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(LESVOS, GREECE)

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ΠΡΟΚΑΤΑΡΤΙΚΗ ΠΕΡΙΓΡΑΦΗ ΤΗΣ ΑΝΩΠΛΕΙΟΚΑΙΝΙΚΗΣ ΠΑΝΙΔΑΣ
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PRELIMINARY NOTE ON THE LATE PLIOCENE FAUNA FROM VATERA (LESVOS, GREECE)*

by

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I. INTRODUCTION

There are six fossil vertebrate yielding sites near Vaterá (Lesvos, Greece), these are the F, E, H, DS, T and U-sites. The material is kept in the Natural History Collection in the Museum of Vrísisa, near Polychnítos on Lesvos Island. It is the aim of this paper to present the preliminary faunal list and describe or discuss some of the characteristic faunal elements. In future publications, each taxon will be more completely described and discussed.

Measurements and their abbreviations

Measurements are taken as indicated by VAN DER MADE & HUSSAIN (1994). In the figures and text measurements are indicated by their abbreviations.

DAP	Antero-posterior diameter
DAPb	Basal DAP
DT	Transverse diameter
DTa	DT of the anterior lobe of a tooth
DTb	Basal DT
DTp	DT of the posterior lobe of a tooth, or the proximal part of a bone
Dist.	Distal
L	Length
Prox.	Proximal.

Collections and their abbreviations

In the text and figure captions reference is made to collections where morphologies were observed and measurements taken. The abbreviations used are the following:

* Προκαταρκτική περιγραφή της Ανωπλειοκαινικής πανίδας των Βατερών (Ν. Λέσβος).

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*** Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, c. José Gutiérrez Abascal 2, 28006 Madrid, Spain.

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***** Natuur Museum Rotterdam, PO Box 23452, 3001 KL Rotterdam, The Netherlands.

AUT	Aristotle University, Thessaloniki
HUJ	Hebrew University of Jerusalem
IGF	Istituto di Geologia, Firenze
IQW	Institut für Quartärpaläontologie, Weimar
IVAU	Instituut voor Aardwetenschappen, Utrecht
MCPV	Musée Crozatier, Le Puy-en-Velay
MNCN	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Muséum National d'Histoire Naturelle, Paris
NHCV	Natural History Collection, Vrissa
NHMB	Naturhistorisches Museum Basel
NHML	Natural History Museum, London
NMMa	Natuurhistorisch Museum, Maastricht
NUA	National and Kapodistrian University of Athens
PINM	Paleontological Institute, Moscow
TMH	Teylers Museum, Haarlem.

II. SYSTEMATICS

F-SITE

The F-site was found following the construction of a track. The first material collected comes from sediment that was not *in situ* anymore. In 1997 the exact position of the locality was determined and the first *in situ* specimens were collected. In 1998 about one square metre was excavated. During 1999 and 2000 the locality was again excavated however, in 2000 the pocket didn't produce fossils anymore. Below the characteristic material collected from 1997 onwards is included. This site yielded about 550 fossils.

Class: Reptilia LINNAEUS, 1758

Order: Chelonia LATREILLE, 1800

Chelonia gen. et sp. indet.

Osteoderms (PO 071 F, PO 254 F, PO 127 F and PO 073 F) (Plate I, A), phalanxes III (PO 067 F, PO 176 F and PO 188 F) (Plate I, B; Table 1) and other bones like a left tibia (PO 184 F) and a left femur (PO 186 F) represent a giant turtle.

Table 1. Measurements (in mm) of the third phalanges.

	L	DAP prox.	DT prox.
PO 067 F	81.4	32.2	28.3
PO 176 F	79.6	29.6	32.3
PO 188 F	—	31.1	33.4

Class: Aves LINNAEUS, 1758

Aves gen. et sp. indet.

A very fragmented radius (PO 513 F) with a length of 88.3 mm and a humerus (PO 081 F) with the size of an eagle (*Aquila*) represent bird remains.

Class: Mammalia LINNAEUS, 1758

Order: Primates LINNAEUS, 1758

Family: Cercopithecidae GRAY, 1821

Genus: *Paradolichopithecus* NECRASOV, SAMSON & RADULESCU, 1961

***Paradolichopithecus arvernensis* (DEPÉRET, 1929)**

An upper premolar (PO 057 F) and an upper canine (PO 056 F) are among the earliest specimens collected. Later two mandibles, a large one PO 114 F (I₁-M₂; Plate I, C) and a smaller one PO 170 F (I₁-M₃) were found *in situ*. The large mandible is subadult, having milk molars in function and premolars in the alveoli. The dentition shows cercopithecoid morphology as described by DELSON (1975): hypsodont, bilophodont, and molariform teeth with four marginal cusps linked by transverse lophids and three foveae separated by the two ridges. The relatively large front teeth lack enamel on the lingual surface as in Papionini, and unlike in Cercopithecini and Colobinae. Both mandibles are unhollowed by fossae, excluding *Papio* and leading to the European genus *Paradolichopithecus*, the sub-Saharan *Parapapio* and the South and South-East Asian *Procynocephalus*. The postcranial elements recovered from the F-site, have a morphology and size similar to the *Paradolichopithecus arvernensis* postcranials VGr 350 found at Valea Grăunceanului (Pliocene; Romania), and include: a right humerus (PO 225 F), a left humerus missing the proximal part (PO 200 F), a right ulna (PO 229 F), a right radius (PO 431 F), a left olecranon (PO 059 F), four radius fragments (PO 501 F, PO 498 F, PO 502 F, PO 630 F), a distal right tibia (PO 228 F), and a right astragalus (PO 157 F).

Order: Carnivora BOWDICH, 1821

Family: Canidae FISCHER DE WALDHEIM, 1817

Genus: *Nyctereutes* TEMMINCK, 1838

***Nyctereutes megamastoides* (POMEL, 1843)**

A hemi-mandible (PO 060 F) (Plate II, A) with C-M₃ belongs to a canid. It has all characteristics that are typical for *Nyctereutes megamastoides*: it has a well-developed subangular lobe, the inferior border of the horizontal ramus is straight and the angle between the horizontal and the vertical ramus is more or less right. In the specimen, the carnassial blade is reduced and the crushing series is well developed. The talonid of the M₁ has two well-developed cuspids of equal size. M₂ has four main cuspids and a strong mesial cingulum.

