

## Chapter 6

# Pre-Pleistocene Land Mammals from Crete

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### Introduction

Pre-Pleistocene terrestrial mammals are known from several Cretan localities (Fig. 6.1). They attracted much attention however, due to their stratigraphic and (bio)geographic interest. All these localities are either above, in, or below marine sediments and one of the localities has become a classic locality for the correlation of marine and continental stratigraphy. The faunas are diverse like mainland fauna and have mainland species. For these reasons, they have played a part in discussions on Miocene geography of the eastern Mediterranean.

The newly described Cretan fossils are stored in the Faculteit Aardwetenschappen, Universiteit Utrecht (FAUU), as well as all material described by H. de Bruijn et al. (1971, 1972, 1979). Some of the Cretan fossils are compared with fossils from other areas in the FAUU, Muséum Guimet in Lyons (MGL) and Muséum national d'Histoire naturelle in Paris (MNHN).

### The Faunas

There are five pre-Pleistocene mammalian faunas or fauna complexes: Petras, Vrysses (or Vrisses), Plakia, Melambes and five localities at Kastellios Hill (Fig. 6.1).

### Melambes

Melambes in Rethymnon province yielded a small fauna. The locality is at the base of the Pandanassa Formation. M. Bonneau and L. Ginsburg (1974) described an M<sup>1</sup> and M<sup>2</sup> and navicuboid which they assigned to *Dorcatherium puyhauberti*. Later, S.E. Kuss (1976) described from the same locality a mandible and calcaneum of *Pliohyrax* sp. and mentioned more remains of *Dorcatherium* sp. and a horncore of an antelope.

The M<sup>1</sup> measures 10.5 x 11.2 mm and the M<sup>2</sup> 12.1 x 12.45 mm (Bonneau and Ginsburg 1974). This is the same size as *Dorcatherium naui* Kaup, 1832 from Eppelsheim. Till MN 6 (Neogene Mammal Units; Mein 1990; de Bruijn et al. 1992), there were several species of *Dorcatherium* in Europe, differing mainly in size (Mottl 1961; Fahlbusch 1985). The dorcatheres resemble the genus *Dorcabune* from Pakistan in the wide and low cheek teeth (and might belong in that genus). Of these species, *Dorcatherium crassum* has molars of the same length as *D. naui* (genotype), but those of the latter species are more hypsodont and narrower and resemble *Dorcatherium* from Pakistan. In addition, *D. naui* seems to have smaller limb bones than *D. crassum* (Fig. 6.3). One of the first occurrences

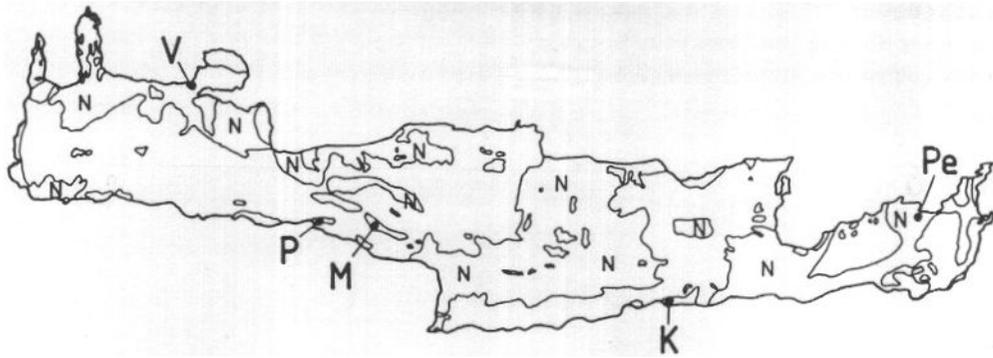


Fig. 6.1. The position of the localities. Legend: K = Kastellios Hill, M = Melambes, P = Plakia, Pe = Petras, V = Vrysses. Neogene deposits are marked "N" (after Zachariasse 1975).

of *D. nauti* is in Paşalar (MN 6; Turkey; Gentry 1990) and one of the last is on Samos (MN 12; Solounias 1981). The type of *D. puyhauberti* Arambourg and Piveteau, 1929 is from the Upper Miocene of Salonika and is probably a junior synonym of *D. nauti*.

Kuss (1976) did not assign the *Pliohyrax* fossils to a species. M.S. Fischer and E.P.J. Heizmann (1992) revised the European and Turkish hyraxes and noted that the specimen from Melambes is much smaller than any specimen from Europe and Turkey, but resembles *Prohyrax hendeyi* from Arrisdraft. The specimen from Melambes is slightly smaller than a *Parapliohyrax* from Beni Melal (Fortelius 1990:table 1). Fischer and Heizmann (1992) considered *Prohyrax*, *Parapliohyrax* and *Pliohyrax* to be closely related. They considered Melambes to be Vallesian and assigned the very early specimen from Paşalar to *Pliohyrax* aff. *kruppii* and the specimen from Melambes to *Pliohyrax* sp.

