow-tine of which is subdivided into two tines lying in a horizontal plane), in the shape of the orbit (Li-758 round; Li-759 oval) and in the wear pattern of the teeth (Li-759 flat; Li-758 lophodont).

4. Li-758 and Li-757 would represent the same species, because of the similar morphology of the orbit, which is round. The third skull (Li-759) would belong to another species, because the orbit is of oval shape. Again we think that the probability that this hypothesis is correct is very low, because the two skulls differ in antler morphology (Li-757 has an antler with only one sub-basilar brow-tine; Li-758 has an antler the brow-tine of which is subdivided into two tines, lying in a horizontal plane), in the thickness of the orbit wall (Li-757 very thick; Li-758 thin) and in the wear pattern of the teeth (Li-757 flat; Li-758 lophodont).

The rejection of the four possibilities outlined above means that we have to accept three taxa in the Liko collection. The three types of skull, representing three different taxa, have the following characteristic features:

1. Skull Li-757 has a very thick dorsal orbital rim (skull type b).
2. Skull Li-758 is characterized by the more or less lophodont teeth, the moderate thickness of the orbital rim (skull type c) and the antlers having two brow-tines at the place of the a1 (antler type 3).
3. Skull Li-759 has a thin orbital wall, an oval orbit (skull type d) and the antlers with a1, a2, p1 and p2.

However, it is very difficult to attribute other skull fragments to any of the three types mentioned.

Furthermore we have skull type a in Gerani 4 and the large skull fragment of Gumbes III (Kuss, 1975b), which Kuss attributed to his large species *Candiacervus rethymnensis*.

So it is concluded that there are at least 5 different types of skulls in the fossil deer material of Crete, belonging to 5 different taxonomic units.

N.B.

Concerning the skulls it is remarkable that all 77 frontal fragments collected from Simonelli Cave have pedicles (Malatesta, 1980). According to Malatesta (p. 70) this remarkable relative frequency indicates that female skulls also had pedicles as a result of some hormonal influence. However, remains from other localities described by Kuss (1975b), Kotsakis *et al.* (1976) and in this paper show that female skulls always lack antlers. The absence of recognizable female frontals in Simonelli Cave is possibly due to the fact that such parts without pedicles are more fragile.

V-6. *Conclusions*

We conclude that the various taxonomic interpretations of the deer material from Crete as proposed by Kuss (1975b), Malatesta (1980) and Kotsakis *et al.* (1979) suppress important information on the diversity of the Cretan deer. These authors' approaches to the classification of the Pleistocene deer are considered unsatisfactory.

Because of the great variation in the size and morphology of the material, the different groups can best be interpreted as representing different taxonomic units.

We conclude that the material contains at least:

- six size groups of post-cranial elements;
- five groups based on the skulls;
- five groups for the antlers;
- three groups based on the size of the teeth.

VI. Association of the material, species units and nomenclature

VI-1. *Association of the elements*

VI-1-a. Making logical combinations

Table 11 gives the distribution of morphogroups (post-cranial skeletal elements, teeth, skulls and antlers) from the Cretan sites. As material of various morphogroups is frequently found together in one locality at the same level, and since most of the material is disarticulated, it is often difficult to make correct associations of cranial and post-cranial elements belonging to a natural taxon. However, especially for the locality Gerani 4 and to a certain extent for Liko as well, it appeared possible to associate some of the groups of the post-cranial skeletal elements with certain cranial-element groups. The most likely combination of morphogroups of different character is based on several criteria such as size, relative abundance of the elements and in one case nature of fossilisation.

VI-1-b. Association of the elements from Gerani 4

From the description and measurements of the deer material from Gerani 4 it becomes clear that there are two size groups of post-cranial skeleton elements (sizes 1 and 2; De Vos, 1979), one type of skull (type a), two sizes of teeth (sizes A and B), two morphotypes of P^2 (morphotype 1 and 2) and two types of antlers (types 1 and 4) (see table 11).

It appears that 99% of the post-cranial skeleton elements found at Gerani 4 belong to size 1, i.e. the smallest deer found on Crete so far. All available skull material belongs to skull type a, the bulk of the teeth material (98%) belongs to size A and their P^2 have morphotype-1. Nearly all the antler material (56 out of 57) is of antler type 1. Because of these frequency data the elements mentioned above are associated with certainty with one group of deer, here indicated as group I, representing one taxonomic unit (table 14).

In Gerani 4 only a few skeletal elements of size 2 (1%) (De Vos, 1979, p. 76) and teeth of size B (2%), having a P^2 in which the hypocone is larger than the protocone (morphotype-2) can be associated with a specific type, because of their relative frequency. These remains together with the single antler of type 4 are associated to our deer group IIc (Table 14). Another argument for associating these elements is the fact that the fossils have a slightly different type of fossilization; they are somewhat darker in colour than the fossils of group I.

VI-1-c. Association of the elements from Liko

The description and measurements of the deer material from Liko indicate that there are four sizes of post-cranial skeletal elements, sizes 2, 3, 4 and 6 (De Vos, 1979), three types of skulls b, c and d, two sizes of teeth B and C. For size B the P^2 has morphotype-1, while in the teeth of size C the P^2 have either morphotype 1 or 3. Whether the latter two morphotypes represent different taxonomic units is not yet clear. Finally, we have four types of antlers 2, 3, 4 and 5 (see table 11).

Associating these morphogroups to form deer groups is rather complicated. In recent deer there is always a positive correlation between the sizes of the skull and post-cranial skeletal elements: species with small skulls also have small-sized post-cranial skeletal elements, species with large skulls have large extremities. So the assumption that size groups of skulls, representing different taxonomic units can be associated with skeletal elements of relatable size is fully warranted.

As the three types of skulls, which are of roughly the same size, are somewhat larger than the ones from Gerani 4 (see table 7), which we associated with post-cranial skeletal elements of size 1, it is reasonable to associate these skulls from Liko with the post-cranial skeletal elements of size 2. Because of these three skull types (b, c and d), we have to recognize three different taxonomic units in size group 2 of the post-cranial skeletal elements: IIa, IIb and IIc. (In Gerani 4 we associate IIc with antler type 4).

It is not possible to associate the rest of the material. On the basis of the size of the post-cranial skeletal elements it is concluded that there are at least four taxonomic units (size 2, 3, 4 and 6). On the basis of skulls there are already three taxonomic units in size 2, so we conclude that the size of the skeletal elements points to three more taxonomic units of deer (III, IV and VI). (Deer group V is based on post-cranial skeletal elements of size 5 from Bate Cave).

VI-2. *Species units*

On the basis of the size of the post-cranial elements it is concluded that there are at least six taxonomic units of Pleistocene deer in the island of Crete (Sizes 1-6). For the locality Liko we concluded from the skulls that there are at least three taxonomic units in size category 2 of the post-cranial skeletal elements. Altogether we have at least eight taxonomic units of deer.

Group I is based on the association of the material from Gerani 4. Groupings IIa, IIb and IIc are based on the association of the material from Liko. Groupings III, IV, V and VI are based only on size differences in the post-cranial skeletal elements. With the material available it is not possible to make further combinations. For example, teeth of size C can go together with post-cranial elements of size 3 or 4, antler type 5 with size 3, 4 or 6.

VI-3. *Nomenclature*

It is not easy to give specific names to our taxonomic groups of deer.

The species concept of Kuss (1975) is quite confusing, as is apparent from a discussion of his *Candiacervus rethymnensis*. The holotype of this species is a metacarpal from Mavro Mouri 4. The size of this holotype corresponds to our size group 4 (our species IV). Furthermore he attributed to his species material which belongs to other taxonomic groupings, as described in this paper. Kuss includes, for example, an antler from Gerani 4, which belongs without doubt to the homogeneous sample from this locality, i.e. to our taxonomic group I. Since Kuss (1975b) chose for the species *rethymnensis* a metacarpal as the holotype and since the measurements of this holotype correspond to our size 4 of the post-cranial skeletal elements, we refer only post-cranial skeletal elements of size 4 to the species *rethymnensis*.

The species *cretensis* has been described by Simonelli (1907). In his material, originating from different localities, the post-cranial size groups 1, 2 and 3 are present. Therefore, the material is considered not to belong to a single species. Simonelli did not designate a holotype, so if we want to restrict the name *cretensis* to one of our natural groupings, we have to choose a lectotype from his material in a suitable way. In the material of Simonelli there is one metacarpal, which falls outside the range of the measurements of the rest of the material. This metacarpal corresponds to our size group 3 and is the most distinct specimen in Simonelli's collection. The rest of his material belongs to size group 1 and 2, of which he had only a small number of specimens. If we choose a lectotype from this latter group, it is not really clear to which of our deer groups it must belong, either group I or group II. Therefore the least ambiguous solution is to select as the lectotype the most characteristic metacarpal. This metacarpal is figured by Simonelli in figures 24 and 25, and its measurements are given on p. 467 (Simonelli, 1907). We therefore refer only post-cranial skeletal material of size group 3 to *C. cretensis*.

No cranial material can be referred to the species *C. cretensis* or *C. rethymnensis* until a find (a complete skeleton or homogeneous sample) proves the relation between cranial and post-cranial elements.

Although it was certainly not our intention to assign the earlier described species units to fairly ill-defined groups, the original material did not give us the opportunity to make a better choice.

On the basis of our group I from Gerani 4 only one new species will be described (*Candiacervus ropalophorus* n.sp.) and it will be added to the earlier described species of Cretan deer (*C. cretensis* and *C. rethymnensis*). Only *Candiacervus ropalophorus* n.sp. can be considered as a clearly recognizable species on the combined characters of cranial and post-cranial elements.

Because of the indistinct ancestors of the Cretan deer (see Chapter IX) the genus name *Candiacervus* Kuss, 1975 will be adopted.

VI-4. *Species*

In Crete the following species are recognized:

Family Cervidae Gray, 1821.
Subfamily Cervinae Baird, 1857.
Genus *Candiacervus* Kuss, 1975.
Type species: *C. cretensis* (Simonelli, 1907).

Type specimen of type species: a metacarpal, figured by Simonelli, 1907, fig. 24 and 25.
Type locality: unknown, possibly a cave near Grida Avlaki.
Differential diagnosis: not based on morphology, but on geography: all Pleistocene deer of the islands of Crete, Karpathos and possibly Amorgos.

Candiacervus ropalophorus n.sp.

Holotype: The male skull Ge4-46 (Plate X).
Stored in: Instituut voor Aardwetenschappen, R.U., Utrecht, the Netherlands.
Additional material: Elements Ge4-1 through 3184, with the exception of Ge4-2702, 1020, 1645, 1671, 1672, 3015, 193 and 2909.
Derivatio nominis: ϱοπαλος = a cudgel thicker towards one end; φέϱω = to bear.
Type locality: Gerani 4, 40 uppermost centimetres of the cave filling.
Occurrence in other localities: Gerani 2, 5 and 6, Mavro Mouri 4c, Sourida, Simonelli Cave, Rethymnon fissure and Kalo Chorafi.
Differential diagnosis: Smallest species of *Candiacervus* (p.c. size 1), with antlers of type 1, and skull of type a.

Short description:

A very small deer (shoulder height about 40 cm) with post-cranial skeletal elements of size 1. The length of the metatarsal ranges from 110-131 mm, with a mean of 121 mm. The metacarpal is relatively short and the limb-bones are relatively more massive than in *Cervus elaphus* (De Vos, 1979). Some metatarsals (6%) are fused with the naviculo-cuboid; 68% of the naviculo-cuboids are fused with the central cuneiform (De Vos, 1979).

The teeth are of size A; the length of the P^2–M^3 ranges from 53.2-71.7 mm, with a mean of 62.8 mm. The P^2 is characterized by a protocone that is similar in size to the hypocone (morphotype-1); between the protocone and hypocone a valley extends from the wear surface downwards to close to the root. The upper molars have a weakly developed cingulum; the occlusal surface of the toothrows of middle-aged animals is flat.

The antlers of type 1 are very long (up to 77 cm) and consist of a beam with a brow-tine at about 10 cm from the burr. At the level of the brow-tine the beam curves backwards and immediately forwards again; the distal end of the beam is bludgeon-shaped.

The 17 male skulls (type a) range in length from 210.5-213.7 mm and have the following characteristics: convex frontals between the orbits; rapid reduction of the width of the snout between the orbits and foramina infraorbitalia; vacuities of small size, small gland pits; cruciform nasals; large foramina supra-orbitalia; thick rims of the dorsal orbital walls; circular orbits; lack of canines.

Candiacervus spp. of size 2

A heterogeneous group of deer with post-cranial elements of size 2; the length of the metatarsals ranges from 123.2-152.5 mm, with a mean of 138 mm; the metacarpal is relatively short and the limb bones are more massive than in *Cer-*

vus elaphus. The teeth are of size B; the length of P^2–M^3 ranges from 62.7-77.5 mm with a mean of 69.9 mm.

On the basis of the morphology of the skull and antlers, three different unnamed taxonomic units are distinguished (IIa, IIb and IIc).

Species IIa

Type specimen: skull Li-757 (Plate XII).
Type locality: Liko, 75 uppermost centimetres of the cave filling.
Other occurrences: Simonelli Cave.

Remarks:

The dorsal rim of the orbital wall is very thick; the orbit is circular; the wear pattern of the teeth is flat; the P^2 has morphotype-1; the antler of type 2 consists of a beam with only one sub-basilar brow-tine.

Species IIb

Type specimen: skull Li-758 (Plate XIII).
Type locality: Liko, 75 uppermost centimetres of the cave filling.

Remarks:

The dorsal rim of the orbital wall is intermediate in thickness between the previous type and the following type (IIc); the orbit is circular; the wear pattern of the teeth is lophodont; the morphology of the P^2 is unknown; the antler of type 3 consists of a beam with two brow-tines.

Species IIc

Type specimen: skull Li-759 (Plate XIV).
Type locality: Liko, 75 uppermost centimetres of the cave filling.
Other occurrences: Gerani 4, Mavro Mouri 4c, Mavro Mouri 3, Simonelli Cave, Gumbes 2 and Kalo Chorafi.

Remarks:

The dorsal rim of the orbital wall is very thin; the orbit is oval, with the longer diameter in the anterior-posterior direction; the wear pattern of the teeth is flat; the morphology of the P^2 is unknown; the antler of type 4 has a1, a2, p1 and p2.