Family: Mustelidae FISCHER DE WALDHEIM, 1817

Genus: *Meles* BRISSON, 1762

***Meles thorali* VIRET, 1951**

The front part of a skull, PO 630 F, and the mandible of a mustelid are present. The upper dentition, as well as the lower dentition, is complete. The measurements of the lower carnassial are given in Table 2 and are similar to those of *Meles thorali* from St. Vallier.

Table 2. Comparison of the measurements of the Lesvos lower carnassial with those of the lower carnassial of *Meles thorali* from St. Vallier (QSV), in mm. Measurements of *Meles thorali* from St. Vallier taken from VIRET (1954).

Lower carnassial	Total length	Length of trigonid	Length of talonid
QSV 1051	17	10	7.8
QSV 8	15.9	9.5	7.3
QSV 16	16.2	9.5	7.1
QSV 19	16.6	9.5	7.7
QSV 13	16.4	9.4	7.2
PO 630 F, left	17.3	9.4	7
PO 630 F, right	17	9.4	7.9

Mustelidae gen. et sp. indet.

A femur (PO 143 F), tibia (PO 144 F) and fibula (PO 145 F) belonging to a single individual (Plate II, B; Table 3) suggest the presence of a mustelid with the size of an otter.

Table 3. Measurements (in mm) of the bones of Mustelidae indet. from VATERÁ.

	L	DAP prox.	DT prox.	DAP dist.	DT dist.
Femur, PO 143 F	112	22.8	30.7	–	–
Tibia, PO 144 F	103.1	25.5	26.7	13.7	20.1
Fibula, PO 145 F	95.3	–	–	–	–

Carnivora gen. and sp. indet.

- 1) A left femur PO 153 F (Plate II, C) missing the distal condyles is concerning the morphology close to those of *Lynx issiodorensis* or *Acinonyx pardinensis*. Length is about 200 mm, DT of midshaft is 14.3 mm, while they are respectively 232 mm and 18.4 mm in *Lynx issiodorensis*.

- 2) Footbones (PO 363 F) that are slightly more robust, but morphologically similar to those of a wild cat.
- 3) A tibia from a canid (PO 479 F) of which the measurements in mm are:
L = 127.1, DAP prox. = 25.5, DT prox. = 26.1, DAP dist. = 11.6, DT dist. = 18.3.

Order: Proboscidea ILLIGER, 1811

Family: Gomphotheriidae CABRERA, 1929

Genus: *Anancus* AYMARD, 1855

***Anancus cf. arvernensis* (CROIZET & JOBERT, 1828)**

The size of a fragmentary metapodial (PO 048 F) suggests the presence of *Anancus arvernensis*.

Order: Perissodactyla OWEN, 1848

Family: Equidae GRAY, 1821

Genus: *Equus* LINNAEUS, 1758

***Equus cf. stenorhis* COCCHI, 1867**

The genus *Equus* is represented by some scanty dental elements of the lower toothrow (PO 065 F, PO 087 F, PO 088 F), as well as by several postcranial remains (Plate IV, A), including an articulated front (PO 444 F) and hind limb (PO 212 F) (see also EISENMANN, this volume). The linguaflexid of the lower cheek teeth is pointed and the metaconid and metastylid are rounded (lingually convex), which indicate stenorhis morphology. The limb bones are long and relatively slender. The morphology of the available limb bones also suggests stenorhis affinities (GROMOVA, 1949; DE GIULI, 1972; PRAT, 1980): a) the metapodials are wider at the suprarticular tubercles than at the distal articulation; b) the calcanea are slender with a weak caput; c) the astragali are relatively narrow; d) the astragalus is articulated to the calcaneum by three facets. The *trigonum phalangis* of the proximal phalanges is, however, relatively long, that is somewhat more advanced.

The metapodials are characterised by great length and slenderness. They are longer than any other Late Pliocene horse sample from Greece (though they are close to Sésklo, especially the metatarsals) and comparable to the stratigraphically younger samples from Olivola and Venta Micena (Figure 1). A comparison of robustness (Figure 2) shows that they better resemble the horses from Olivola and Sésklo, which are referred to *Equus stenorhis* (DE GIULI, 1972; ATHANASSIOU, 1996, 2001).

In general, the *Equus* material from F-Site belongs to a big horse with slender limb bones.