Bonneau and Ginsburg (1974) suggested that Melambes was of the same age as Kastellios Hill, that is Vallesian, but could not offer any biostratigraphic arguments for that other than the presence of the *Dorcatherium*. The presence of *Dorcatherium nauti* indicates an age of MN 6 to MN 12 for Melambes. The locality is at the base of the Pandanassa Formation suggesting that it is as old as or older than Plakia, which is assigned to MN 7/8. Considering the possibility that Melambes is about as old as Paşalar and possibly intermediate in age between Arrisdraft (Early Miocene) and Beni Mellal (MN 7/8), the interpretation of hyracoid phylogeny might slightly change. The Melambes mandible is here assigned to cf. *Prohyrax hendeyi*.

## Plakia

De Bruijn and J.E. Meulenkamp (1972) described the mammalian micro-fauna from Plakia near the

south coast of Crete in Rethymnon province. The locality is in the Pandanassa Formation, which is overlain by marine sediments containing an early-middle Tortonian foraminifera assemblage and therefore the Pandanassa Formation is considered to be pre-Tortonian.

The fauna was reported to contain: the sciurids *Spermophilinus* cf. *bredai*, *Blackia?* sp. and *Forsythia* sp., the cricetids *Democricetodon* aff. *kretensis*, *Cotymus* sp. and the glirid *Glirundinus* sp. Also, there is one tooth of a suid and it is of interest to note that there are many small crocodile teeth. Because of the evolutionary stage of *Democricetodon* and the absence of *Progonomys*, Plakia was considered to be intermediate between on the one hand La Grive and on the other Can Llobateres and Kastellios Hill. Plakia was also considered to be earlier than the entry of *Hipparion*. In current biostratigraphy this is the later part of MN 7/8. The locality is at the base of the Yeni Eskihisar pollen zone, which is correlated with the later part of MN 7/8 (Steininger et al. 1990).

The suid tooth (Fig. 6.2D) is low and elongate with one main cusp and one posterior ridge. It probably represents a milk tooth because of the low and elongate shape and a  $D_2$  because  $D_3$  tend to have more than one posterior ridge. The specimen is broken. Its length must have been over 9.8 mm, width of the anterior lobe  $\geq 3.6$ ; width of the posterior lobe  $\geq 4.0$  and height  $\geq 6.2$  mm. The tooth does not have a listriodont or tetraconodont morphology, leaving *Hyotherium soemmeringi* and *Propotamochoerus palaeochoerus* as the most likely candidates. The *H. soemmeringi*  $D_2$  seems to be narrower. *P. palaeochoerus* entered Europe in the latter part of MN 7/8 (van der Made and Moyà-Solà 1989), which would then be the most likely age of Plakia. The last certain occurrence of *H. soemmeringi* is in MN 6 (van der Made 1990).