Candiacervus cretensis (Simonelli)

Lectotype: metacarpal figured by Simonelli (1907, fig. 24 and 25).
Type locality: unknown, possibly a cave near Grida Avlaki.
Other occurrences: Liko, Mavro Mouri 4c, Rethymnon fissure and Kharoumes 2.

Diagnosis by Kuss (1975b, p. 29):

"Kleine Art des Genus *Candiacervus* von rund 0.55 m Schulterhöhe. Schnauze kurz, aber etwas länger als bei *C. cerigensis*. Foramina supraorbitalia weit. Ethmoidallücken maximal 10 mm lang, Tränengruben sehr schwach oder fehlend. Geweih im Laufe des Jüngeren Pleistozäns in Abwandlung begriffen vom Vierender zum Achtender. Stangen erwachsener Tiere ± verplattet".

Revised diagnosis: *Candiacervus* species of size group 3.
Short description:

The metacarpals are intermediate in massivity between *Candiacervus ropalophorus* n.sp. and *Candiacervus rethymnensis*. The length of the metatarsal is 180 mm. At present no skull, teeth or antler material can be attributed to this species.

Candiacervus rethymnensis Kuss 1975

Holotype: Right metacarpal III + IV, table VI, fig. 0 (Kuss, 1975). Collection of the Geological-Palaeontological Institute of the University of Freiburg i. Br.
Type locality: Mavro Mouri 4, West of Rethymnon, Crete (Kuss, 1970, plate 1, text p. 77).
Other occurrences: Gerani 2, Mavro Mouri 4c, Sourida, Rethymnon fissure, Liko and possibly Simonelli Cave.
Diagnosis by Kuss (1975b, p. 42):

"Cervide, der *Candiacervus cretensis* (Simonelli) morphologisch ähnlich, jedoch um 1/3 bis 1/2 grösser ist. Backenzähne mit kraftigem Innencingulum, z.T. mit Basalpfeiler. Geweih des erwachsenen Hirsches im Normalfall nur mit Augensprosse. Metapodien in den Proportionen mehr *Cervus*-artig als bei *C. cretensis*. – Weitaus seltener als *C. cretensis*".

Revised diagnosis: *Candiacervus* of size group 4 of the post-cranial skeletal elements.
Short description:

The metacarpals are *Cervus elaphus*-like in relative length and proportions; the length of the metatarsals ranges from 217.5-241.8 mm, with a mean of 229.6 mm. At present no skull, teeth or antler material can be attributed to this species.

Species V: *Candiacervus* species of size 5 of the post-cranial skeletal elements.
Type locality: Bate Cave.

Remarks:

This species is based only on the size of the post-cranial skeletal elements (size 5); the metapodials of this and the following species are extremely thin, quite unlike any known continental form (Kotsakis *et al.*, 1980); the length of the metatarsals ranges from 301-307 mm, with a mean of 304 mm.

Species VI: *Candiacervus* species of size 6 of the post-cranial skeletal elements.
Type locality: Bate Cave.
Other occurrence: Liko.

Remarks:

This species is based only on the post-cranial skeletal elements of size 6; the metapodials are extremely thin; the length of the single metatarsal is 406.

VII. Stratigraphy and faunal succession

VII-1. *Stratigraphic data on some localities*

In the previous chapter we concluded that there are at least eight groups of fossil deer, each representing a species. Not all species have been found together at one locality: sometimes only one was found (Gerani 5), sometimes two (Gerani 4) occasionally even more (in Liko at least six).

Only at a few localities has more than one lithostratigraphical unit been distinguished. These localities are: Gerani 2, Kutri, Gerani 3 and Milatos 3.

VII-1-a. Gerani 2

All our material coming from the main layer Gerani 2_3 can be placed in the species *Candiacervus ropalophorus*. On top of this layer there is a level with pottery fragments and remains of man-introduced mammals (*Oryctolagus*, *Rattus*). In this layer the endemic murid *Mus minotaurus* still occurs, while the endemic cervids are absent.

In addition to these levels already described by Kuss (1970) and Mayhew (1977), the remains of older cave fillings were observed in the floor and attached to the roof of the cave. Evidently this is what remained of an older cave filling, which probably had been eroded by sea during some transgressive phase during the Pleistocene.

Underneath the layer Gerani 2_3 the sediment yielded further material of the small deer *C. ropalophorus* and one astragalus (Ge2_4-1) of size 4, which we attribute to the larger species *C. rethymnensis*. No signs of mixture have been noted. The combination indicates that *C. rethymnensis* and *C. ropalophorus* probably lived at the same time.

VII-1-b. Kutri (= Phalasarna)

At this locality Bate (1905) distinguished two successive layers, each about one metre thick. According to Bate the upper layer contained abundant remains of "Antilope", while in the lower layer "horns and teeth of a deer" were found. According to Kuss (1966, pp. 179-180) all material from this locality can be attributed to a deer of small size, except for three bones from the lower layer, which he attributed to a deer of larger size. He also suggested that the deer of larger size is older than the deer of smaller size; however, we could not verify this suggestion during a visit to Bate's Collection in the British Museum.

VII-1-c. Gerani 3

In the locality Gerani 3 deer remains of small and of large size were found.

However, it is unknown whether they originate from the same level. According to Kuss (1970, p. 75) human neolithic artefacts and bones of domesticated and wild animals were found at this locality together with many remains of endemic deer. In 1970 (p. 75) Kuss wondered whether the layers contain reworking, but he rejected this idea in 1973 (p. 58). We assume that we are dealing with some kind of mixture, because in Gerani 2 deer-remains were absent in the layer with neolithic remains.

VII-1-d. Milatos 3

At this site there are two levels with different endemic murids. In the lower level there are remains of the genus *Kritimys*, in the upper levels teeth of *Mus minotaurus* have been found. In the stalagmite and calcrete column containing remains of *Kritimys*, a tiny fragment of a cervid molar was observed. Mayhew (1977) concluded that layers with *Kritimys* pre-date the layers with *Mus minotaurus.*

VII-2. *Biostratigraphical succession*

It is impossible to establish lithostratigraphic correlations of the localities, because we are dealing with fillings of caves, collapsed caves and fissures. Several attempts have been made to establish a biostratigraphy based on phylogeny. For such a biostratigraphy it is necessary to consider the entire faunal assemblages of the localities.

A list of the localities with their faunal assemblages will be given on page 48, 49 and 50, but many assemblages are poorly known.

Figure 37 gives localities the faunal assemblage of which is considered to be fairly well known. In the list *Candiacervus* sp. indet. means that we are unable to ascribe the reported deer material with certainty to any of our eight species.

There are localities with the genus *Mus*, localities with the genus *Kritimys* and three localities (Stavros cave inside, Stavros micro and Milatos 3) from which both genera have been reported. On the basis of the separate occurrences of *Mus* and *Kritimys* Kuss (1970) distinguished a *Mus minotaurus* fauna and a *Kritimys* fauna. He supposed that the *Kritimys* fauna is the older one. Mayhew (1977) confirmed this succession, on the basis of the finds in Milatos 3, where *Mus minotaurus* was found in the upper levels and *Kritimys* in the cemented cave floor.

Mayhew (1977) supposed that the genus *Kritimys* increased in size during the Middle Pleistocene (the *Kritimys* aff. *kiridus* ±*Kritimys kiridus* ±*Kritimys catreus* lineage). According to this concept the localities with the smallest species of the genus *Kritimys* are the oldest.

Within the genus *Mus* Mayhew (1977) established a lineage of which the species also became larger in the course of time. The small *Mus bateae* leads to the larger *Mus minotaurus*, because the locality with *Mus bateae* (Stavros micro) would pre-date the localities with *Mus minotaurus* (Mayhew, 1977).

Kuss (1975a) supposed that the species *Hippopotamus creutzburgi* decreased in size in the course of the interval represented by the *Kritimys* faunas. He

Locality	No. on map (fig. 1)	Remains of	According to
Gerani 5	20	*C. ropalophorus*	De Vos 1979, this paper
Gerani 6	21	*C. ropalophorus*	De Vos 1979, this paper
Gerani $2_{2,3,4}$	17	*Mus minotaurus*	pers. observation
$2_{3,4}$		*C. ropalophorus*	De Vos 1979, this paper
2_{4}		*C. rethymnensis*	De Vos 1979, this paper
$2_{2\text{-}4}$		*Crocidura* sp.	pers. observation
2_{2}		cultural level with non-endemic mammals	pers. observation
Gerani 4	19	*Mus minotaurus*	pers. observation
		C. ropalophorus	De Vos, 1979, this paper
		C. sp. IIc	idem
		Crocidura sp.	pers. observation
Bate Cave	22	*Mus minotaurus*	Kotsakis *et al.* 1976
		Candiacervus sp. indet.	this paper, De Vos, 1979
		C. sp. V	idem
		C. sp. VI	idem
		Crocidura sp.	Kotsakis *et al.* 1976
Liko	15	*Mus minotaurus*	Mayhew, 1977, p. 187
		Crocidura sp.	idem
		C. spp. IIa, IIb, IIc	this paper
		C. cretensis	this paper
		C. rethymnensis	this paper
		C. sp. VI	this paper
		Isolalutra cretensis	Symeonidis & Sondaar, 1975
Mavro Mouri 4c	28	*Mus minotaurus*	Mayhew, 1977, p. 187
		Elephas creutzburgi	Kuss, 1970, p. 77
		C. ropalophorus	this paper, De Vos, 1979
		C. sp. II	idem
		C. cretensis	idem
		C. rethymnensis	idem
Sourida	23	*Mus minotaurus*	Mayhew, 1977, p. 188
		Elephas creutzburgi	pers. observation
		C. ropalophorus	De Vos, 1979; this paper
		C. sp. II	idem
		C. rethymnensis	idem
Rethymnon fissure	24	*Mus minotaurus*	Mayhew, 1977, p. 189
		Crocidura sp.	idem
		Elephas creutzburgi	pers. observation
		C. ropalophorus	De Vos, 1979; this paper
		C. sp. II	idem
		C. cretensis	idem
		C. rethymnensis	idem
Kalo Chorafi	43	*Mus minotaurus*	Kuss, 1965
		Elephas creutzburgi	idem
		C. ropalophorus	this paper, De Vos, 1979
		C. sp. II	idem
Simonelli Cave	33	*C. ropalophorus*	this paper
		C. sp. II	idem
		possibly *C.* sp. IV	idem
		Elephas creutzburgi	Malatesta, 1980

Locality	No. on map (fig. 1)	Remains of	According to
Kharoumes 2	54	*C.* sp. II	this paper, De Vos, 1979
		C. cretensis	idem
Kharoumes 3	52	*Elephas antiquus*	Kuss, 1970, p. 79
		C. sp. indet.	pers. observation
Milatos 2, 4	46/44	*Mus minotaurus*	Mayhew, 1977, p. 193
		Crocidura sp.	idem, p. 190
Milatos 3	45	*C.* sp. indet.	pers. observation
Stalagmitic column		*Kritimys catreus*	Mayhew, 1977, p. 190
upper layer		*Mus minotaurus*	idem, p. 193
lower layer		*Kritimys catreus*	idem, p. 190
layer unknown		*Crocidura* sp.	Reumer, pers. comm.
Stavros cave inside	7	*Kritimys catreus*	Mayhew, 1977
		Crocidura sp.	Reumer, pers. comm.
		Mus minotaurus	Mayhew, 1977, p. 193
Stavros macro		*Kritimys catreus*	idem, p. 186
		Crocidura sp.	idem
		H. creutzburgi parvus	Kuss, 1975a
		C. sp. II	De Vos, 1979, this paper
Stavros micro		*Mus bateae*	Mayhew, 1977, p. 186
		Kritimys catreus	idem
		Crocidura sp.	idem
		dormouse	idem, p. 199
Stavros cave outside		*Kritimys catreus*	idem, p. 186
		H. creutzburgi parvus	Kuss, 1975a
Katho Zakros	56	*Kritimys catreus*	idem
		H. cr. parvus	idem
Kharoumes 5	51	*C.* sp. indet.	Dermitzakis, 1977
		Kritimys catreus	idem
		H. cr. creutzburgi	Kuss, 1975a
Kharoumes 4	53	*C.* sp. indet.	Kuss, 1970
		Kritimys catreus	Mayhew, 1977, p. 191
		H. cr. creutzburgi	Kuss, 1975a
Katharo	48	*H. cr. creutzburgi*	Kuss, 1975a
Kharoumes A		*Kritimys catreus*	Mayhew, 1977, p. 191
		Crocidura sp.	idem
Xeros	57	*Kritimys catreus*	idem
		Crocidura sp.	Reumer, pers. comm.
Bali 2	42	*Kritimys catreus*	Mayhew, 1977, p. 200
		Crocidura sp.	idem
Milatos 1	47	*Kritimys catreus*	idem
Cape Maleka 1	9	*Elephas creticus*	Bate, 1907
		Kritimys kiridus	Mayhew, 1977, p. 205
Cape Maleka	11	*Kritimys kiridus*	idem
Sitia 1	49	*Kritimys* aff. *kiridus*	idem, p. 206
		Apodemus sp.	idem
Gumbes 1b	34	*C.* sp. indet.	this paper
		large elephant	pers. observation

Localities with general lists from the literature.