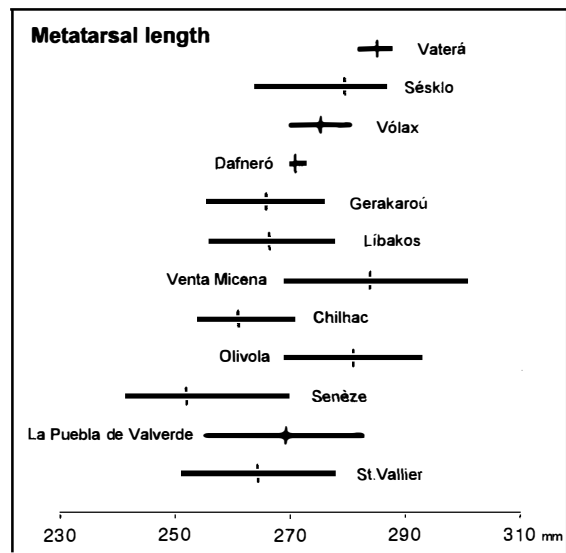
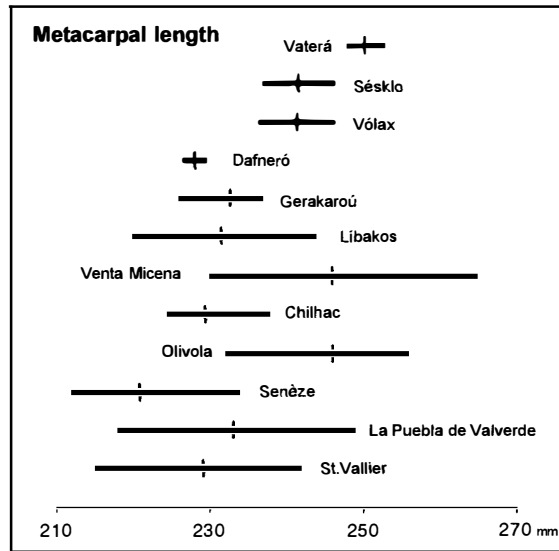
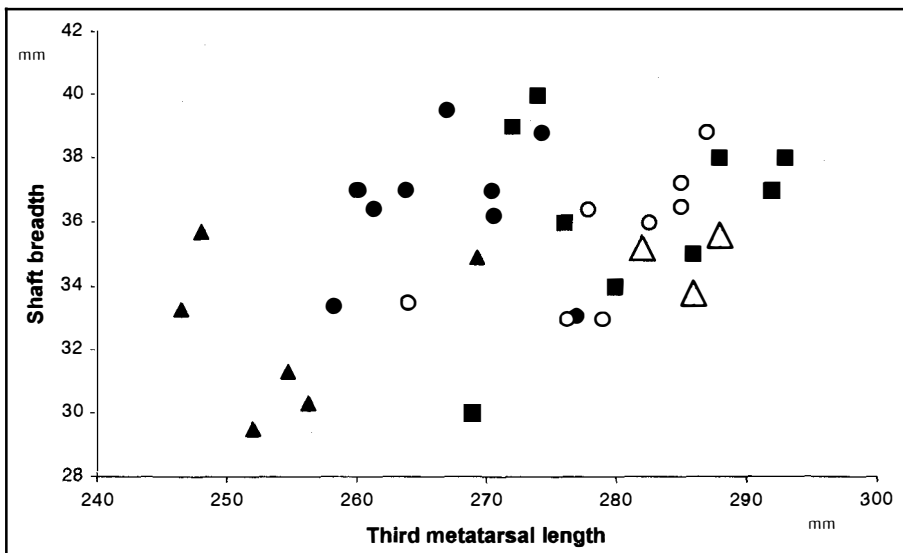
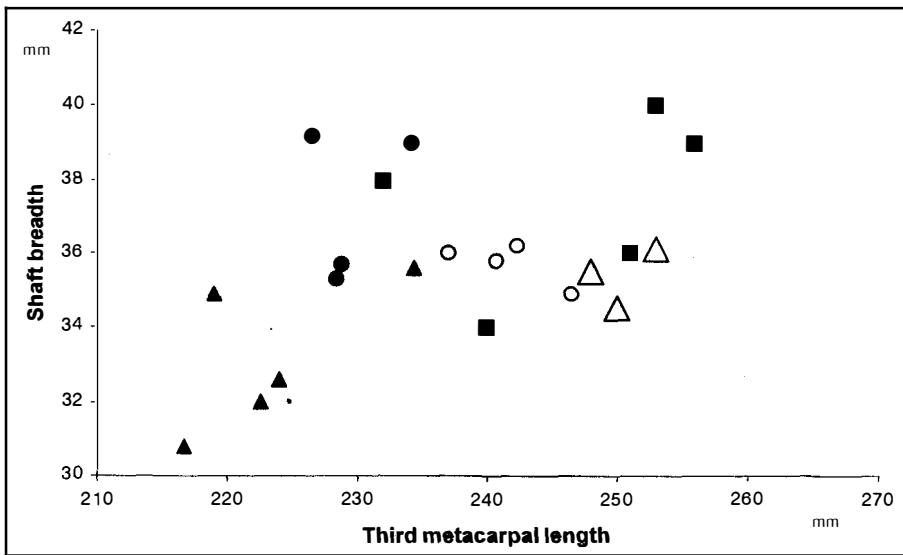


Fig. 1 Comparative diagrams of the metapodial length (metrical variation and mean) of several *Equus* samples. Data according to EISENMANN (1979), PRAT (1980), BOEUF (1983), MARIN (1987), STEENSMA (1988), KOUFOS (1992), KOUFOS & KOSTOPOULOS (1993), KOUFOS & VLACHOU (1997) and ATHANASSIOU (2001).



● St. Vallier ▲ Senèze ■ Olivola ○ Sésκλο △ Vatera

Fig. 2 Bivariate diagrams of the metapodial length and minimal shaft breadth of European *Equus* samples. St. Vallier and Senèze specimens measured in NHMB; Olivola and Sésκλο according to DE GIULI (1972) and ATHANASSIOU (2001) respectively.

Order: Artiodactyla OWEN, 1848
Family: Cervidae GOLDFUSS, 1820
Genus: *Dama* FRISCH, 1775

***Dama cf. rhenana* (DUBOIS, 1904)**

The presence of a *Dama*-like cervid is indicated by a fragmentary skull of a male with shed antlers (PO 134 F) (Plate IV, D) and its maxillaries (PO 134b and c), a front part of a skull from an old individual, an isolated left maxillary (PO 134 F a) and postcranial remains, including metacarpal PO 122 F and metatarsal PO 160 F.

The pedicles of skull PO 134 F are placed at the back of the orbit and are directed backward and upward, not so much outward as in the *Dama*-like deer, *Cervus*, *Eucladoceros*, etc. The remains are smaller and the pedicles point less outward than in material from Kuruksai (Tadzhikistan; PINM) and Udunga (PINM) assigned to *Axis* (VISLOBOKOVA, 1988; VISLOBOKOVA *et al.*, 1995).

Dama-like deer occur in the Late Pliocene to Recent in Western Europe. After placing all these forms in *Dama*, AZZAROLI (1953, 1992) considered that the relationship between the earlier and later forms was not demonstrated and placed the early forms in “*Pseudodama*”, however without demonstrating them being different. Both the study of the gradual morphological and metrical transition from the earlier to the later forms and a cladistic analysis suggest that all forms should be placed in *Dama* (VAN DER MADE, 1996, 1999a, 1999b; PFEIFER, 1997, 1999). The measurements of the maxillaries from Vaterá fit with those of *Dama*-like deer from other localities, including Tegelen, type locality of *Dama rhenana* (Tables 4, 5). The same is the case with the metapodials (Table 6; SPAAN, 1992, tables 45 and 51).

Table 4. Measurements in mm of the maxillaries from Vaterá.

Maxillary	P ² -M ³	P ² -P ⁴	M ¹ -M ³
PO 134a sin.	88.4	37.3	52.7
PO 134b dex.	85.0	38.2	50.4
PO 134c sin.	87.3	38.6	50.4
PO 461 dex. (old)	82.0	34.7	45.1
PO 461 sin. (old)	82.1	36.1	44.3

Table 5. Measurements of *Dama* from: Peyrolles, Senèze, St. Vallier and Tegelen (*Cervus* of SPAAN, 1992, table 31).