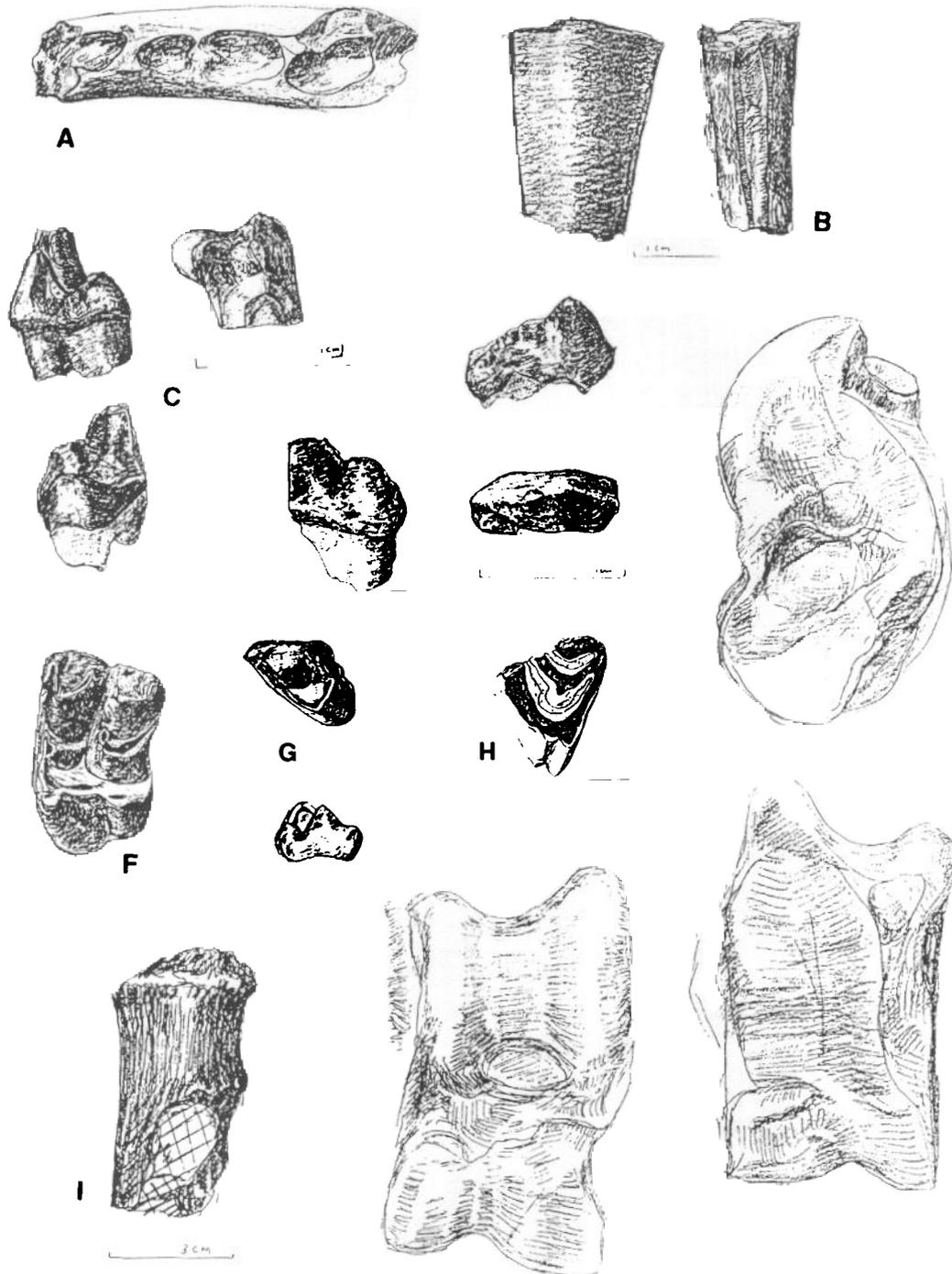


Fig. 6.2. A) Carnivora indet., right mandible with alveoles of  $P_3$  to  $M_1$ , "Occlusal view". B) *Taucanamo?*/*Yunnanochoerus?*/Carnivora, upper canine from Kastellios Hill 2. 1) side view, 2) anterior view. C) Carnivora indet., left  $P^4$  from Kastellios Hill "eastern slope". 1) anterior view, 2) occlusal view, 3) lingual view, 4) buccal view. D) Cf. *Propotamochoerus palaeochoerus* left  $D_2$  from Plakia. 1) lingual view, 2) occlusal view. E) Cf. *Dorcabune anthracoteroides* from Kastellios Hill "eastern slope", left astragalus. 1) External view, 2) anterior view, 3) posterior view. F) *Schizogalerix sinapensis* from Kastellios Hill 1, left  $M^2$ . Occlusal view. G) *Schizogalerix sinapensis* from Kastellios Hill 1, left  $M^3$ . 1) Occlusal view, 2) buccal view. H) *Prolagus* sp. left  $P^3$  from Vrysses. Occlusal view. I) Cervinae indet. right pedicle, surface find from Kastellios Hill. Internal view. All specimens in the FAUU. Figs. A-H drawn with a Wild microscope, fig. I drawn without utensils. The 2 mm bar indicates the scale for figs. F-H, the 1 cm bar for figs. A - E and the 3 cm bar for fig. I.

The presence of crocodiles in Plakia is interesting, since it is a late occurrence, however, far south. In central Europe crocodiles occurred till somewhere in MN 6. Sandelzhausen must be one of the latest faunas in Central Europe with crocodiles (and with *H. soemmeringi*). At the end of MN 6, a number of mammalian taxa disappeared from Europe, but lived on in warmer (sub)tropical climates and the event was believed to involve a decrease in temperature (van der Made 1992).

Crocodile remains from Plakia collected by Kuss in 1977-78 are preserved in the Staatliches Museum für Naturkunde Karlsruhe, Germany.

### Kastellios Hill

For a long time, there were two competing opinions on the correlation of Late Miocene continental and marine deposits. The entry of *Hipparion* into Europe and thus the lower limit of (what is called now) the Vallesian was either correlated to the lower limit of the Pliocene or it was correlated to the Tortonian, that is lower Upper Miocene. Kastellios Hill became a classic locality after de Bruijn, P.Y. Sondaar and W.J. Zachariasse (1971) showed that here deposits containing Early Tortonian marine fossils overly deposits containing *Hipparion*.