Cave deposit between		Ruminants, Rodents	Bate, 1905, p. 194;

Locality	No. on map (fig. 1)	Remains of	According to
Chanea and Suda	6	and shrew	Mayhew, 1977
		Mus minotaurus	
Gumbes 1	34	*Mus minotaurus*	Kuss & Misonne, 1968
Gumbes 2 = Grida Avlaki	35	*Mus minotaurus*	Kuss & Misonne, 1968, p. 58
		C. sp. indet.	idem
		Human skeleton	Kuss, 1970, p. 74
Skaleta	39	*Mus minotaurus*	Kuss & Misonne, 1968
		C. sp. indet.	idem
		Sus sp.	Kuss, 1970, p. 74
		minoic pottery	idem
Bali 1	41	*Kritimys catreus*	Kuss & Misonne, 1968
		Kritimys kiridus	idem
Cape Maleka 2	10	*Kritimys kiridus*	idem
		Kritimys catreus	idem
Gerani 1	16	*C.* sp. indet.	Kuss, 1975b
Gerani 3	18	*C.* sp. indet.	Kuss, 1970, p. 76
		Human bones, bovids, dog, hare neolithic artefacts	idem, p. 75
Mavro Mouri 1	25	*C.* sp. indet.	Kuss, 1970, p. 77
Mavro Mouri 2	26	*C.* sp. indet.	idem
Mavro Mouri 3	27	*C.* sp. indet.	idem
Mavro Mouri 4	28	a few fossils	idem
Mavro Mouri 6	30	no data are given	idem
Mavro Mouri 7	31	idem	idem
Mavro Mouri 8	32	subrecent animals	idem
Katholiko	8	no bone remains	Kuss, 1965, p. 195
Sphinari	1	ruminants and rodents	idem, p. 197
Kutri 1	2	"Antilope" and "horns and teeth of deer"	Bate, 1905
Kutri 2	2	Mammals	Kuss, 1965, p. 196
Ravduka	3	Ruminants	idem
Tripiti	4	Ruminants and rodents	idem, p. 194
Exopolis	14	*C.* sp. indet.	Kuss, 1965, p. 345
		Elephas?	idem
		murids	idem
Gumbes 3	36	*C.* sp. indet.	Kuss, 1975b, p. 43
		culture layers/ elephant bones	Kuss, 1970, p. 78
Panajia 1	37	*Elephas*	idem
Panajia 2	38	??	idem
Melidoni	13	*C.* sp. indet.	Kuss, 1965, p. 345
Marathi	12	idem	idem, p. 344
Kharoumes 1	55	*Kritimys* sp.	Kuss, 1970, p. 79
		H. cr. creutzburgi	Kuss, 1975a
Kharoumes 7	50	*C.* sp. indet.	Kuss, 1975a
		Kritimys sp.	idem
Peristeri	40	??	Kuss, 1970, p. 78
Gonia	5	*C.* sp. indet.	Dermitzakis, 1977

therefore distinguished an older fauna with *Hippopotamus creutzburgi creutzburgi*, and a younger fauna with *Hippopotamus creutzburgi parvus*. Both subspecies are found together with *Kritimys catreus*. We are inclined to accept Kuss' lineage concept and on the basis of the hippos we thus subdivide the hippo faunas with *Kritimys catreus* into an older and a younger subfauna.

Kuss (1973) distinguished three species of elephants in Crete: viz., the pigmy form *Elephas creticus*, only known from Cape Maleka 1 on Akrotiri, the mainland species *Elephas antiquus* and its local descendant *Elephas creutzburgi*, which is a little smaller. According to Kuss (1965) *Elephas creutzburgi* is the youngest, while *Elephas creticus* is the oldest. This hypothesis is supported by the fact that *Elephas creticus* is found together with *Kritimys* and *Elephas creutzburgi* with *Mus minotaurus*.

VII-3. *Biostratigraphic conclusions*

Lithostratigraphic data can not support a correct biostratigraphy. So we accept the phylogeny on murids (Mayhew, 1977), hippos (Kuss, 1975a) and elephants (Kuss, 1973) as being the most likely framework in the range chart of figure 37. This means that the theory on phylogeny of the deer (Kuss, 1975b) cannot be accepted. Then we can consider the following faunas:

1. There is an earlier *Kritimys* Zone and a later *Mus* Zone. In both Zones *Crocidura* sp. is present. The *Kritimys* Zone ends when *Mus* enters the record.
2. In the *Kritimys* Zone there is a *Kritimys kiridus* Sub-zone and a *Kritimys catreus* Sub-zone. The *Kritimys kiridus* Sub-zone pre-dates the *Kritimys catreus* Sub-zone.
3. In the *Mus* Zone there is a *Mus bateae* Sub-zone and a *Mus minotaurus* Sub-zone. The *Mus-minotaurus* Sub-zone is the younger one.
4. In the *Kritimys catreus* Sub-zone a refinement can be made, based on the ranges of *Hippopotamus*. The earliest part of the Sub-zone is lacking *Hippopotamus*, this is followed by a *Hippopotamus creutzburgi creutzburgi* Range-zone, a *H.c. parvus* Range-zone, and another part without *Hippopotamus*.
5. There are three species of elephants: *Elephas creticus* in the *Kritimys kiridus* Sub-zone, *Elephas antiquus* and its smaller descendant *Elephas creutzburgi*. The latter seems to mark the middle part of the *Mus minotaurus* Zone.
6. Remains of *Candiacervus* s.l. are present in the *Kritimys* Zone as well as in the *Mus* Zone. The history of the deer will be discussed in the following chapters. The range chart gives the impression that proliferation of *Candiacervus* species did not occur prior to the *Mus minotaurus* Sub-zone.

VIII. Origin and evolution of *CANDIACERVUS*

VIII-1. *The successive faunal pictures*

From our range chart of figure 37 it is obvious that our Pleistocene faunas are strongly endemic throughout. Reading all the literature on the various Cretan species we have to acknowledge that authors have made various guesses, but no more, about the ancestry of the mice, hippos, elephants and deer. Evidently there must have been long chains of morphological changes on the island, but so far we have no documentation about them. These changes might well have been rapid, but if the assumptions about the island history of Crete are correct (e.g. Drooger & Meulenkamp, 1973) the last connections with the mainland could well have been during the Late Miocene. This means that there would have been ample time for local development of various groups to such an extent that their ancestry can no longer be retraced from their morphology.

However, we do not believe that we are dealing with relicts of Tertiary faunas, as suggested by Kuss (1973, 1975b). If our range chart is correct, we favour the assumption of successive arrivals by swimming or rafting; otherwise we would have been unable to establish the zonation based on discrete ranges.

According to the range chart the first mammal to arrive on Crete was the ancestor of *Kritimys* aff. *kiridus*, known from Sitia 1 only. This taxon, which is not well known, must have been the ancestor of *Kritimys kiridus* and *Kritimys catreus*, both of which are distinctly endemic. The origin of *Kritimys* is unknown. The best guess seems to be that of Mayhew (1977), who suggested that *Kritimys* came from Asia Minor via Rhodes, during the Late Pliocene, but for the actual ancestor Pleistocene African mice have been proposed. Kuss & Misonne (1968) thought that the African genus *Praomys* is closest to *Kritimys*. Jaeger (1975) described *Praomys* (*Berberomys*) *pomeli* from the Pleistocene of Maghreb; he believes the species to be ancestral to *Kritimys*.

The next arrival on Crete was probably the ancestor of the pigmy *Elephas creticus*. Since this elephant, known from one locality (Cape Maleka 1) only, already shows strong endemic characters, we evidently lack a fair part of its history. So it is not certain that the elephants arrived later than the mice. Elephants are good swimmers (Johnson, 1980) and frequently they are the first of the larger mammals to arrive on an island. There is much evidence (Sondaar, 1977) that elephants were the only Pleistocene large mammals present on islands, e.g. Flores, Timor and Naxos. Such poor faunas may indicate that, at the moment the elephants arrived, the island was so far from the mainland that only elephants could reach it. Once the elephants arrived on Crete they must have evolved into *Elephas creticus*.

Kritimys kiridus evolved to *Kritimys catreus*, and during the range of the latter species *Hippopotamus* and deer arrived on Crete, probably during a period when the distance between the island and the mainland had become reduced by a lowering of the sea-level. The arrival of hippos and deer thus probably took place during a glacial period. The hippos we found had already developed to endemic forms with a specialised locomotion (Boekschoten & Sondaar, 1967); they became smaller in the course of time (Kuss, 1975).

In the localities Kharoumes 4 and 5 and in Stavros macro the hippos are accompanied by deer that cannot be ascribed to any of our eight species. The record of the deer in the *Kritimys* Zone is very poor. Since in the older localities the sediment is strongly indurated we can only state that deer are present. Only in the case of Stavros macro could we ascertain that the deer is *Candiacervus* sp. II (on the weak basis of four first phalanges and two second phalanges).

Later invasions brought *Mus* and again elephants, the latter possibly accompanied by more deer. The *Mus minotaurus* group, which evidently was rather successful on Crete, again shows strongly endemic characters. Kuss & Misonne (1968) have suggested a relationship of *Mus minotaurus* with the Indian species *Mus pahari*, *Mus mayori* and *Mus shortridgei*, as well as with the African species *Mus bufo*. In the opinion of Mayhew (1977) the suggestion of Jaeger (1975) that *Mus minotaurus* descended from an ancestor resembling *Mus musculus* is the most acceptable one. It is considered likely that the extinction of *Kritimys* is a consequence of competition with *Mus*.

The first newly arrived elephant (*E. antiquus* = *E. namadicus* according to Maglio, 1973) is one of the arrivals which was of European origin. The elephants rapidly became smaller in the course of time, which development led to the endemic species *Elephas creutzburgi*.

During the range of this elephant species the deer show a distinct radiation into a large number of species. Possibly there remained descendants of the earlier invasion which had occupied particular niches and therefore the assumedly newly arrived deer had to occupy other niches. The hypsodonty of the teeth of *Candiacervus ropalophorus* and *Candiacervus* sp. II suggests that the acquisition of grazing habits enlarged the number of biotopes outside the realm of forested niches. The radiation also resulted in large-sized species with very slender extremities. The mode of life of such animals remains enigmatic. These large forms were very rare; actually they have been found at two localities only (Liko and Bate Cave). It is possible that the development of these larger deer with assumedly a conservative type of diet caused the extinction of the elephants, after which Crete became an island of deer and mice.

Both in Simonelli Cave (Suriano, in Malatesta, 1980) and at Liko (Weesie, pers. comm.) cold-loving birds have been found. Possibly these sites represent glacial periods and, because in Simonelli Cave the elephants are present and in Liko they are absent, they probably correspond to two different glacial periods.

After the cold period of Liko the climate presumably became warmer and as a consequence the island got smaller as the sea level rose. The change in island size may have caused a reduction of habitats and the extinction of the deer taxa, with the exception of the small *Candiacervus ropalophorus*, which is the only species in the localities Gerani 2 (main layer), Gerani 5 and 6, if these really are the youngest localities.

The extinction of *C. ropalophorus* was probably caused by domestic animals introduced by Man. This we deduce from the finds in Gerani 2. Above the main layer $Ge2_3$ in which we still find *C. ropalophorus* there is a layer without this species, but with traces of human activities and domesticated animals. In this layer *Mus minotaurus* is still present. There is no clear sedimentary break between this layer and layer $Ge2_3$. The extinction of *C. ropalophorus* must have taken place in the Holocene, after the arrival of Man, which is thought to have taken place in the Neolithic. The somewhat later extinction of *Mus minotaurus* probably was caused by the competition of *Rattus* and recent *Mus*, which accompany every human invasion.

VIII-2. *The origin of the Cretan deer*

The range chart fig. 37 shows that the Cretan deer went through a long period of poorly documented history before the fossils are sufficiently distinct and numerous to unravel their morphology. During that period they had become so specialised that ancestral features are difficult to recognize. We need not be amazed that the literature contains diverse speculations on the origin of the Cretan deer.

Our best documentation is on the metapodials, which are either too massive or too slender to be compared with those of mainland species. Only those of *C. rethymnensis* are comparable in massitivity to the metapodials of *Cervus elaphus*; the latter species is commonly used as a reference for mainland species. Unfortunately *Candiacervus rethymnensis* is not the first species to appear in our record. If we accept that such a form must be at the basis of all our deer, we evidently again lack an important part of the history.

More useful than metapodials for the reconstruction of phylogeny are the skulls and the antlers. However, the skulls and the antlers of the later deer from Crete are so different from those of the known Pleistocene mainland species that no distinct clues for relationships are available. It has been suggested (Simonelli, 1907/08; Azzaroli, 1952; Radulesco & Samson, 1967; Sickenberg, 1975) that the sub-basilar position of the brow-tine in our antler types 1, 2 and 4 (our species *C. ropalophorus*, *Candiacervus* sp. IIa, IIb and IIc) points to a relationship with certain mainland genera (*Megaceros*, *Praemegaceros*, *Eucladoceros*, *Cervus*, *Croizetoceros*). These names stand for quite a large group of species, but it is especially the species *verticornis* which is mentioned most frequently (Azzaroli, 1952; Malatesta, 1980). We have no objection to such a hypothesis, but it leaves us with too wide a choice for the actual invaders of Crete. In our opinion the position of the brow-tine is an insufficient argument that there is phylogenetic relationship between specific mainland forms and the Cretan deer, as was suggested by Simonelli (1907/1908), Azzaroli (1952), Radulesco & Samson (1967) and Sickenberg (1975).

It also seems unlikely that Cretan deer had their origin on other Mediterranean islands Corsica and Sardinia, since these islands are too far from Crete. It is much more likely that the various island species each had their own development from possibly the same, but unspecified parental stock.

VIII-3. *The speciation of the Cretan deer*

It is tempting to speculate on the possible mode of development of the eight different taxa of Cretan deer. Because localities with ample deer material are scarce, our reconstruction strongly depends on preconceived ideas about how evolution generally operates. We must be careful with conclusions based on the available material, because we may be comparing fossils of different immigrated stocks, which were not related at all, but merely show similar morphology caused by parallel evolutionary trends. Unfortunately the material is especially scarce for the stratigraphically older localities.

We can safely conclude that the ancestor(s) amongst the mainland species must have had metapodials similar in massivity to those of our *Candiacervus rethymnensis*. If the seven other Cretan species are descended from such a stock we have to accept that evolution led to more massive as well as to more slender metapodials. Trends towards greater massivity of the limb bones are quite common in island speciation; these trends are commonly explained as an adaptation to mountainous terrains. The absence of predators would be another argument that such greater stability and reduction in speed caused no harm during escape. The development to long and slender metapodials is more difficult to explain, unless one wishes to assume that increasing height of the animals was an advantage in browsing.

Irrespective of whether these adaptive trends occurred or not, the major problem is why so many different species developed on one island, presumably during the same time. On the mainland we usually never find more than three deer species together in the same area, but never eight, which moreover are morphologically much closer. Probably the array of specialization was much wider than is usual for deer. The wear pattern of *C. ropalophorus* suggests that this species lived mainly on grass, and also for the group of *Candiacervus* II species goat-like living patterns (i.e. eating grasses as well as shrubs) are quite likely. Unfortunately we do not know what the teeth of the other species were like, but it is likely that some of them continued with the old browsing habits.