	Locality	<i>n</i>	<i>min</i>	\bar{x}	<i>max</i>
P ² –M ³	Peyrolles	1	–	78	–
	Senèze	23	81	87.4	92
	St. Vallier	22	78.5	82.9	89.5
	Tegelen	5	82	84.7	88
M ¹ –M ³	Peyrolles	3	46	48.8	51
	Senèze	43	46	51.6	56
	St. Vallier	46	45	48.0	52
	Tegelen	8	45.5	48.5	50.5
P ² –P ⁴	Peyrolles	3	34.5	35.0	35.5
	Senèze	32	37	39.0	42.5
	St. Vallier	27	34.5	37.1	40.5
	Tegelen	6	36	37.8	40.5

Table 6. Measurements (in mm) of the metacarpal and metatarsal from Vatera.

	L	DAP prox.	DT prox.	DAP dist.	DT dist.
MC PO 122 F	222	25.0	33.5	23.5	37.9
MT PO 160 F	252	33.5	32.8	24.9	38.2

Family: Giraffidae GRAY, 1821

Genus: *Mitilanotherium* SAMSON & RADULESCO, 1966

***Mitilanotherium cf. inexpectatum* SAMSON & RADULESCO, 1966**

A complete first phalanx (PO 061 F), as well as fragmentary first (PO 506 F, PO 507 F), second (PO 062 F) and third phalanx (PO 063 F), (fragments of) carpals (PO 133 F), an astragalus (PO 508 F) and an articulated distal humerus and proximal radius (PO 097 F) of a giraffid are found.

The first phalanx is more elongate than in large deer and bovines and is close to the specimen from Vólax (or Wolaks; NUA) that was attributed to *Macedonitherium martinii* (SICKENBERG, 1967) (Figure 3). Elongate first phalanges is a character that occurs already in giraffids from the Middle Miocene Chinji Formation.

Relatively small Plio-Pleistocene giraffids are known from Eastern Europe and Western Asia and have been named *Mitilanotherium inexpectatum* SAMSON & RADULESCO, 1966, *Macedonitherium martinii* SICKENBERG, 1967 and *Sogdianotherium kuruksaense* SHARAPOV, 1974. As metrical and morphological differences are small, these genera are synonyms,

and the species probably as well. A future comparison with the similar sized *Giraffa gracilis* ARAMBOURG, 1933 from the Omo area might be interesting. The giraffe from Ubeidiyah (HUI) is much larger and does not belong to the same species.

Mitilanotherium is known from the Greek localities Vólax (SICKENBERG, 1967), Líbakos (STEENSMA, 1988), Dafneró (KOSTOPOULOS, 1996) and Sésκλο (ATHANASSIOU, 1996), the Romanian localities Fintîna lui Mitilan and Valea Grâunceanului (SAMSON & RADULESCO, 1966), the Turkish locality of Gülyazı (VANDER MEULEN & VAN KOLFSCHOTEN, 1986) and from Kuruksai in Tadzhikistan (SHARAPOV, 1974). In all these localities, the material is scarce. A comparison of the material from Vaterá is possible to the samples from Romania, Vólax, Líbakos and Sésκλο, but not to those from Tadzhikistan, because no postcranials were found, and Turkey, since that material has not yet been described. As seen in Table 7, the dimensions of the humerus and the astragalus are practically the same in the compared samples. The apparently higher DT of the Romanian astragali is an artifact of the slightly different way of measuring (see footnote of Table 7). The radius from Vaterá seems to be 10-15% smaller than the other known specimens, while the first phalanx is somewhat longer and proximally deeper. The morphological and metrical resemblance of the giraffid from Vaterá to *Mitilanotherium* specimens allows the attribution of the material to *Mitilanotherium* cf. *inexpectatum*.

Table 7. Metrical comparison of the *Mitilanotherium* material (in mm).

Humerus	Vaterá	Vólax	Líbakos	Sésκλο	Romanian sites
Distal articular DT	88.5	—	—	90	—
Minimal trochlear diameter	39.6	40.0	—	40.3	—
Radius	Vaterá	Vólax	Líbakos	Sésκλο	Romanian sites
Maximal proximal DT	95.7	—	104.7	105.5	102–108
Proximal articular DAP	47.2	—	53.3	50.0	—
Proximal articular DT	88.8	—	98.4	97.0	96.5–100
Astragalus	Vaterá	Vólax	Líbakos	Sésκλο	Romanian sites
DT of the proximal trochlea	50.6	—	—	52.5	54–58*
First phalanx	Vaterá	Vólax	Líbakos	Sésκλο	Romanian sites
L	98.8	91.6	—	—	—
Proximal articular DAP	37	28	—	—	—
Proximal articular DT	33.8	34.2	—	—	—
Middle shaft DT	25.5	23.4	—	—	—
Distal articular DAP	27.2	26.5	—	—	—
Distal articular DT	27.0	28.4	—	—	—

* Maximal width of the bone.