Kastellios Hill is situated a few kilometers from the south coast and some 80 km east of the Plakia and Melambes localities. The section, which is exposed at the west slope of the hill, shows an interfingering of continental and marine sediments. At 4 levels (K1, K2, K3, K5) mammalian fossils were collected and at one level marine fossils (K4). The localities are in sequence: K1 is the lowest and K5 the highest and K4 is thus younger than K1, K2 and K3. In addition, mammals were collected at the eastern slope of Kastellios Hill. In 1976, additional micromammals were collected by de Bruijn from K1 as well as some surface finds of large mammals (de Bruijn and Zachariasse 1979). Magnetostratigraphy of the section indicated an age between 10.99 and 10.30 My for all localities (Sen et al. 1986).

The K1 fauna was reported to contain the cricetid *Cricetulodon* cf. *sabadellensis*, the murid *Progonomys woelferi*, the glirid *Muscardinus* cf. *crusafonti*, the sciurid *Spermophilinus bredai*, and *Hipparion*. There are also an M<sup>2</sup> and M<sup>3</sup> of an insectivore. This fauna was placed in MN 9, though S. Sen et al. (1986) argue for MN 10.

The insectivore M<sup>2</sup> (Fig. 6.2F) has a large protoconule and metaconule, and is very wide compared to its length. Neogene Turkish insectivores were

revised by B. Engesser (1980). The characters of the M<sup>2</sup> are found in *Schizogalerix*. There are two types, one with wide M<sup>2</sup> and one with narrow M<sup>2</sup>. The tooth from Kastellios measures 2.0 x 3.2 mm and groups with the wide type. In the Kastellios tooth, the hypocone has a very clear posterior wing. Similarly, the posterior wing of the protoconule is well developed. The mesostyle is split into two structures which are well apart and separated by a deep and wide transverse valley; there is no crest or connection between the two cusps (as in Amama and not as in Amasya; Engesser 1980:fig. 10). The ridge formed by the mesostyle, metacone and metastyle is moderately V-shaped and the upper ends of the "V" (the styles) are not moved inwards (towards each other). The paracone forms a similar structure. These characters are intermediate between *S. anatolica* and the *Schizogalerix* from Amama II (though, this form is known from the M<sup>1</sup> and not from the M<sup>2</sup>). *Schizogalerix sinapensis* Sen, 1991 from Sinap Tepe (Turkey) is intermediate in morphology and in age (MN 9) between these two forms (MN 8 and MN 12, respectively). The M<sup>2</sup> from Kastellios Hill and Sinap are identical. The M<sup>3</sup> (Fig. 6.2G) from Kastellios Hill has a complete separation between the paracone and metacone, with no ridges running into the separating valley. The tooth measures 1.4 x 1.3 mm.

The *Hipparion* from K1 is mentioned by de Bruijn and Zachariasse (1979), but not by de Bruijn et al. (1971). Maybe it is the canine found in 1976 (see 1976 finds).

From the K2 locality, left and right P<sup>2</sup>-M<sup>3</sup>, a P<sub>2</sub> or P<sub>3</sub> and the proximal part of a second metacarpal of *Hipparion* were described and some fragmentary incisors were mentioned. The locality is currently placed in MN 10, or near the MN 9/10 transition (de Bruijn and Zachariasse 1979; Steininger et al. 1990).

The incisors include a left I<sup>3</sup> in a premaxillary (16.8 x 9.3 mm at the occlusal surface), right I<sup>1</sup> (>12.5 x >11.8) and a right premaxillary with the root of a I<sup>2</sup>. The metacarpus measures 17.5 x 12.2 mm at the proximal end. Besides, there is a right M<sub>3</sub> (anterior width measured at the enamel 7.6 and at the cementum 10.4 mm) and a left cuboid (antero-posterior length ≥31.8 mm, height 22.5 mm and width 18.8 mm). One incisor was reported to be from K1 (Sondaar et al. 1986), which must be one of these specimens. The incisors, metacarpus, M<sub>3</sub> and cuboid are not numbered and were stored together with material from Kastellios Hill 3. The exact provenance of these specimens is unclear.

In addition, there is a fragment of an upper molar of a bovid and a fragment of an upper canine (in a tube with label stating their provenance as K2). The tip and root of the canine are broken off (Fig. 6.2B).