Such a complex composition of the faunas of the Cretan deer is difficult to reconcile with the existing theories of one invasion (Malatesta, 1980) or two invasions (Kuss, 1975) and a reduction in size after each arrival.

Malatesta (1980) assumes that there was only one invasion and that all taxa originated from this single ancestral stock. The large specimens were explained as aberrant specimens.

Kuss (1975b) supposed that there were two invasions and that subsequent evolution led to smaller species, his *C. cretensis* and to his *C. rethymnensis*, respectively. For both species Kuss (1975b) supposed a reduction in size with time.

Both models cannot explain the presence of three or more species at many localities. Moreover, our range chart does not give the impression that size reduction was the overall trend. It is true, size reduction did occur and the smallest species *Candiacervus ropalophorus* is the one surviving longest, but nowhere can we find clear evidence for a gradual size decrease. It seems more likely that a sudden radiation caused the wide variation of species and that thereafter each species remained more or less stable. But maybe we are idealizing the value of our range chart.

Nevertheless, we believe that there were at least two successive invasions of deer, mainly because it seems to be difficult to explain simultaneous genetic isolation of so many groups from a single invading stock. The range chart gives ample opportunity for a first invasion in the *Kritimys* Zone from which presumably the relatively small deer *Candiacervus* sp. II originated (and possibly *C. ropalophorus* and *C. cretensis*) present in Kharoumes 2 in hard sediment). The second invasion left more traces of the original stock in *C. rethymnensis* from which our large forms would have originated. It is also possible that our *C. cretensis* originated from the parental stock of the second invasion.

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TABLES

	Gerani 2	Gerani 4	Gerani 5	Gerani 6	Sourida	Mavro Mouri 4c	Liko	Rethymnon fissure	Gumbes 1b
P^2-M^3	4	70	-	-	-	2	28	-	-
P^2-P^4	4	58	-	-	-	7	22	-	-
M^1-M^3	6	75	1	-	3	5	26	-	-
P^2	5	59	-	-	4	23	21	8	1
P^3	5	67	1	-	4	13	21	13	-
P^4	6	78	2	-	3	16	27	7	-
M^1	6	84	2	2	6	8	36	-	1
M^2	6	97	1	2	6	12	37	-	1
M^3	6	84	2	2	7	39	34	5	-
P_2-M_3	5	43	-	3	6	-	18	-	1
P_2-P_4	6	47	-	1	2	-	36	-	1
M_1-M_3	7	78	1	3	10	1	51	-	1
P_2	5	44	-	1	4	5	39	1	1
P_3	8	70	3	3	10	2	53	1	1
P_4	7	85	6	5	9	2	54	2	1
M_1	7	88	5	4	13	4	56	2	1
M_2	7	83	5	5	13	4	59	3	1
M_3	7	82	3	5	13	8	54	13	1
Skulls ♂	-	17	-	-	-	-	3	-	-
♀	-	22	-	-	-	-	2	-	-
antlers/ fragments	-	57	-	-	-	8	266	-	-

Table 1. The number of cranial and dental elements studied from each locality.

	Locality	N	Min. - Max.	M	SD	V
P^2-M^3	Gerani 4	70	53.2 -71.7	62.79	3.67	5.84
	Liko	28	62.7 -90.0	73.70	8.02	10.88
	Mavro Mouri 4c	2	69.2 -72.6	70.90	2.40	3.38
P^2-P^4	Gerani 4	58	22.3 -31.4	25.96	1.89	7.28
	Liko	22	25.5 -40.8	31.02	4.13	13.31
	Mavro Mouri 4c	7	25.1 -30.8	28.89	1.98	6.85
M^1-M^3	Gerani 4	75	31.3 -43.9	37.38	2.80	7.49
	Liko	26	33.7 -55.8	43.46	5.90	13.57
	Mavro Mouri 4c	5	34.8 -43.4	38.60	3.47	8.98
P_2-M_3	Gerani 4	43	62.2 -72.8	67.22	2.51	3.73
	Liko	18	67.6 -82.6	75.37	4.27	5.66
	Mavro Mouri 4c	1	76.8	-	-	-
P_2-P_4	Gerani 4	47	22.0 -27.6	24.87	1.34	5.38
	Liko	36	24.6 -35.4	28.19	2.16	7.66
M_1-M_3	Gerani 4	78	39.8 -48.2	43.07	1.77	4.10
	Liko	51	40.8 -56.5	47.95	3.47	7.23
	Mavro Mouri 4c	1	48.0	-	-	-

Table 2. Measurements of the toothrows of the Cretan deer from different localities.

	Locality	N	Min. - Max.	M	SD	V
P^2 Length	Gerani 4	59	8.4 - 11.6	9.45	0.67	7.08
	Liko	21	9.1 - 12.2	10.42	0.88	8.44
	Mavro Mouri 4c	23	8.1 - 11.8	9.83	0.96	9.76
	RES	8	8.2 - 11.5	9.48	1.07	11.28
Width	Gerani 4	59	9.0 - 11.8	10.41	0.65	6.24
	Liko	20	9.5 - 14.0	12.10	1.33	10.99
	Mavro Mouri 4c	23	8.5 - 13.9	11.27	1.46	12.95
	RES	8	9.6 - 13.7	11.58	1.77	15.28
P^3 Length	Gerani 4	67	7.2 - 10.1	8.48	0.73	8.60
	Liko	21	8.2 - 12.1	9.62	1.17	12.16
	Mavro Mouri 4c	14	6.3 - 10.9	9.38	1.21	12.89
	RES	14	8.0 - 11.2	9.58	1.07	11.16
Width	Gerani 4	65	9.2 - 13.2	11.50	0.67	5.82
	Liko	20	11.6 - 16.1	13.65	1.42	10.40
	Mavro Mouri 4c	13	10.7 - 15.0	13.11	1.45	11.06
	RES	13	10.0 - 16.8	13.91	2.10	15.09
P^4 Length	Gerani 4	78	5.6 - 9.6	7.53	1.01	13.41
	Liko	27	6.6 - 11.6	8.81	1.21	13.73
	Mavro Mouri 4c	16	7.0 - 10.7	8.94	1.15	12.86
	RES	7	6.8 - 9.8	8.67	1.04	11.99
Width	Gerani 4	72	11.9 - 15.0	13.00	0.63	4.84
	Liko	24	12.5 - 18.1	14.74	1.51	10.24
	Mavro Mouri 4c	13	13.4 - 15.5	14.42	0.64	4.43
	RES	7	11.6 - 14.0	12.51	0.84	6.79

Table 3. Measurements of the upper premolars from different localities

	Locality	N	Min. - Max.	M	SD	V
M^1 Length	Gerani 4	84	9.0 - 15.6	11.57	1.46	12.61
	Liko	36	10.2 - 17.6	13.35	2.23	16.70
	Mavro Mouri 4c	8	9.0 - 15.7	12.30	2.08	16.91
Width	Gerani 4	78	13.2 - 16.4	14.69	0.71	4.83
	Liko	33	13.2 - 19.3	16.25	1.46	8.98
	Mavro Mouri 4c	8	14.0 - 16.7	15.50	0.92	5.95
M^2 Length	Gerani 4	97	10.2 - 16.2	13.01	1.31	10.06
	Liko	37	10.6 - 18.5	14.58	2.12	14.54
	Mavro Mouri 4c	12	12.6 - 16.1	13.89	1.14	8.20
Width	Gerani 4	96	14.0 - 18.1	15.67	0.84	5.36
	Liko	36	15.0 - 21.2	17.50	1.58	9.02
	Mavro Mouri 4c	12	15.2 - 18.2	16.63	0.92	5.53
M^3 Length	Gerani 4	84	11.2 - 14.7	13.13	0.92	7.00
	Liko	34	10.7 - 17.4	14.82	1.54	10.39
	Mavro Mouri 4c	39	11.4 - 15.8	14.09	1.03	7.31
	RES	5	14.2 - 15.2	14.74	0.41	2.78
Width	Gerani 4	72	13.0 - 17.3	14.89	0.87	5.84
	Liko	34	14.5 - 20.4	16.85	1.49	8.84
	Mavro Mouri 4c	36	14.4 - 18.2	16.30	1.20	7.36
	RES	5	14.9 - 17.6	16.18	1.02	6.30

Table 4. Measurements of the upper molars from different localities.

	Locality	N	Min. - Max.	M	SD	V
P_2 Length	Gerani 4	44	6.2 - 8.1	7.15	0.46	6.43
	Liko	39	6.6 - 10.6	8.15	0.89	10.92
	Mavro Mouri 4c	5	7.0 - 9.4	8.22	0.96	11.67
	RES	1	9.4	-	-	-
Width	Gerani 4	44	4.4 - 5.8	5.04	0.36	7.14
	Liko	39	4.6 - 7.4	5.83	0.72	12.34
	Mavro Mouri 4c	5	4.7 - 6.8	5.96	0.98	16.44
	RES	1	6.4	-	-	-
P_3 Length	Gerani 4	70	7.8 - 10.8	9.13	0.67	7.33
	Liko	53	8.2 - 13.4	10.06	0.94	9.34
	Mavro Mouri 4c	2	6.9 - 8.8	7.85	1.34	17.07
	RES	1	11.6	-	-	-
Width	Gerani 4	68	5.4 - 7.2	6.38	0.42	6.58
	Liko	52	5.8 - 8.9	7.10	0.70	9.85
	Mavro Mouri 4c	2	6.4 - 8.4	7.40	1.41	2.00
	RES	1	7.4	-	-	-
P_4 Length	Gerani 4	85	7.6 - 10.6	9.30	0.63	6.77
	Liko	54	7.9 - 12.1	10.20	0.83	8.13
	Mavro Mouri 4c	2	9.4 - 10.2	9.80	0.57	5.81
	RES	2	10.2 - 12.0	11.10	1.27	11.44
Width	Gerani 4	82	6.1 - 8.6	7.39	0.50	6.76
	Liko	50	6.6 - 9.9	8.19	0.67	8.18
	Mavro Mouri 4c	2	7.5 - 8.9	8.20	0.99	12.07
	RES	2	8.0 - 8.7	8.35	0.49	5.86

Table 5. Measurements of the lower premolars from different localities.

	Locality	N	Min. - Max.	M	SD	V
M_1 Length	Gerani 4	88	9.8 - 15.1	12.26	1.08	8.80
	Liko	56	11.2 - 16.3	13.60	1.36	10.00
	Mavro Mouri 4c	4	13.1 - 14.5	13.58	0.66	4.86
	RES	2	13.9 - 16.1	15.00	1.56	10.40
Width	Gerani 4	79	8.2 - 10.4	9.27	0.46	4.96
	Liko	49	8.7 - 12.4	10.29	0.93	9.03
	Mavro Mouri 4c	4	9.4 - 10.9	10.05	0.62	6.16
	RES	2	10.4 - 10.6	10.50	0.14	1.33
M_2 Length	Gerani 4	83	11.4 - 16.3	13.81	1.06	7.67
	Liko	59	12.5 - 18.6	15.07	1.31	8.69
	Mavro Mouri 4c	4	14.4 - 16.9	16.10	1.16	7.20
	RES	3	12.2 - 15.0	14.03	1.59	11.33
Width	Gerani 4	67	8.4 - 10.3	9.37	0.49	5.22
	Liko	49	8.6 - 12.5	10.51	0.94	8.94
	Mavro Mouri 4c	3	9.2 - 10.9	10.17	0.87	8.55
	RES	3	9.1 - 10.7	10.10	0.87	8.61
M_3 Length	Gerani 4	82	15.6 - 19.9	17.43	0.82	4.70
	Liko	54	16.7 - 23.4	19.33	1.50	7.75
	Mavro Mouri 4c	8	16.9 - 20.9	19.16	1.46	7.62
	RES	13	17.9 - 21.9	19.08	1.08	5.66
Width	Gerani 4	67	7.9 - 10.2	8.90	0.51	5.73
	Liko	47	8.2 - 12.6	10.11	1.05	10.88
	Mavro Mouri 4c	5	8.9 - 11.2	9.88	0.93	9.41
	RES	15	8.6 - 11.7	10.21	0.94	9.20

Table 6. Measurements of the lower molars from different localities.

Locality	sex	skull no	basilar length (prosthion-basion) 1	width byzygomatic (zygion-zygion) 2	height of the linea-nuchalis superior to the basion 3	width of the occipitale (othion-othion) 4	DAP of the orbit 5	height of the orbit 6	index 1 : 2/1	index 2 : 6/5	index 3 : 4/3
Gerani 4	male	1	-	105.8	54.4	83.3	29.9	28.2	-	0.95	1.53
		2	-	109.2	-	-	32.0	32.2	-	0.98	-
		3	-	-	57.3	90.5	-	-	-	-	1.57
		4	-	-	57.2	-	31.2	31.0	-	0.99	-
		5	-	-	-	-	30.2	29.6	-	0.98	-
		6	-	102.7	54.7	84.9	30.6	29.5	-	0.96	1.55
		7	-	-	54.4	-	-	-	-	-	-
		8	-	112.9	57.1	89.1	33.9	31.9	-	0.94	1.56
		9	-	110.0	-	81.9	29.8	30.0	-	0.99	-
		11	-	-	55.9	-	-	-	-	-	-
		12	-	-	-	-	30.3	32.4	-	1.06	-
		14	-	-	54.8	82.0	-	-	-	-	1.49
		18	196.7	109.1	52.9	82.0	29.8	29.2	0.55	1.03	1.55
		17	-	99.8	50.0	81.4	30.4	29.8	-	0.96	1.62
		46	195.3	110.2	57.6	91.2	31.3	32.0	0.56	1.05	1.58
		47	196.3	110.0	54.0	82.0	29.6	30.2	0.56	1.02	1.51
Li		759	-	115.7	63.6	91.9	35.2	29.8	-	0.85	1.44
		757	218.8	120.5	60.2	98.2	32.8	34.8	0.55	0.94	1.63
		758	-	-	64.8	93.8	32.3	31.2	-	0.97	1.44
Gerani 4	female	19	-	-	51.2	-	29.5	27.9	-	0.95	-
		20	-	-	54.9	74.5	30.7	29.8	-	0.97	1.35
		21	-	-	53.6	72.1	28.8	28.6	-	0.99	1.34
		23	-	96.2	53.2	74.2	30.2	27.9	-	0.92	1.39
		24	-	-	55.6	75.3	31.4	28.6	-	0.90	1.35
		25	-	-	49.5	71.9	29.6	28.6	-	0.97	1.45
		26	-	-	51.9	72.7	-	-	-	-	1.40
		27	-	-	53.9	70.6	-	-	-	-	1.30
		28	-	-	-	-	29.1	29.2	-	1.00	-
		31	-	95.0	-	-	29.2	28.5	-	0.98	-
		33	-	-	52.7	74.3	29.4	29.2	-	0.99	1.40
		34	-	-	51.0	73.0	29.2	28.6	-	0.98	1.43
		35	-	100.9	54.4	76.1	30.5	29.1	-	0.95	1.39
		36	-	90.6	49.4	69.5	27.8	27.3	-	0.98	1.40
		37	-	92.0	51.8	68.5	31.3	29.4	-	0.94	1.32
		39	192.0	-	50.1	68.1	28.2	28.2	-	1.00	1.35
		40	-	-	50.8	71.7	31.0	28.6	-	0.92	1.41
		42	-	-	51.4	68.1	-	-	-	-	1.32
		43	-	-	50.1	73.9	29.8	29.6	-	0.99	1.47
		45	-	99.3	52.7	73.3	28.0	27.6	-	0.99	1.39
		48	192.9	95.1	53.4	72.7	29.0	27.7	0.49	0.92	1.36
Li		756	-	-	53.4	74.8	31.2	30.4	-	0.97	1.40