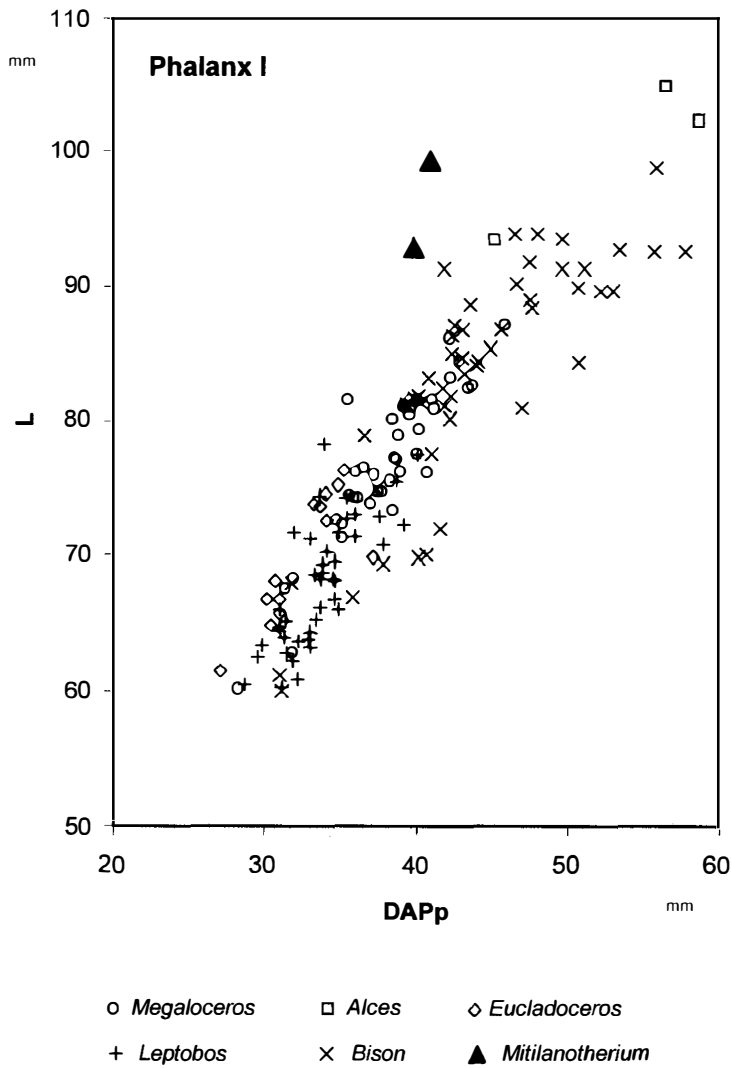


Fig. 3 Bivariate plot of the first phalanx. *Megaloceros* from Ireland (NHM), Ubeidiyah (HUI), Voigtstedt (IQW), Süßenborn (IQW), Soleilhac (MCPV) and East and West Runton (NHM). *Eucladoceros* from Tegelen (NHMM), Olivola (IGF), Il Tasso (IGF) and Untermassfeld (IQW). *Alces* from Voigtstedt (IQW) and Süßenborn (IQW). *Leptobos* from Montopoli (IGF), Ubeidiyah (HUI), Olivola (IGF), Matasino (IGF), Pýrgos (IVAU) and Láchar (MNCN). *Bison* from Untermassfeld (IQW), Voigtstedt (IQW), Pirro Nord (IGF), Appolonia 1 (AUT), Süßenborn (IQW), Soleilhac (MCPV), Bacton (NHM) and Bilzingsleben (FBB). *Mitilanotherium* from Vólax (small specimen; NUA) and Vaterá (large specimen; NHCV).

Family: Bovidae GRAY, 1821
Subfamily: Antilopinae BAIRD, 1857

The F-site yielded antelope dental and postcranial material with a bimodal distribution (Figures 4, 5). Some of the larger specimens cluster with *Gazella bouvrinae*, described by KOSTOPOULOS & ATHANASSIOU (1997), while the bulk of the material is close to the smaller specimens from Spain that are usually assigned to *Gazella borbonica* (ALBERDI *et al.*, 1997; ARRIBAS HERRERA & BERNAD GARCÍA, 1994). In particular in the M³ the specimens from Vaterá are very small compared to the Spanish material (Figure 5). It is of interest that a small P₄ has the metaconid placed far backward as in the Spanish specimens and unlike in *G. bouvrinae*.

There are four types of antilopine horn cores:

- A) Very large and long with elliptical cross-section (PO 077 F).
- B) Short horn cores of almost circular cross-section (PO 515 F);
- C) Rather short horn cores of elliptical cross-section (PO 510 F, 511 F, 514 F, 516 F);
- D) Short and straight horn cores (PO 197 F, PO 478 F, PO 614 F, PO 124 F).

Type A has exactly the same morphology with *Gazella* sp. B from Sésklo (strong horn cores, large supra-orbital foramens, very strong and prominent sutures) (ATHANASSIOU, 1996; KOSTOPOULOS & ATHANASSIOU, 1997), but it has even stronger horn cores (Plate V, B).

Type B resembles *G. bouvrinae* KOSTOPOULOS, 1996 in the dimensions of the horn core base, especially those of the sample from Gerakarou (KOSTOPOULOS & ATHANASSIOU, 1997). However, the single available specimen does not allow measurements of the total length and at 7 cm above the base.

Type C has comparable cross section dimensions to the sample of the male *G. borbonica* from La Puebla de Valverde and other European localities (Figure 6). However, the horn cores do not seem to be that long as those of the latter species, which are 160-200 mm long (HEINTZ, 1975). The length of the type C horn cores is unknown, though it was probably not greater than 130 mm.

Type D is associated to two skull fragments. The horn cores are small (Table 8), rather short (80-90 mm long) and straight. The orbits and auditory bullae are large and the brain case is very convex in lateral view (Plate V, A). The relatively small supra-orbital foramens and rather strong bend of the braincase are differences from African gazelles (GENTRY, 1978).

Table 8. Measurements (in mm) of the horn cores of type D.

	DAP at the base	DT at the base	Estimated L
PO 197 F sin.	13.0	11.9	75.6
PO 197 F dex.	12.9	11.8	76.1
PO 478 F sin.	12.1	11.3	84.2
PO 478 F dex.	12.7	11.7	88.3
PO 124 F	12.2	11.0	–
PO 614 F	12.5	10.9	–

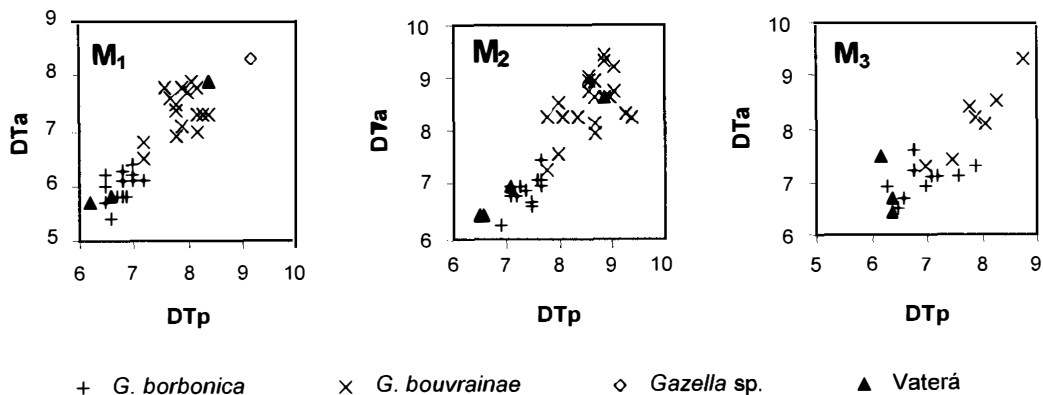


Fig. 4 Bivariate plots of the lower molars of *Gazella*. *Gazella bouvrinae* from Dafneró (AUT), Gerakarouí (AUT) and Sésklo (NUA). *Gazella* sp. from Sésklo (NUA). *Gazella borbonica* from El Rincón (MNCN) and Villarroya (MNCN). Vaterá includes at least two species: *Gazella* cf. *bouvrinae* and *Gazella* aff. *borbonica* (NHCV).