The section is symmetrical and oval and measures 10.6 x 6.4 mm. The tooth has a sharp posterior edge and an anterior wear facet. The facet is wide, nearly flat and nearly perpendicular to the long axis of the tooth. Several millimeters of the tooth were worn away. Ruminant canines never have anterior facets, nor are they symmetrical. The tooth might represent a kind of sabre-toothed cat or a "peccary", such as *Taucanamo*. The sabre-toothed cats tend to reduce the lower canines and are not expected to have such heavy anterior wear. *Taucanamo* tends to have canines with only the apical part completely covered with enamel, away from the tip, the sides of the tooth are not covered with enamel, but are bare dentine or tend to get a cementum covering. The Kastellios canine has enamel all around, where a *Taucanamo* canine would lack enamel. *Schizochocerus* has very wide canines (up to 15 mm). *Yunnanochocerus* is a related form found only in Pakistan and China of which the upper canines are not known (van der Made and Han 1994). *Taucanamo*, is not known from later than MN 8 (MN 9 citations turn out to belong to other suoids).

The K3 locality was reported to contain the murids *Progonomys cathalai*, *Progonomys woelferi* and the scaphoid of a ruminant. K3 is placed in MN 10, or near the MN 9/10 transition (de Bruijn and Zachariasse 1979; Steininger et al. 1990).

The scaphoid is small (21.6 x 11.6 x 17.1 mm - l x w x h). There is also a third lobe of a bovid  $M_3$  (width 5.2 mm).

The K5 locality yielded a  $P^3$  or  $P^4$  of *Hipparion*.

The locality Kastellios "eastern slope" were reported to have yielded fragments of a mustelid  $P^4$ , a fragmentary  $M_3$  of a bovid and a  $D_4$  and a  $M_1$  or  $M_2$  of *Dorcatherium*.

The  $P^4$  (Fig. 6.2C) has a protocone that is situated nearly as much forward as the parastyle, it projects much lingually and there is a valley between the two cusps. The roots below the protocone and parastyle are fused, but have separate pulp cavities. The anterior border of the tooth is concave. The parastyle is as large as and higher than the protocone. It has sharp anterior and posterior edges. The latter one meeting the anterior sharp edge of the paracone. The tip of the paracone is broken off, as well as the posterior part of the tooth. The width of the tooth at the protocone is 8.3 mm and just behind it a paracone 5.6 mm. This type of  $P^4$  is found in a number of very different carnivores. Some which are close in size and age are the viverrid *Tungurictis punica* from the pre-*Hipparion* beds of Bled Douarah (MN 7/8) with a  $P^4$  with a maximum width of 8.5 mm (Kurtén 1976), the felid *Pseudaelurus quadridentatus* from Los Valles de Fuentidueña (MN 9) with a  $P^4$  that has a maximum width of 10.4 mm

(Ginsburg et al. 1981) and the hyenaid *Protictitherium* (aff.) *gaillardi* from various Greek and Spanish Vallesian localities ranging between 72.-8.5 (de Bonis and Koufos 1991).

Besides the  $P^4$  there is a right mandible of a carnivore (Fig. 6.2A) with the posterior alveole of the  $P_3$ , both alveoles of the  $P_4$  and the anterior alveole of the  $M_1$ . The combined length of the alveoles for the  $P_4$  is 9.4. The depth of the mandible at the middle of the  $P_4$  is 12.0 mm. This specimen may belong to the same species as the  $P^4$ . The mandible is much less deep than the mandible of *Pseudaelurus quadridentatus*, though the approximate size of the  $P_3$  is similar (Filhol 1891:pl. 4, fig. 1), but the depth must be similar to that in *Protictitherium* aff. *gaillardi* from the Ravin de la Pluie (MN 10; compare with the slightly larger *P. cf. crassum*; De Bonis and Koufos 1991:pl. 2, fig. 7).

The bovid left  $M_3$  had a width at the distal lobe of 9.3 mm. There is a scrap of another lower molar and half a left  $D_4$  (width of the anterior lobe 5.9 mm). These specimens are of the size and morphology of *Tragoptax gaudryi*, but may very well represent another species. There are also the remains of a smaller  $D_4$  (width anterior lobe 3.2 mm and of the second lobe 4.3 mm). It is morphologically different and represents a second bovid species. No teeth of *Dorcatherium* were found in the collection; might the two  $D_4$  have given rise to the citation of that genus?