Table 7. Measurements of the skulls from the localities Gerani 4 and Liko

Gerani 4 skulls	sex	N	Min. - Max.	M	SD	V
basilar length (prosthion-basion)	♂	3	195.3-196.7	196.10	0.72	0.36
	♀	2	192.0-192.9	192.45	0.64	0.33
width byzygomatic (zygion-zygion)	♂	9	99.8-112.9	107.74	4.17	3.87
	♀	7	90.6-100.9	95.59	3.67	3.83
height of the linea-nuchalis superior to the basion	♂	13	50.0- 57.8	55.24	2.24	4.05
	♀	18	49.4- 55.6	52.31	1.82	3.47
DAP of the orbit	♂	21	28.2- 33.9	30.74	1.46	4.74
	♀	21	27.9- 31.4	29.42	0.89	3.02
height of the orbit	♂	22	28.2- 33.6	30.53	1.53	5.01
	♀	22	27.3- 29.8	28.50	0.69	2.42

Table 8. Survey of the parameters of table 7.

		t	number of degrees of freedom	probability smaller than	level 95%
P^2-M^3	length	9.3444	96	0.001	+
P^2-P^4	length	12.2961	78	0.001	+
M^1-M^3	length	6.9796	99	0.001	+
P^2	length	5.2318	78	0.001	+
	width	7.5182	77	0.001	+
P^3	length	5.3450	86	0.001	+
	width	9.3555	83	0.001	+
P^4	length	5.3874	103	0.001	+
	width	8.0555	94	0.001	+
M^1	length	5.1811	118	0.001	+
	width	7.5811	109	0.001	+
M^2	length	5.1659	132	0.001	+
	width	8.5919	130	0.001	+
M^3	length	7.3480	116	0.001	+
	width	8.5235	104	0.001	+
P_2-M_3	length	9.3029	59	0.001	+
P_2-P_4	length	8.6033	81	0.001	+
M_1-M_3	length	10.5165	127	0.001	+
P_2	length	6.5362	81	0.001	+
	width	6.4308	81	0.001	+
P_3	length	6.4059	121	0.001	+
	width	6.9978	118	0.001	+
P_4	length	7.2429	137	0.001	+
	width	7.8211	130	0.001	+
M_1	length	6.5529	142	0.001	+
	width	8.2657	126	0.001	+
M_2	length	6.3238	140	0.001	+
	width	8.4836	114	0.001	+
M_3	length	9.5218	134	0.001	+
	width	10. 4926	112	0.001	+

Table 9. Comparison between teeth from Gerani 4 (size A) and Liko (size B).

	$P^2 - M^3$			$P^2 - P^4$			$M^1 - M^3$		
	N	Min. - Max.	M	N	Min. - Max.	M	N	Min. - Max.	M
size A	70	53.2 - 71.7	62.7	58	22.3 - 31.4	25.9	75	31.9 - 43.9	37.3
size B	18	62.7 - 77.5	69.9	15	25.5 - 33.2	28.6	21	33.7 - 46.8	41.1
size C	4	85.2 - 90.9	88.3	4	34.4 - 36.2	35.1	4	52.2 - 53.0	52.5

Table 10. Comparison of the ranges and means of the three different teeth size groups (upper tooth-rows).

	size of post-cranial skeletal elements						types of skull				size of teeth morphotype P^2			type of antler				
	1	2	3	4	5	6	a	b	c	d	A	B	C	1	2	3	4	5
Gerani 2	+			+							1			+				
Gerani 4	+	+					+				1	2		+			+	
Gerani 5	+										1			+				
Gerani 6	+										1			+				
Liko		+	+	+		+		+	+	+		1	1,3		+	+	+	
Mavro Mouri 4c	+	+	+	+							1	1,2						
Stavros macro		+																
Bate cave					+	+												
Sourida	+	+		+							1	2						
Mavro Mouri 3																	+	
Simonelli Cave	+	+		?													+	+
Gumbes 2																	+	
Rethymnon fissure	+	+	+	+							1	1,2						
Kalo Chorafi	+	+												+			+	+
Kharoumes 2		+	+															

Table 11. Distribution of the recognizable types in the material over the studied localities

	size B from Gerani 4							
	Ge4-3015		Ge4-193					
	P^2	P^3	M_1-M_3	P_3	P_4	M_1	M_2	M_3
length	11.4	9.9	50.8	10.1	11.8	14.6	16.7	21.6
width	13.2	15.3	-	8.5	9.2	10.9	10.9	10.7

Table 12. Measurements of teeth material from Gerani 4 of size B.

		t	number of degrees of freedom	probability smaller than	level 95%
P^2	length	2.8860	58	0.01	+
	width	4.2563	28	0.001	+
P^3	length	1.9308	66	0.1	-
	width	5.6285	64	0.001	+
M_1-M_3	length	4.3395	77	0.001	+
P_3	length	1.4375	69	0.2	-
	width	5.0109	67	0.001	+
P_4	length	3.9451	84	0.001	+
	width	3 5981	81	0.001	+
M_1	length	2.1544	87	0.05	+
	width	3.5212	78	0.001	+
M_2	length	2.7103	82	0.01	+
	width	3.0994	66	0.01	+
M_3	length	5.0546	81	0.001	+
	width	3.5033	66	0.001	+

Table 13. Comparison between the measurements of material of size A from Gerani 4 with those of size B from Liko.

Taxonomic deer groupings	size post-cranial skeletal elements	Teeth morphotype P^2	size	skull type	antler type
I *Candiacervus ropalophorus*	1	1	A	a	1
IIa	2	1	B	b	2
IIb	2	?	B	c	3
IIc	2	2	B	d	4
III *Candiacervus cretensis*	3				
IV *Candiacervus rethymnensis*	4				
V	5				
VI	6				

Table 14. The different taxonomic deer groups of Crete with their characters.

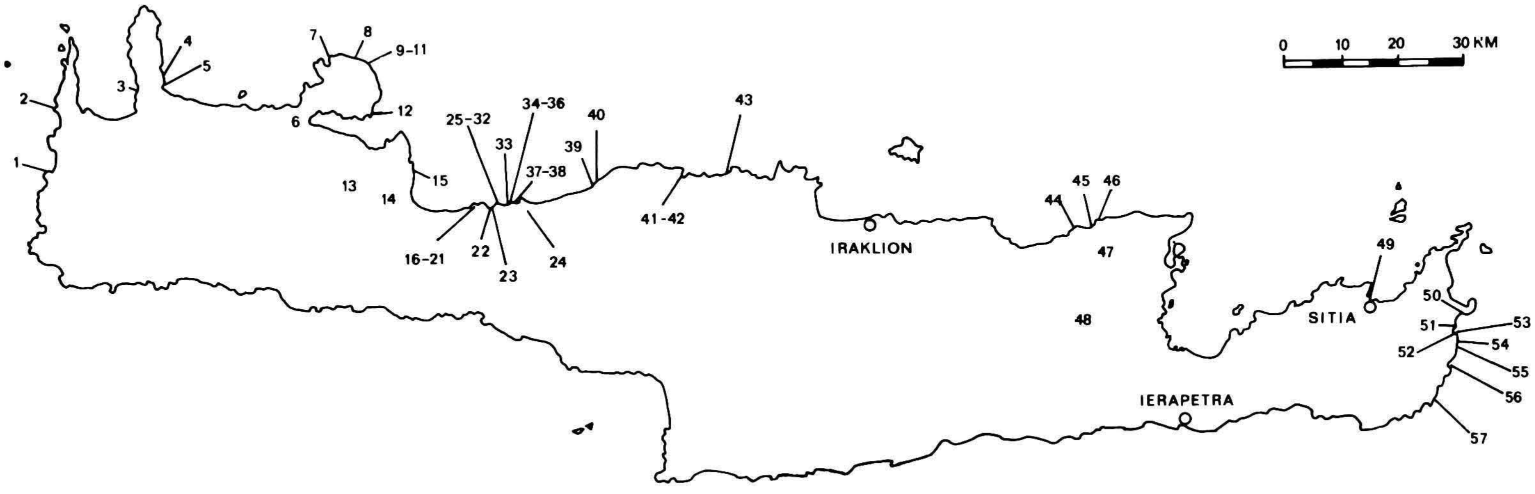


Fig. 1. Map of Crete indicating the positions of the localities mentioned in this paper.

1. Sphinari
2. Kutri
3. Ravduka
4. Tripiti
5. Gonia
6. Caves between Chania and Souda
7. Stavros localities
8. Katholiko
9. Cape Maleka 1
10. Cape Maleka 2
11. Cape Maleka 3
12. Marathi
13. Melidoni
14. Exopolis
15. Liko
16. Gerani 1
17. Gerani 2
18. Gerani 3
19. Gerani 4
20. Gerani 5
21. Gerani 6
22. Bate Cave
23. Sourida
24. Rethymnon fissure
25. Mavro Mouri 1
26. Mavro Mouri 2
27. Mavro Mouri 3
28. Mavro Mouri 4c
29. Mavro Mouri 5
30. Mavro Mouri 6
31. Mavro Mouri 7
32. Mavro Mouri 8
33. Simonelli Cave
34. Gumbes 1b
35. Gumbes 2 (= Grida Avlaki)
36. Gumbes 3
37. Panaija 1
38. Panaija 2
39. Skaleta
40. Peristeri
41. Bali 1
42. Bali 2
43. Kalo Chorafi
44. Milatos 4
45. Milatos 3
46. Milatos 2
47. Milatos 1
48. Katharo
49. Sitia 1
50. Kharoumes 7
51. Kharoumes 5
52. Kharoumes 3
53. Kharoumes 4
54. Kharoumes 2
55. Kharoumes 1
56. Kato Zakros
57. Xeros

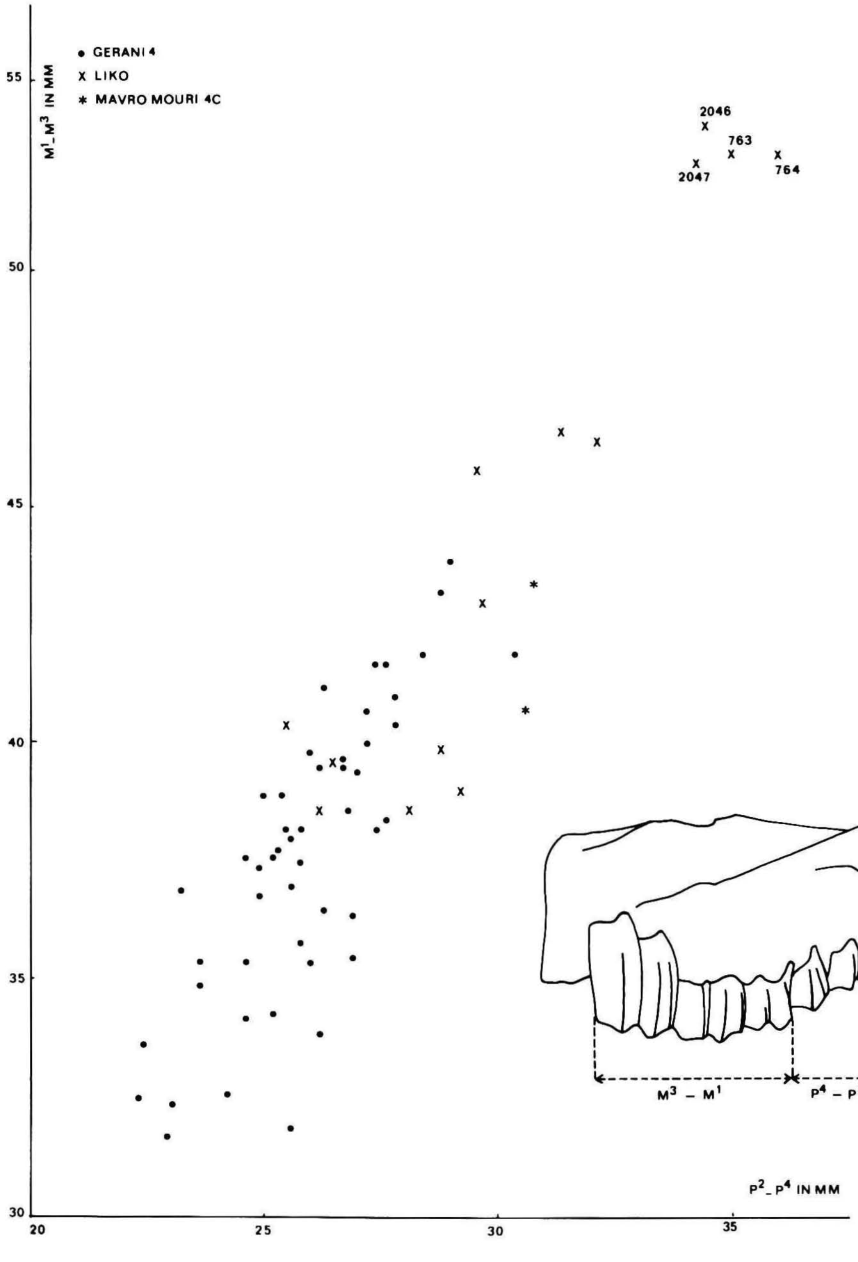


Fig. 2. The relation between the length of the M^1–M^3 and the length of the P^2–P^4 from different localities.