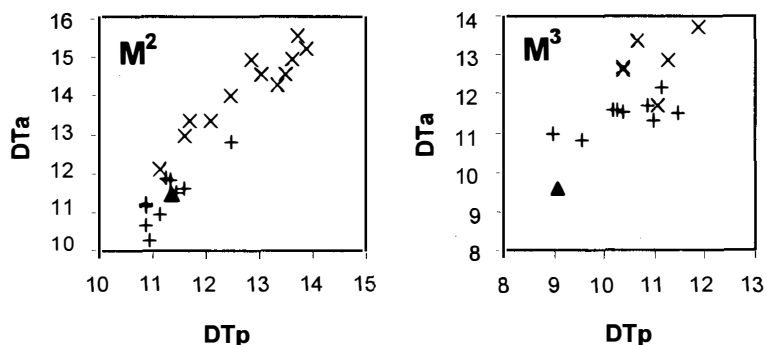


Fig. 5 Bivariate plots of the second and third upper molars. Legend and provenance of data as in figure 4, save for no data from Villarroya.

Three species of *Gazella* are reported from the latest Pliocene of Greece (KOSTOPOULOS & ATHANASSIOU, 1997): the medium-sized *Gazella borbonica*, the somewhat larger *G. bouvrinae* and a still larger, until now not named form, which is referred by ATHANASSIOU (this volume) to a new species. However, there are also other possible ways, in which the gazelline fossils can be assigned to species, as the genus *Gazella* presents marked sexual dimorphism. The females of some species do not have horn cores, but in others, like *G. borbonica*, the females have horn cores, that are much smaller than those of the males (HEINTZ, 1969). Up to now horn cores of female *G. borbonica* have not been identified from Greece.

The horncores from El Rincón and also those from the Norwich Crag have been

assigned to the sexually bimodal species *G. borbonica*, and form two clusters (Figure 6), while the dental material gives single clusters for each element (Figures 4, 5). This suggests that sexual bimodality is great in horn cores but small in dental material. In general, the female horn cores seem to have a more rounded section, while the male horn cores tend to be more flattened.

The antelope association of Vaterá could, therefore, be interpreted in the following possible ways: One extreme (favored by AA) is: 1) horn core type A is assigned to the large until now not named species, mentioned above, 2) horn core type B to *Gazella* cf. *bouvrainae*, 3) horn core type C to *Gazella* aff. *borbonica*, and 4) horn core type D to a different antelope genus, possibly neotragine. Another extreme (favored by JvdM) is: 1) small teeth and bones, and horn core types D (females) and C (males) are assigned to *Gazella* aff. *borbonica* (particularly the M3 are relatively small), and 2) larger teeth and bones and horn core type B (female) and possibly A (males) to *G. cf. bouvrainae*; alternatively type A might be a male of the large not named species. Still other, intermediate ways exist.

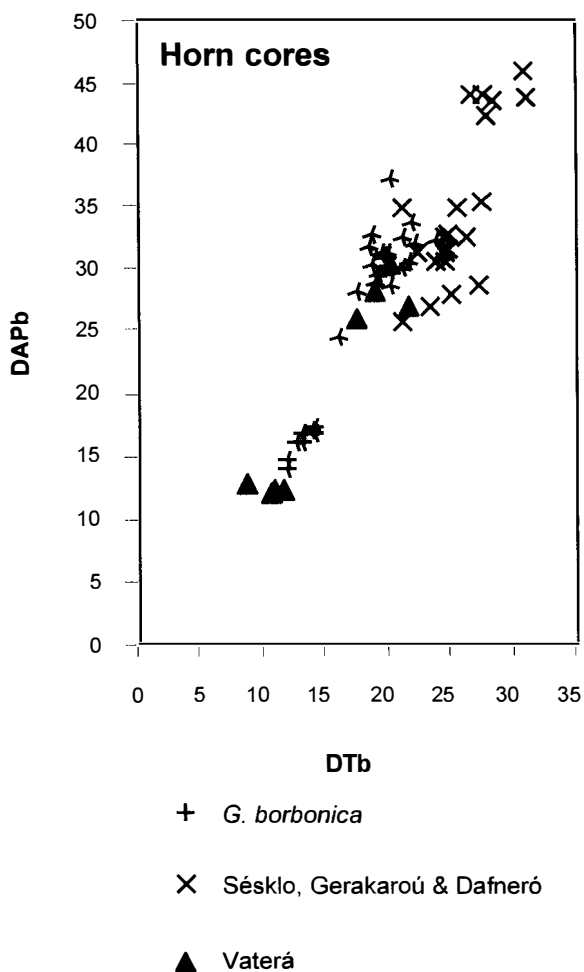


Fig. 6 Bivariate plots of the horn cores of *Gazella*. Provenance of data as in figure 4, save for no data from Villarroya; in stead 3 specimens from the Norwich Crag are included (NHML).

Nevertheless, the presence of both *Gazella* aff. *borbonica* and *Gazella* cf. *bouvrainae* is accepted in all interpretations.

Genus: *Gazellospira* PILGRIM & SCHAUB, 1939

***Gazellospira* cf. *torticornis* (AYMARD, 1854)**

The presence of *Gazellospira* is indicated by a frontal with a left horn core (PO 512), resembling the material of *Gazellospira torticornis* from Senèze, described and figured by PILGRIM & SCHAUB (1939). The left horn core shows anti-corkscrew torsion of 166° per 10 cm (measured as by VAN DER MADE & HUSSAIN, 1994). Some postcranial material can also be referred to this species.

Gazellospira torticornis is known from Europe to China (DUVERNOIS & GUÉRIN, 1989). Most of these localities are Late Pliocene (MN 16 onwards). Material from Ubeidiyah (HUI) assigned to “?*Gazellospira*” (GERAADS, 1986) does not include the very diagnostic horn cores and certainly not all this material belongs to this species. In Greece it is known from Vólax, Dafneró, Sésklo, Pýrgos, Halykés and Vaterá (VAN DER MEULEN & VAN KOLFSCHOTEN, 1986; ATHANASSIOU, 1996; KOSTOPOULOS, 1996; NUA, AUT, IVAU, NHCV). The somewhat smaller Asian species *Gazellospira gromovae* DMITRIEVA, 1975 has less robust horn cores (DMITRIEVA, 1977), which do not resemble the one found at Vaterá.