One of the most interesting finds is an astragalus of tragulid morphology (Fig. 6.2E). Since it is not mentioned by de Bruijn et al. (1971) it may have been collected in 1976. It was stored with the K2 material. The astragalus is not a bovid or cervid astragalus, because it is more elongate (Fig. 6.3), the proximal and distal rollers are oblique and because of details of its morphology of the proximal articulation facet and external side. Its morphology is identical to that of large tragulid astragali from the Nagri Formation and its size is slightly superior to these. Its length is externally 37.1 mm, in the middle 28.2 mm and internally 33.8 mm. Its width is proximally 18.9 mm and distally 20.0 mm. There are several tragulid species in the Nagri Formation, most of them small ones, the large ones are *Dorcatherium majus*, which is abundant, and *Dorcabune anthracotheroides*, which is much rarer. The latter species was originally described from the Chinji Formation (Pilgrim 1915). The astragali of *Dorcatherium nauai* tend to be small compared to the ones of *D. crassum* from Sansan, which is a brachyodont species like *Dorcabune* and are much smaller than those attributed to *D. majus* and *D. anthracotheroides*. This shows that the astragalus from Kastellios Hill does not belong to *D. nauai* and it suggests that the brachyodont species with wider molars (*D. crassum*)

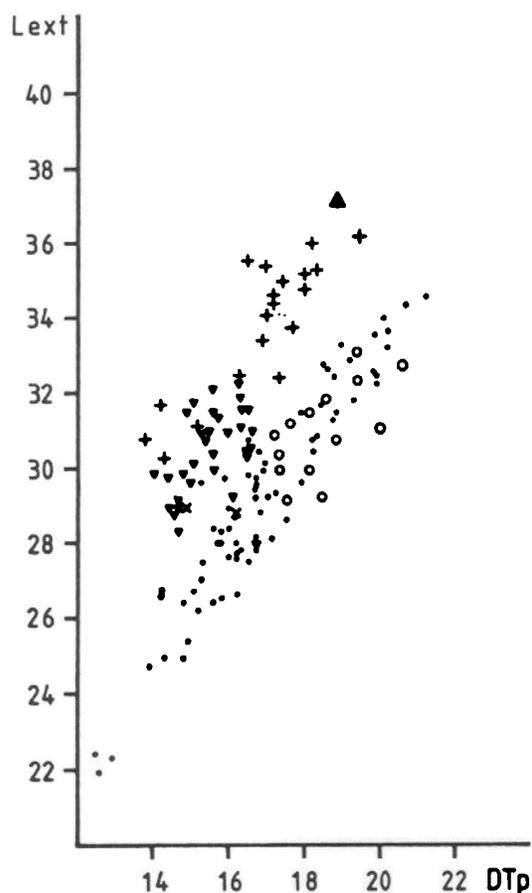


Fig. 6.3. Bivariate plot of proximal width (DTp) versus external length (Lext) of astragali. Legend: triangle point upwards = cf. *Dorcabune anthracotheroides* from Kastellios Hill; triangles points downwards = *Dorcatherium crassum* from Sansan (MNHNP); crosses = *Dorcatherium majus* and *Dorcabune anthracotheroides* from the Nagri Formation (FAUU); oblique crosses = *Dorcatherium naui* from various European localities; dots = bovids from the Chinji Formation (FAUU); circles = cervids from La Grive (MGL).

tend to have larger astragali than the hypsodont species with molars of the same length (*D. naui*). If this is really the case, *D. anthracotheroides* has larger astragali than *D. majus*, and since the species is rare, the extreme sizes may not be represented in the sample. Thus, the Kastellios Hill astragalus may well represent *Dorcabune anthracotheroides* or else it has to be a new species, since there is no other large tragulid of this age.

The 1976 finds include a right pedicle of a cervid, the distal and proximal parts of a right humerus of a bovid and an upper canine of *Hipparion*. These finds are either K1 or surface finds, since they are stored

with K1 material, but surface finds have also been collected (de Bruijn, pers. comm.).

The *Hipparion* canine measures 10.5 x 9.2 mm. The proximal facet of the humerus has a width of 34.4 mm; the proximal antero-posterior diameter of the bone is 54.5 mm. The width of the distal facet is 36.4 mm. The radius of the distal roller measured at different places: internally >17.5; the internal gully 17.2; the ridge 22.6; the external gully 19.3 and externally 26.0 mm.

The cervid pedicle (Fig. 6.2I) includes the basal part with a small part of the brain case; distally the antler is broken just above and through the rose. The pedicle was situated well behind the orbit and was much inclined. It is short. The length of the pedicle from brain case to rose cannot precisely be measured, but exceeds only slightly 23.2 mm. Just below the rose, the antero-posterior diameter of the pedicle is 30.8 mm and the transverse diameter 31.0 mm. The position on the skull, orientation and length relative to diameter indicate that the cervid belonged to the Cervinae. In Spain, the Muntiacinae were the dominant cervids during the Vallesian and the earliest Cervinae entered during the Turolean (Azanza 1989). All Spanish cervines have smaller pedicles, but the length relative to the diameter approaches the Kastellios pedicle. *Pliocervus pentelici* is cited from Pikermi, Samos and Marageh (MN 11-13) and Cervinae indet. from Pikermi (Solounias 1981) and the cervine *Cervavitus* from Dorn Dürkheim (MN 11; Azanza 1989). A pedicle from Marageh is small like *Pliocervus matheroni* (type locality Mont Léberon; MN 12); the section of the pedicle is 20-22 mm (Tobien 1980). The holotype of *Pliocervus pentelici* has a pedicle with a section of 34 mm and a length of 56 (Dames 1883). The length seems larger than the specimen from Kastellios Hill, but it is not clear how the length was measured, internally as here, or externally from the orbit to the rose, resulting in a higher value. The specimen is assigned here to cf. *Pliocervus pentelici*.