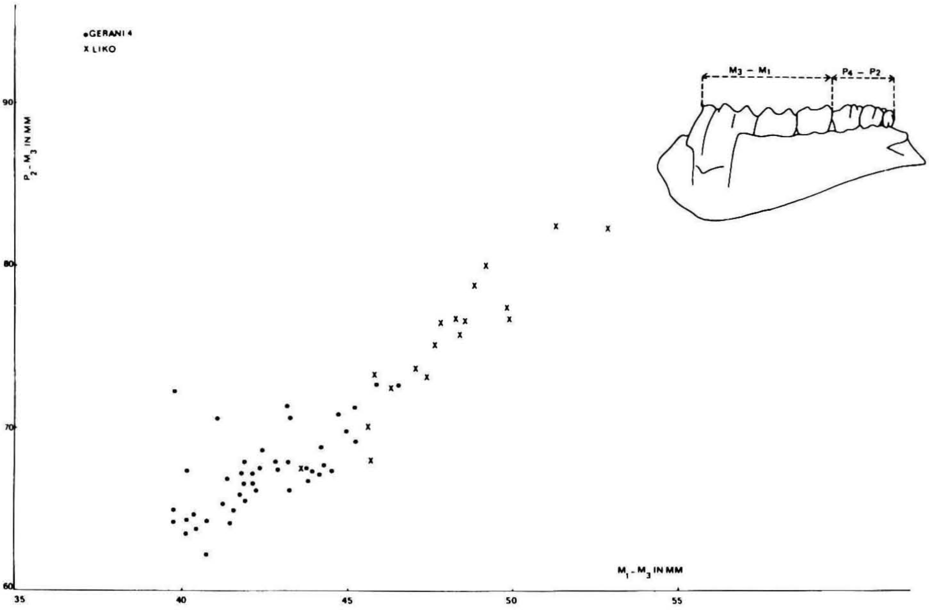


Fig. 3. The relation between the length of P_2–M_3 and M_1–M_3 from different localities.

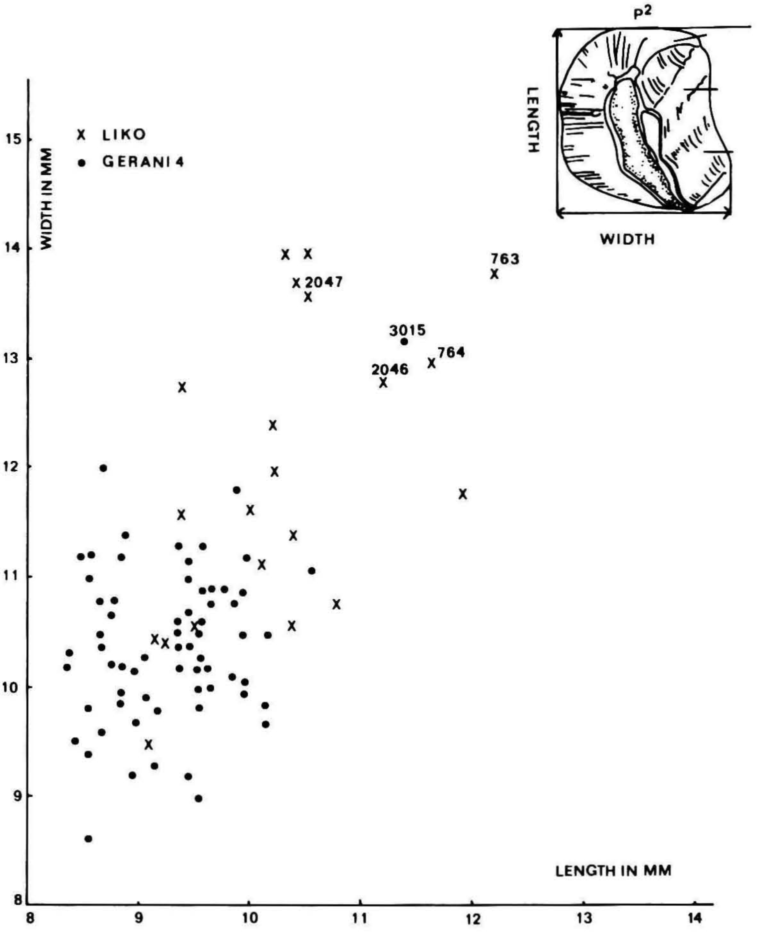


Fig. 4a. The relation between the length and the width of the P^2 from Gerani 4 and Liko.

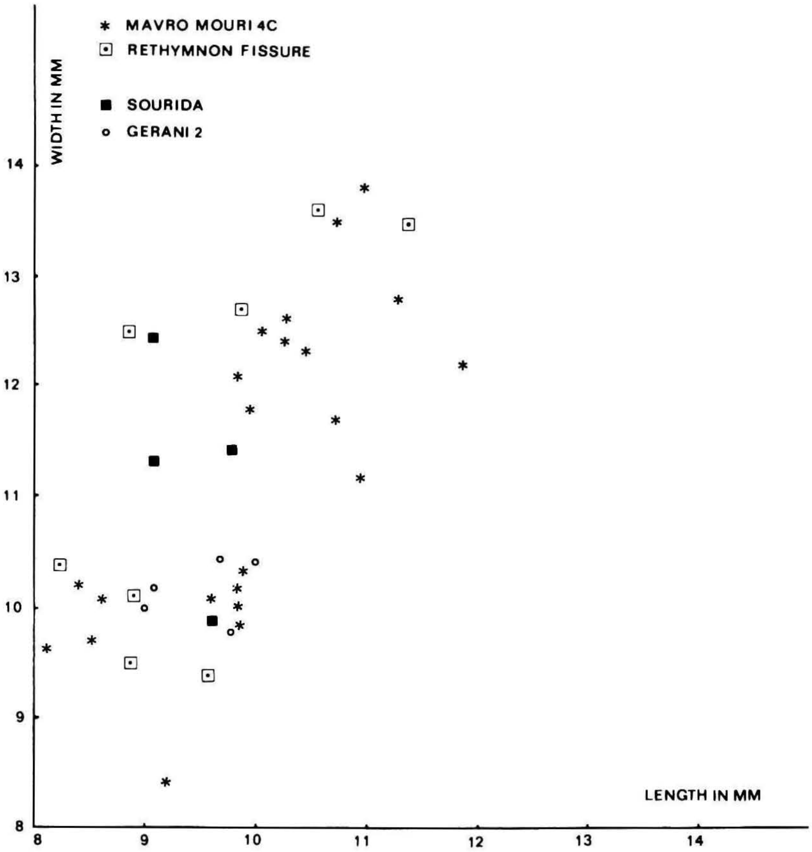


Fig. 4b. The relation between the length and the width of the P^2 from different localities.

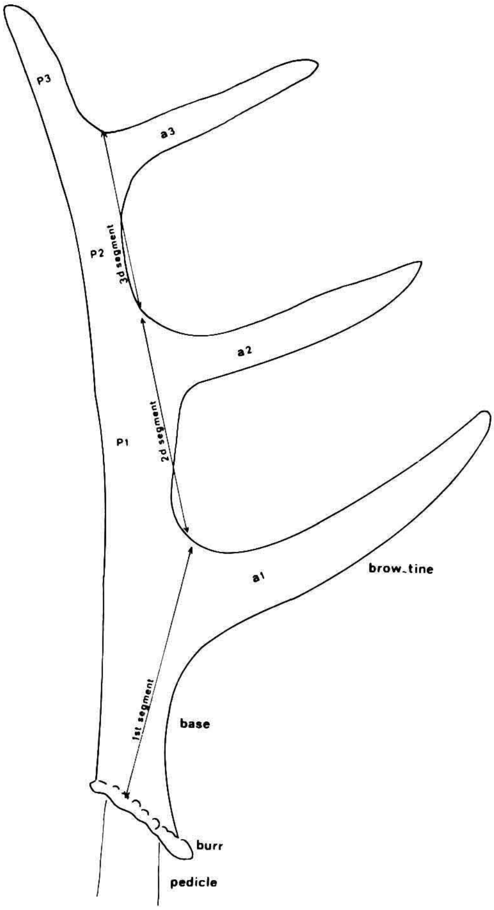


Fig. 5. Illustration of the nomenclature and the methodology of measuring of antlers (a left antler seen from the inner side).

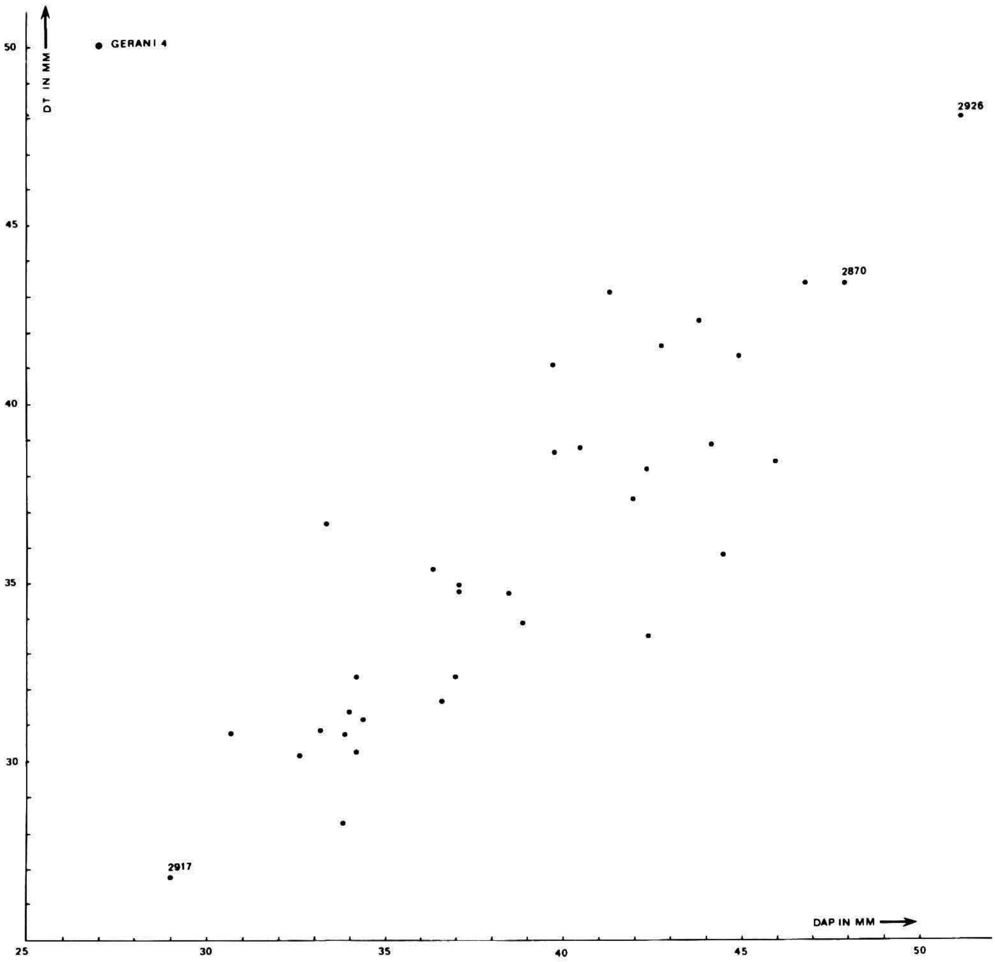


Fig. 6. The relation between the DAP and DT of the burrs of full-grown antlers from Gerani 4.

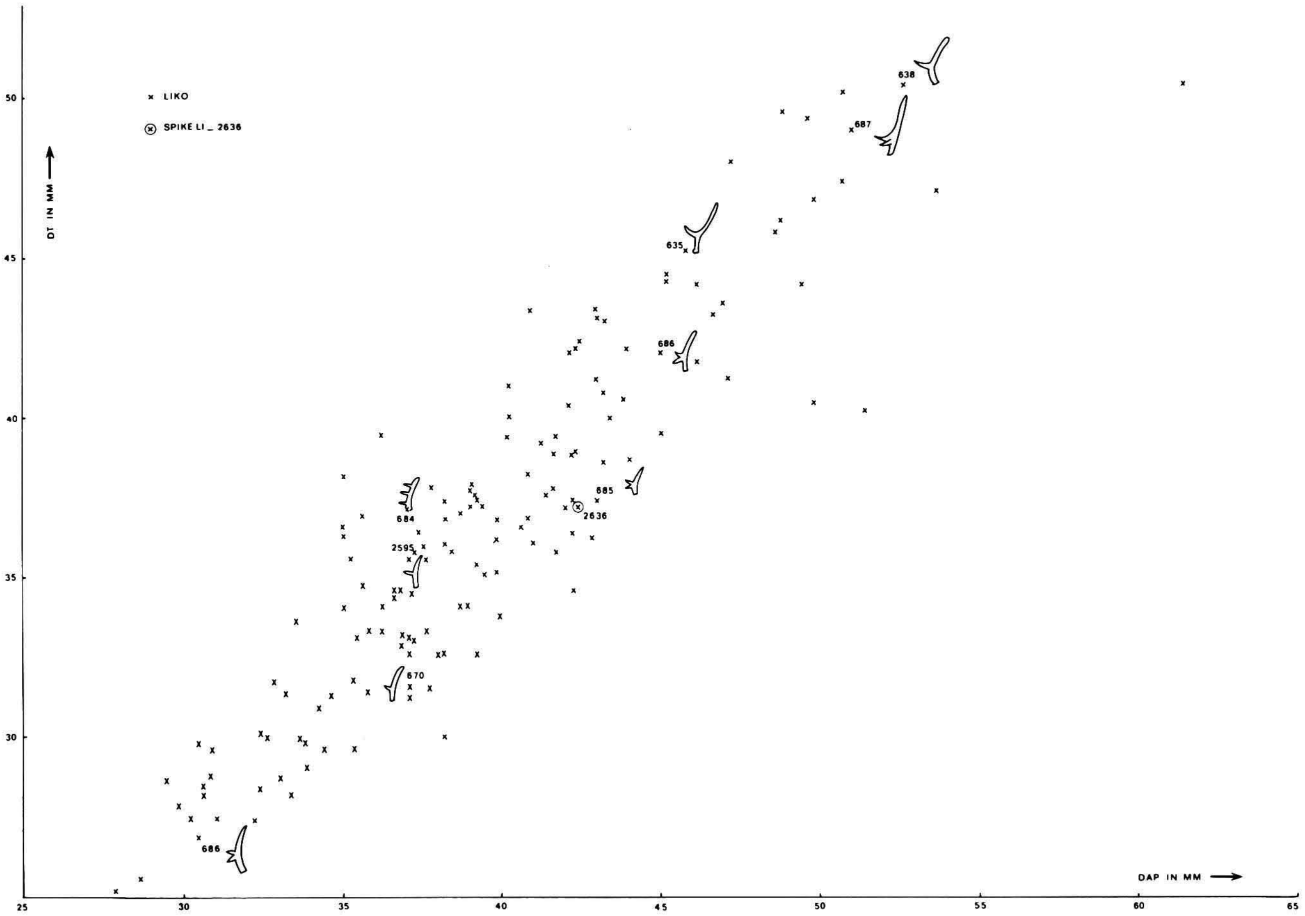


Fig. 7. The relation between the DAP and DT of the burrs of full-grown antlers, with the exception of spike Li-2636 from Liko.