The metatarsals are small (eg. DTd 33.3, 35.6) compared to Villarroya (34.6, 36.8, 36.8, 38.2; MNCN), La Puebla de Valverde (37.6; MNCN) and Sésklo (36.0, 38.3, 38.6, 39.0, 39.0, 39.1; NUA) and similar to those from Pýrgos (33.3, 33.7). The length (≥ 248.0 , 235.9) is smaller than in Villarroya (255.6, 264.2, > 271.7 ; MNCN), but comparable to that from Pýrgos (230.4, > 22.1 ; IVAU).

The material from Vaterá is assigned to *Gazellospira* on the basis of the horn core morphology, but is on the small side for what is considered to be *G. torticornis*.

Genus: *Leptobos* RÜTIMEYER, 1877-78

cf. *Leptobos* sp.

The remaining distal part of metacarpal PO 509 F resembles *Leptobos*. Too little is preserved to know whether the specimen was long as in the giraffids or short as in the bovids. The size is a little larger than in *Leptobos* from Perrier and St. Vallier (see Tables 13 & 14). The specimen is very similar to the metacarpal PO 608 DS described below.

H-SITE

Order: Proboscidea ILLIGER, 1811

Family: Gomphotheriidae CABRERA, 1929

Genus: *Anancus* AYMARD, 1855

Anancus arvernensis (CROIZET & JOBERT, 1828)

This site contains only four specimens. They are a complete, very worn left molar (PO 008 H) (Plate III, A), a fragment of a right molar (PO 009 H) and two tusk fragments (PO 010 H and PO 011 H), all from *Anancus arvernensis*. The length of the left molar is 200 mm, the width is 77.0 mm.

U-SITE

Order: Proboscidea ILLIGER, 1811

Family: Elephantidae GRAY, 1821

Genus: *Mammuthus* BURNETT, 1830

cf. *Mammuthus meridionalis* (NESTL, 1825)

From an unknown site there is a molar fragment (PO 515 U) of cf. *Mammuthus meridionalis* present (Plate III, B).

E-SITE

Order: Carnivora BOWDICH, 1821

Family: Canidae FISCHER DE WALDHEIM, 1817

Genus: *Nyctereutes* TEMMINCK, 1838

Nyctereutes cf. *megamastoides* (POMEL, 1843)

A dextral toothrow (PO 004 E) with C, P₁, P₃–M₂ is present. This specimen was considered by DERMITZAKIS *et al.* (1991) to belong certainly to a small canid. However, they stated already that “if is of a *Vulpes*, it is a strange one”. Although it is difficult to see the characters of the mandible in the preserved fragment, the dental morphology of this specimen is characteristic for the genus *Nyctereutes*: the canine is low crowned and curved, M₁ has a short and low trigonid and the talonid is well developed with a hypoconid and endoconid of equal size, linked together with a cristid.

Family: Felidae GRAY, 1821

Machairodontinae gen. et sp. indet.

A fragmented proximal part of a left femur (PO 007 E) probably of a sabre-toothed cat is present.

Order: Perissodactyla OWEN, 1848
Family: Equidae GRAY, 1821
Genus: *Equus* LINNAEUS, 1758

***Equus* sp.**

An astragalus (PO 001 E) and a metatarsal (PO 005 E; Table 9) of a rather robust horse are present. The specimens are larger and more robust than those of the F-site (Plate IV, B). DERMITZAKIS *et al.* (1991) stated that ratio diagrams show that the proportions are closer to that of *Equus stenonis*.

Table 9. Measurements of the metatarsals of *Equus* from the E and F sites (in mm).

	PO 005 E	PO 118 F
L	317	278
DT prox.	61.5	53.7
DAP dist.	44.2	38.8
DT dist.	58.0	49.4

Order: Artiodactyla OWEN, 1848
Family: Bovidae GRAY, 1821

Bovidae gen. et sp. indet.

Two upper molars that fit together: M² (PO 002 E; DAP = 17.2, DT = 19.4) and M³ (PO 003 E; DAP = 19.3, DT = 19.1).

T-SITE

Class: Reptilia LINNAEUS, 1758
Order: Chelonia LATREILLE, 1800
Genus: *Testudo* LINNAEUS, 1758

***Testudo* sp.**

From this site a partial carapax and plastron (PO 098 T) of *Testudo* sp. is present (Plate VII, A, B). The width of the plastron is 86 mm.

DS-SITE

This site has been excavated and about 60 fossils are known.

Class: Aves LINNAEUS, 1758

Aves gen. et sp. indet.

Two associated thoracale vertebrae (PO 560 DS) are present. The length of the vertebrate body is 22.2 mm and 22.0 mm respectively. The maximum width is 17.0 mm, the height is 13.3 mm, and width is 10.4 mm.

Class: Mammalia LINNAEUS, 1758

Order: Carnivora BOWDICH, 1821

Family: Felidae GRAY, 1821

Felidae gen. et sp. indet.

Ulna (PO 561 DS)

An ulna (PO 561 DS) of a large felid is present (Plate VI, A). The proximal part is broken. The length of the articulation facet with the radius is 34.7 mm. The maximal DAP is 60.9 mm.

Tibia (PO 562 DS)

A distal part of a tibia (PO 562 DS) of a large felid is present: DAP dist. = 43.2 mm; DT dist. = 50.6 mm.

Tibia (PO 563 DS)

A complete tibia (PO 563 DS) represents a smaller felid. L = 255 mm; DAP prox. = 60.9 mm; DT prox. = 59.2 mm; DAP dist. = 26.3 mm; DT dist. = 37.7 mm.

Carnivora gen. et sp. indet.

Ulna (PO 609 DS)

A proximal ulna fragment of a small carnivore is present. It consists of facets, which articulates with the humerus and the radius. The length of the articulation facet with the humerus is 29.0 mm, the length of the articulation facet with the radius is 25.4 mm.

Canine (PO 564 DS)

A very weathered canine represents a small carnivore. Total length of the canine (root + crown) is 41.9 mm, width is 7.1 mm.

Incisor (PO 565 DS)

A very weathered incisor represents a small carnivore. Total length of the incisor (root + crown) is 24.8 mm, width is 4.3 mm.

Radius (PO 569 DS)

A proximal part of a radius (PO 569 DS) represents a small carnivore. DAP is 12.3 mm, DT is 17.9 mm.