Cervinae apparently entered earlier in southeast and central Europe than in Spain and the specimen from Kastellios Hill is still older (MN 10 versus MN 11 for the next earliest citation). If the find is a surface find, could it not be from younger deposits? The pedicle from Kastellios Hill is short like that of some of the Pleistocene endemic deer, though these do not seem to have a perfectly round section, as is the case in the specimen from Kastellios Hill. Kastellios Hill is capped by marine limestones and no Pliocene or Pleistocene deposits are reported from there (de Bruijn et al. 1971). The green marls attached to the pedicle are identical to the marls clinging to other fossils from Kastellios Hill. The pedicle seems to be genuinely Miocene. The specimen is too fragmentary for far-

reaching conclusions, but in view of the posterior palaeogeographic evolution of the Cretan area and the remaining morphology of the specimen, a close relationship between the Miocene and Pleistocene deer seems unlikely.

### Vrysses

L. Benda, H. Hiltermann, Kuss and N.K. Symeonides (1968) assigned molar fragments from Vrysses near Khania to *Mastodon* sp. The fragments were found in a lignite mine along with many other fossil bones, which were lost. The lignites form part of the Pandanassa Formation (Sondaar et al. 1986).

The fragments do not allow for a precise determination, however, Benda et al. indicate that the fossils resemble proboscideans from Samos, Pikermi and Kos. These species are today not placed in *Mastodon*, but this is not the right place to discuss generic affinities of all species that might have occurred on Crete.

De Bruijn collected samples at Vrysses, but not in the lignite mine, which however did not yield more mammalian fossils than a rodent incisor and left P<sup>3</sup> of *Prolagus* sp. (de Bruijn, pers comm.) (Fig. 6.2H). These fossils are stored in the FAUU.

Benda et al. believed a Late Miocene age ("Pliocene" in their terminology) most likely for the proboscidian remains.

### Petras

J.J.M. Leinders and Meulenkamp (1978) described a P<sup>4</sup> of *Microstonyx* from Petras near Sitia. The tooth was found at the passage from the mainly continental Skopi Formation to the overlying marine Akhadia Formation. The foraminifera from the Akhadia Formation are of Tortonian age. It was left open whether the tooth belonged to *M. major* (including *M. erymanthius*) or *M. antiquus*.

The tooth has a well developed sagittal cusp (*sensu* Pickford 1988) and thus belongs to the Suinae. For a review of the European Suinae see van der Made and S. Moyà-Solà (1989). Suinae cited from North Africa and the Middle East include *Sus*, *Propotamochoerus* and *Kolpochoerus* (Geraads et al. 1986; Geraads 1993). The tooth is large (16.7 × 21.0 mm) and is larger than in any species of *Sus*, *Propotamochoerus*, or *Kolpochoerus*. The size is about that of a small *Microstonyx major* or a large *M. erymanthius* (van der Made, in prep.) and inferior

to that of *M. antiquus* from Turkey. *Microstonyx* is known to have dwarfed on the (palaeo)island of Toscane. The Petras form might be a dwarfed *M. antiquus*, but this does not seem to be likely, since the other Cretan faunas of the same age (but of different areas) do not indicate island environments.

*Microstonyx major* and *M. erymanthius* occurred in Europe and Turkey from MN 10 to MN 13 or late Vallesian and the whole of the Turolian. In view of the fact that the overlying Akhladia Formation is Tortonian and that MN 13 usually is equated with the Messinian, MN 10 or MN 11 are more likely for the locality of Petras than MN 12 or MN 13.

*Microstonyx* has not been found in North Africa, but is a common genus in Europe and Turkey and thus suggests geographical connections to Eurasia.

## Faunal Evolution

The Melambes fauna is placed in MN 6 or early in MN 7/8. The Plakia fauna in the same formation is placed in late MN 7/8. The older Kastellios Hill faunas are late MN 9 or early MN 10 and the younger ones might be Turolian, if the deer is taken into consideration. The Petras tooth is probably MN 10 or MN 11. The locality of Vrysses might be Vallesian or Turolian.