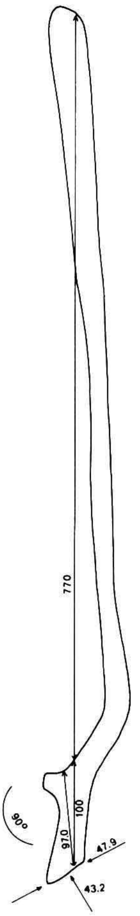


Fig. 8. Ge-2870, right antler, seen from the inside. Type-specimen of antler type-1.

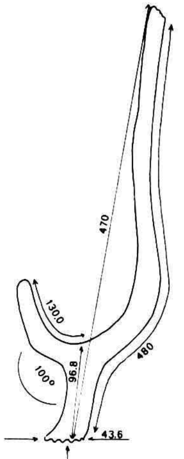


Fig. 9. Li-2593, right antler, seen from the inside. Type-specimen of antler type-2.

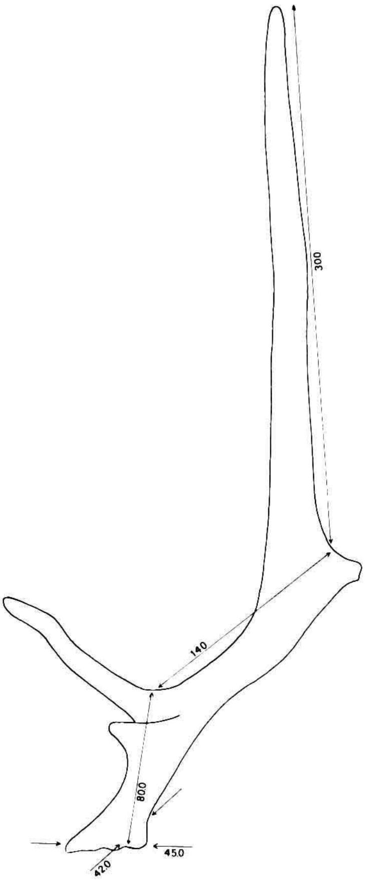


Fig. 10. Li-686, right antler, seen from the inside. Type-specimen of antler type-3.

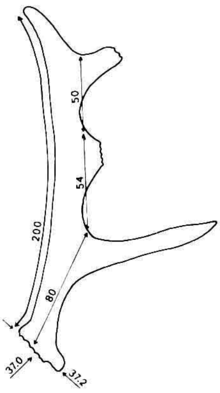


Fig. 11. Li-684, left antler, seen from the inside. Type-specimen of antler type-4.

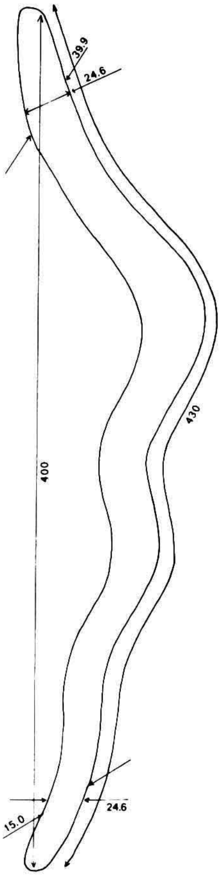


Fig. 12. A bludgeon-shaped distal end of the beam with a wavy appearance. (Specimen Ge4-3522).

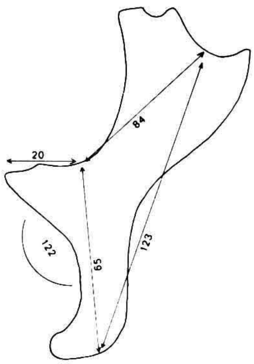


Fig. 13. Ge-2909, right antler, seen from the inside. (antler-type 4).

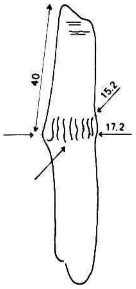


Fig. 14. Li-2614, spike attached to the pedicle.

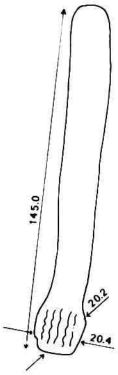


Fig. 15. Li-2627, shed spike.

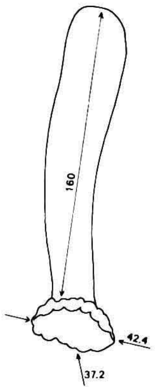


Fig. 16. Li-2636, shed spike.

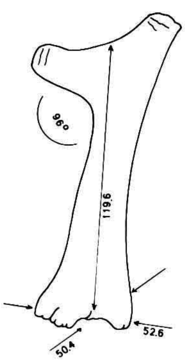


Fig. 17. Li-688, right antler, seen from the inside.

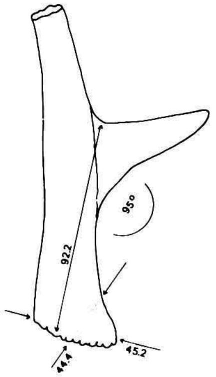


Fig. 18. Li-2585, left antler, seen from the inside.

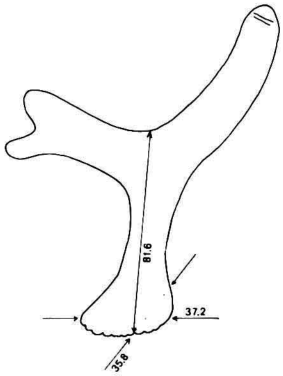


Fig. 19. Li-2595, right antler, seen from the inside.

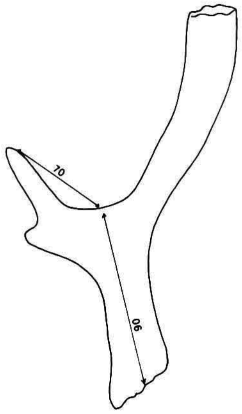


Fig. 20. Li-669, right antler, seen from the inside.

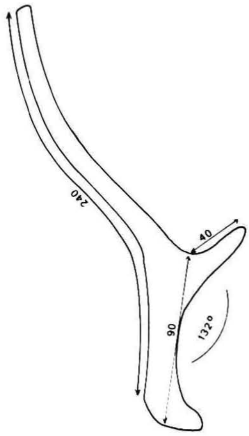


Fig. 21. Li-657, left antler,
seen from the inside.

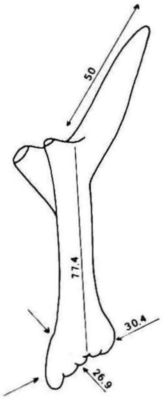


Fig. 22. Li-688, right antler,
seen from the inside (antler-type 3).

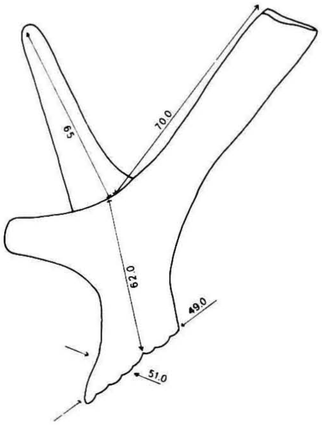


Fig. 23. Li-687, right antler,
seen from the inside (antler-type 3).

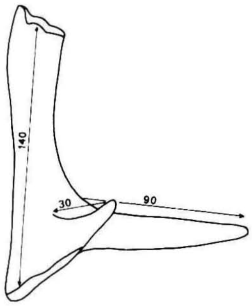


Fig. 24. Li-2607, left antler,
seen from the inside (antler-type 3).

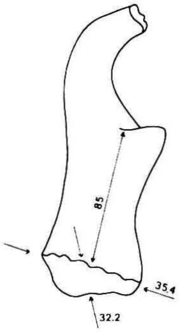


Fig. 25. Li-2608, left antler,
seen from the inside (antler-type 3).

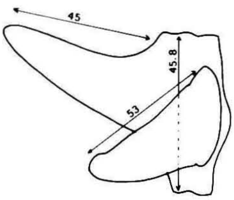


Fig. 26. Li-2609, right antler,
seen from the inside (antler-type 3).

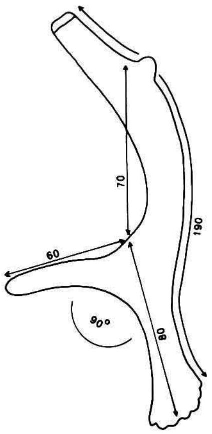


Fig. 27. Li-643, right antler,
seen from the inside (antler-type 4).

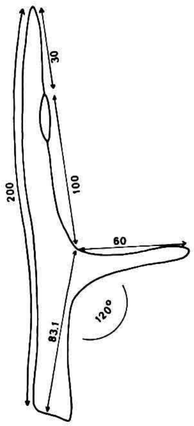


Fig. 28. Li-2603, left antler,
seen from the inside (antler-type 4).

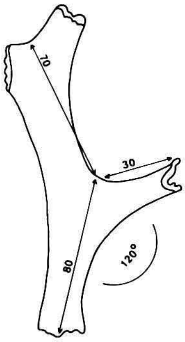


Fig. 29. Li-2601, left antler,
seen from the inside (antler-type 4).

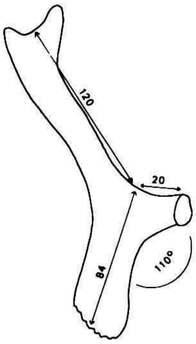


Fig. 30. Li-677, left antler,
seen from the inside (antler-type 4).

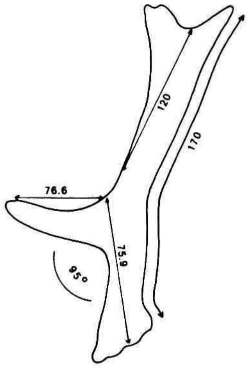


Fig. 31. Li-2604, right antler,
seen from the inside (antler-type 4).

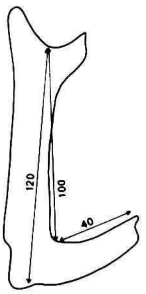


Fig. 32. Li-2600, left antler,
seen from the inside (antler-type 4).

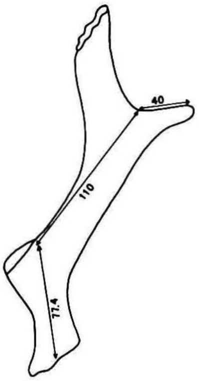


Fig. 33. Li-2605, right antler,
seen from the inside (antlr-type 4).

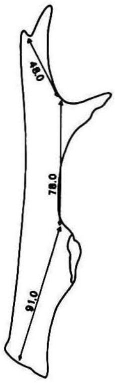


Fig. 34. Li-2598, left antler,
seen from the inside (antler-type 4).

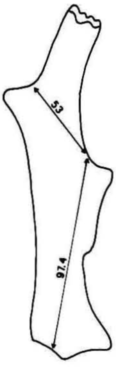


Fig. 35. Li-2602, left antler,
seen from the inside (antler-type 4).

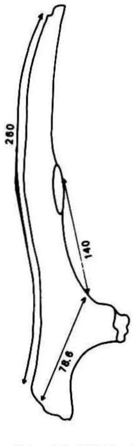


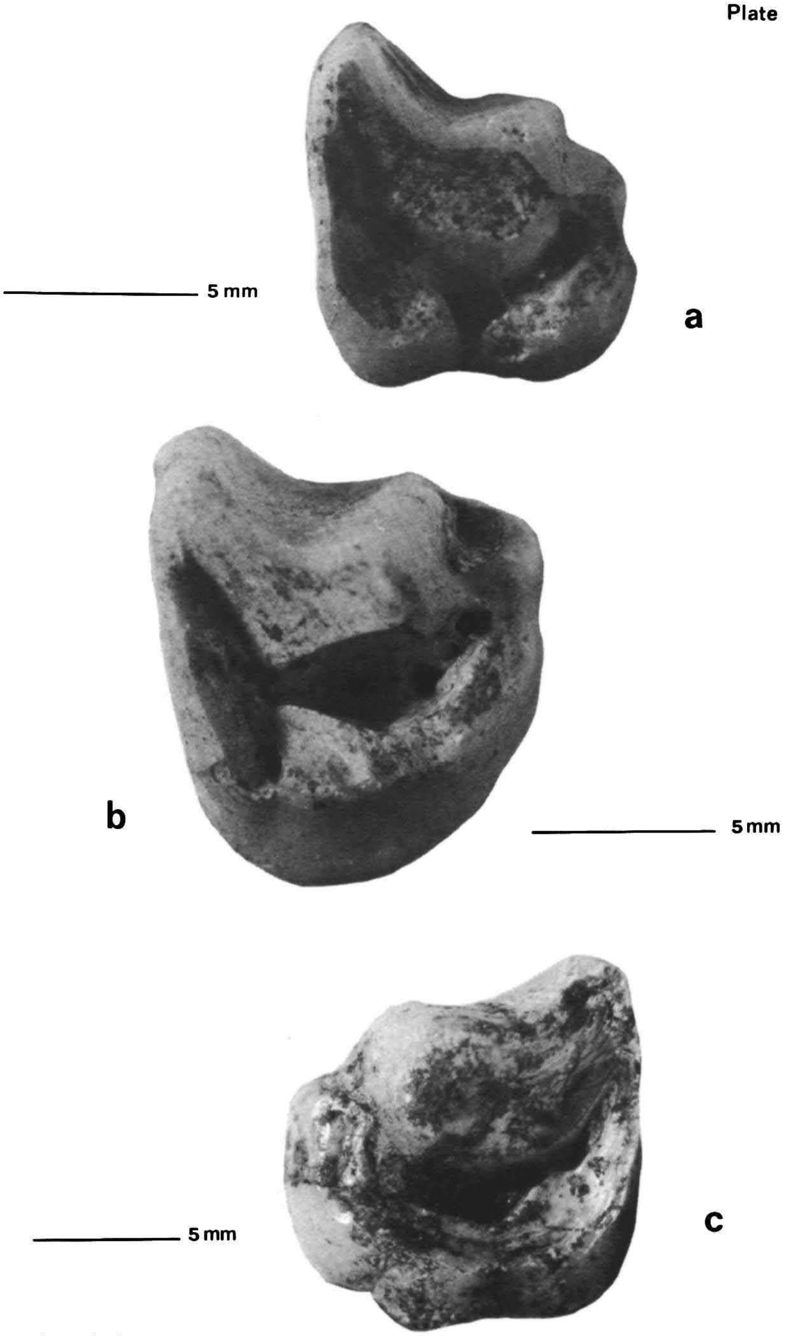
Fig. 36. Li-2599, left antler,
seen from the inside (antler-type 4).