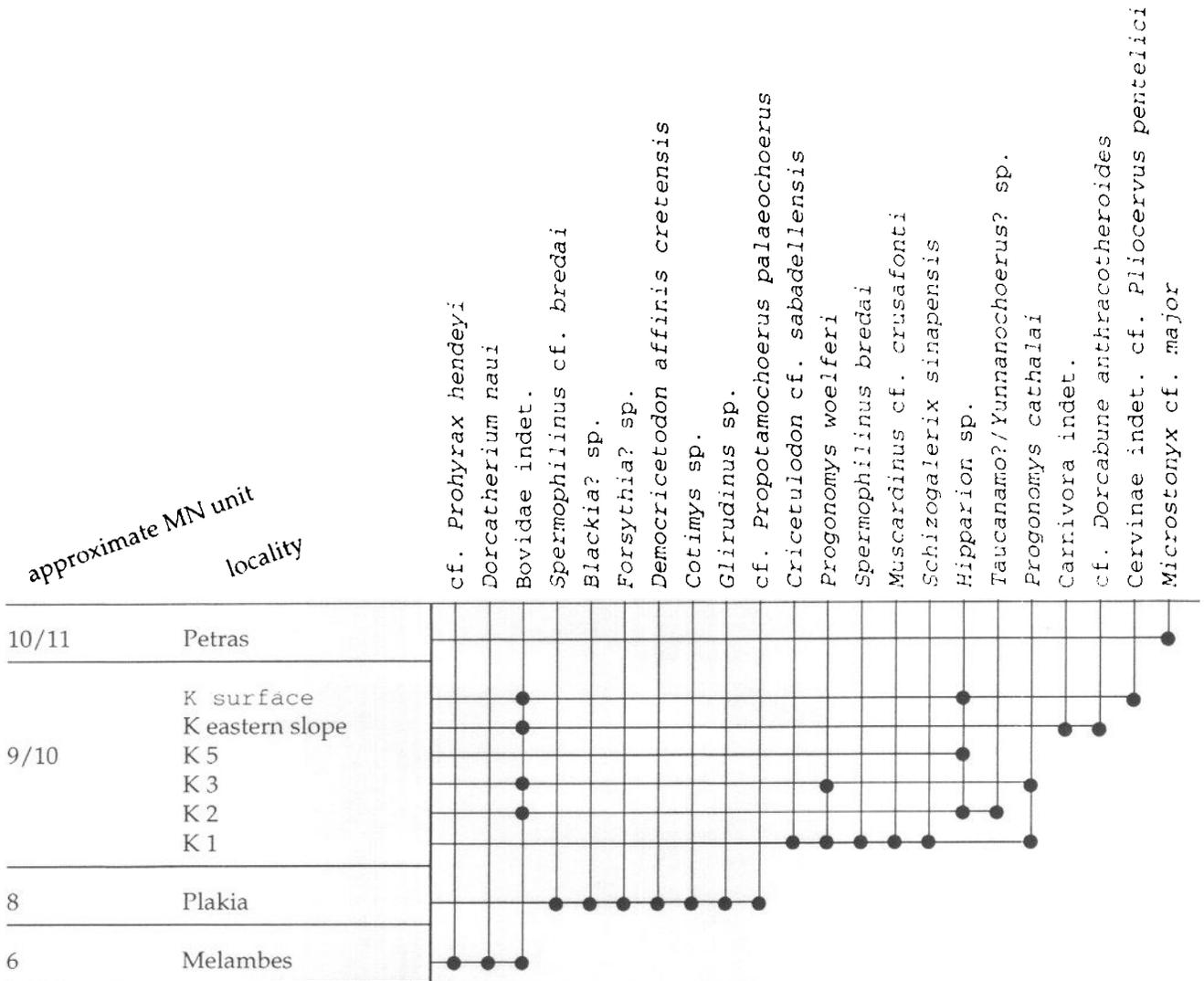
The sequence of faunas (Fig. 6.4) and each individual fauna are very incomplete compared to the faunas from Europe and Turkey. However, a series of important entries of immigrants can (tentatively) be recognized on Crete, such as *Dorcatherium nauyi* (latter part MN 6), *Propotamochoerus palaeochoerus* (latter part MN 7/8), *Progonomys* and *Hipparion* (MN 9) and the Cervinae (entry in MN 11 in Spain).

All faunas are mainland faunas and not endemic island faunas, this is not only indicated by the species diversity, the presence of carnivores and *Hipparion* (which are never found in island faunas) and the presence of mainland taxa (instead of endemic taxa), but also by the repeated entry of new taxa. Most of the taxa have European or Turkish affinities. The most conspicuous exceptions are the hyrax (Africa) and *Dorcabune anthracotheroides* (Pakistan).

## Acknowledgements

I thank Drs. de Bruijn and Sondaar for discussion and comments.

Fig. 6.4. Range chart for the pre-Pleistocene land mammals from Crete.



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