Species Localities	*Candiacervus sp. indet.*	*Candiacervus ropalophorus nov. sp.*	*Candiacervus ssp. II*	*Candiacervus cretensis*	*Candiacervus rethymnensis*	*Candiacervus sp. V*	*Candiacervus sp. VI*	*Mus minotaurus*	*Mus bateae*	*Kritimys catreus*	*Kritimys kiridus*	*Kritimys aff. kiridus*	*Crocidura sp.*	*Elephas creutzburgi*	*Elephas antiquus*	*Elephas creticus*	*Hippopotamus creutzburgi creutzburgi*	*Hippopotamus creutzburgi parvus*	*Isolalutra cretensis*	Zones	
Gerani 2_2								●												*Mus minotaurus* Sub-zone	*Mus* Zone
Gerani 5		●																			
Gerani 6		●																			
Gerani 2_3		●						●													
Gerani 4		●	●					●					●								
Gerani 2_4		●			●			●					●								
Bate Cave	●					●	●	●					●								
Liko			●	●	●		●	●					●						●		
Mavro Mouri 4c		●	●	●	●			●						●							
Sourida		●	●		●			●						●							
Rethymnon fissure		●	●	●	●			●					●	●							
Kalo Chorafi		●	●					●						●							
Simonelli Cave		●	●		?									●							
Kharoumes 3	●														●						
Kharoumes 2			●	●																	
Milatos 2 and 4								●					●								
Milatos 3 upper								●					●								
Stavros Cave inside								●		●			●								
Stavros micro									●	●			●							*M. bateae* S.-zone	
Milatos 3 lower										●										*Kritimys catreus* Sub-zone	*Kritimys* Zone
Milatos 3 stalagmitic column	●									●											
Stavros macro			●							●			●					●			
Stavros Cave outside										●								●			
Katho Zakros										●								●			
Kharoumes 5	●									●							●				
Kharoumes 4	●									●							●				
Katharo																	●				
Kharoumes A										●			●								
Xeros										●			●								
Milatos 1										●											
Bali 2										●			●								
Cape Maleka 1											●					●				*Kritimys kiridus* Sub-zone	
Cape Maleka 3											●										
Sitia 1												●									

Fig. 37. Selected Cretan localities with their endemic fossil mammal assemblages.

PLATES

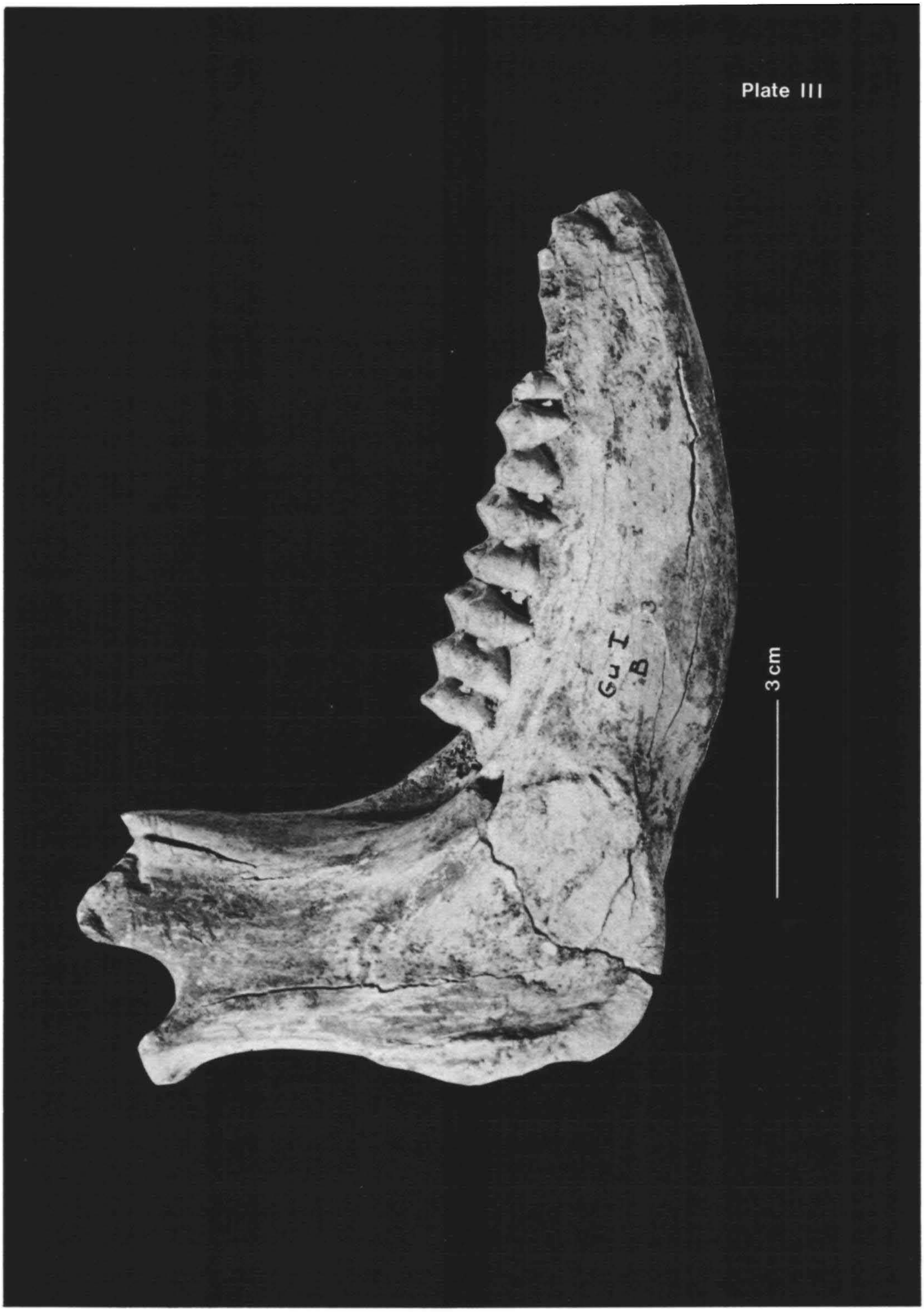
Plate I



Explanation of Plate I.

a. right upper P^2 (specimen RES-455) showing morphotype-1; b. right upper P^2 (specimen RES-458) showing morphotype-2; c. left upper P^2 (specimen Li-764) showing morphotype-3.

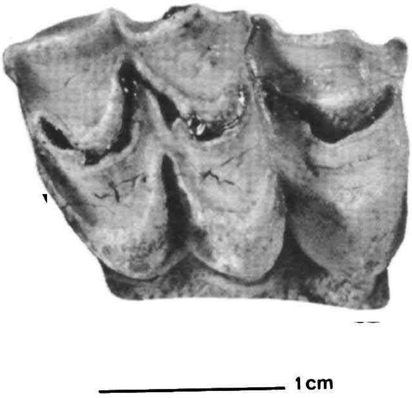
Explanation of Plate II.
Left mandible (specimen Ge4-131) showing a wear pattern of teeth which results in a flat occlusal surface.



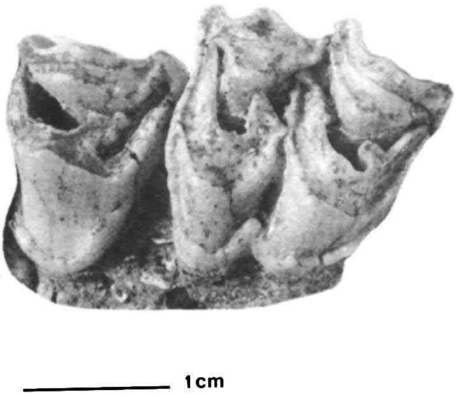
Explanation of Plate III.
Right mandible (specimen Gulb-13) showing a wear pattern of teeth which emphasises a distinct relief, indicated as a lophodont wear pattern.

Plate IV

a



b



Explanation of Plate IV.
a. Right upper P^4–M^1 (specimen Ge4-48) showing a weak cingulum; b. Left upper P^4–M^1 (specimen Li-2046) showing a strong cingulum.

Explanation of Plate V.
Type specimen (Ge4-2870) of antler type 1.

Explanation of Plate VI.
Type specimen (Li-2593) of antler type 2.

Plate VII

Explanation of Plate VII.
Type specimen (Li-686) of antler type 3.

Explanation of Plate VIII.
Type specimen (Li-684) of antler type 4.

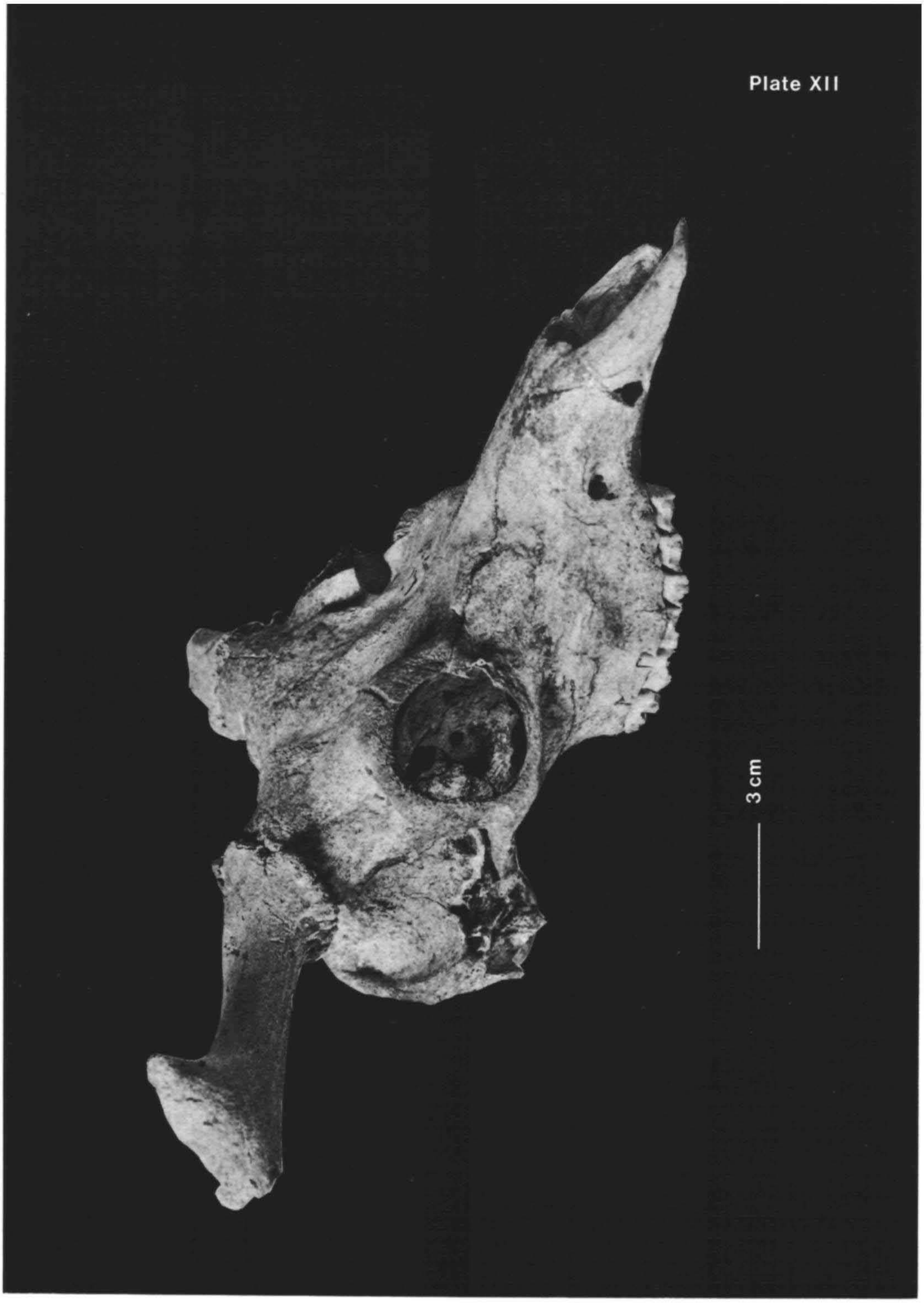
Explanation of Plate IX.
Type specimen (no number) of antler type 5.

Explanation of Plate X.
Male skull (specimen Ge4-46) of type a; Holotype of *Candiacervus ropalophorus* n. sp.

Plate XI

Explanation of Plate XI.
Female skull of type a (specimen Ge4-48).

Plate XII



Explanation of Plate XII.
Male skull; type specimen (Li-757) of skull type b.

Explanation of Plate XIII.
Male skull; type specimen (Li-758) of skull type c.

Plate XIV

Explanation of Plate XIV.
Male skull; type specimen (Li-759) of skull type c.