Order: Proboscidea ILLIGER, 1811
Family: Elephantidae GRAY, 1821
Genus: *Mammuthus* BURNETT, 1830

cf. Mammuthus meridionalis (NESTI, 1825)

Small fragments (PO 568 DS) of a Proboscidean molar are present. Probably they belong to *Mammuthus meridionalis*.

Order: Perissodactyla OWEN, 1848
Family: Equidae GRAY, 1821
Genus: *Equus* LINNAEUS, 1758

Equus sp.

Equus sp. is represented by a juvenile tibia (PO 578 DS) of which the measurements are: DAP is 47.37 mm, DT is 66.6 mm and a complete calcaneum (PO 604 DS).

Family: Rhinocerotidae OWEN, 1845
Genus: *Stephanorhinus* KRETZOI, 1942

Stephanorhinus cf. etruscus (FALCONER, 1859)

A rhino species is represented by an epistropheus (PO 575 DS), complete right femur (PO 570 DS) (Plate IV, C), a left femur (PO 571 DS) of which the proximal and distal parts are broken off and lost. Further a proximal part of an ulna (PO 573 DS), a distal part of a tibia (PO 576 DS), of which the anterior part is broken and a metapodial (PO 574). A biometrical comparison with Villafranchian rhinos (Tables 10 and 11) shows that the size is similar to *Stephanorhinus etruscus*.

Table 10. Comparison of the measurements of the Lesvos femur with those of Plio-Villafranchian rhinos. Measurements taken from GUÉRIN (1980, Table 104).

Femur	PO 570 DS	<i>S. megarhinus</i>			<i>S. jeanvireti</i>			<i>S. etruscus etruscus</i>		
		<i>n</i>	\bar{x}	<i>min – max</i>	<i>n</i>	\bar{x}	<i>min – max</i>	<i>n</i>	\bar{x}	<i>min – max</i>
L	475	14	550.04	481–600	10	510.75	494–519	17	441.94	406–474
DT dist.	133.7	17	158.53	133–174	12	151.08	143–160	21	124.1	115–135

Table 11. Comparison of the measurements of the Lesvos femur with those of Plio-Villafranchian rhinos. Measurements taken from GUÉRIN (1980, Table 104).

Femur	PO 571 DS	<i>S. megarhinus</i>			<i>S. jeanvireti</i>			<i>S. etruscus etruscus</i>		
		<i>n</i>	\bar{x}	<i>min – max</i>	<i>n</i>	\bar{x}	<i>min – max</i>	<i>n</i>	\bar{x}	<i>min – max</i>
DT 3rd tro.	110.0	14	161.79	150–177	8	145.13	128–164	17	121.53	101–140

Order Artiodactyla OWEN, 1848
Family Bovidae GRAY, 1821
Subfamily: Antilopinae BAIRD, 1857

Antilopinae gen. et sp. indet.

A horn core PO 600 DS that is spine-like similar to those of the Type D from the F-Site. The measurements at the base are: DAP is 13.2 mm, DT is 11.6 mm. A second phalanx (PO 583 DS) might belong to this form, or, because of its size (Table 12), might belong to a larger gazelle.

Table 12 Measurements (in mm) of the second phalanges of the Artiodactyla from the DS site.

Phalanx II	PO 591 DS	PO 583 DS
L	40.0	24.1
DAP prox.	29.8	14.2
DT prox.	21.4	9.6
DAP dist.	25.8	10.8
DT dist.	18.9	8.1

Genus: *Leptobos* RÜTIMEYER, 1877-78

cf. *Leptobos* sp.

A metacarpal (PO 608 DS) of a large bovid (Plate VI, B) is as gracile as in *Leptobos* and *Bison menneri* and is in the metrical overlap of the two (Tables 13 & 14; SHER, 1997). A distal part of a radius (PO 607 DS) with gnawing marks: DAP = 48.5 mm and DT = 88.9 mm. Phalanx PO 591 DS has the size of *Leptobos* (Table 12), though it is rather narrow. Within the context of the fauna, it is more likely that these fossils belong to *Leptobos* than to *Bison*.

Table 13. Measurements (in mm) of the metacarpals of cf. *Leptobos* from the F and DS-Sites.

	PO 608 DS	PO 509 F
L	267	—
DAP prox.	41.3	—
DT prox.	69.6	—
DAP dist.	39.5	39.7
DT dist.	68.4	66.7

Family: Cervidae GRAY, 1821

Cervidae gen. et sp. indet.

A cervid is represented by a piece of antler (PO 099 DS) of which the dimensions are: DAP = 26.9 mm, DT = 34.8 mm.

Table 14. Measurements of metacarpal of different species and subspecies of *Leptobos* as indicated by DUVERNOIS (1990, table 20) and of *Bison menneri* from SHER (1997).

	<i>n</i>	\bar{x}	<i>min</i>	<i>max</i>
<i>L. etruscus</i>				
L	53	245.46	223.5	266
DAP prox.	59	40.26	35.5	46
DT prox.	60	63.35	55	69.5
DAP dist.	65	34.74	30	40
DT dist.	68	59.95	51	66.5
<i>L. bravardi</i>				
L	6	260.5	256	267
DAP prox.	8	40.81	38.5	43
DT prox.	9	61.72	57.5	64.5
DAP dist.	10	35.85	34	39
DT dist.	8	59.56	57	64
<i>L. elatus elatus</i>				
L	10	247.35	242.5	253.5
DAP prox.	12	36.16	32.5	39
DT prox.	12	54.91	52.5	57.5
DAP dist.	10	32	30	33.5
DT dist.	11	52.31	48.5	55.5
<i>L. elatus merlai</i>				
L	11	242.04	231	256
DAP prox.	8	39.62	35	45
DT prox.	7	58.14	51	66
DAP dist.	11	32.31	29.5	35.5
DT dist.	11	56.81	52	63
<i>L. furtivus</i>				
L	13	231.8	216.5	246.5
DAP prox.	16	35.43	32	38
DT prox.	16	53.43	49	56.5
DAP dist.	14	30.21	27.5	32.5
DT dist.	16	50.96	47.5	55
<i>B. menneri</i>				
L	33	262.0	277.5	297.0
DAP prox.	44	40.0	46.5	53.0
DT prox.	44	68.0	77.0	88.0
DAP dist.	33	38.0	43.7	48.5
DT dist.	34	68.0	76.5	87.0

III. DISCUSSION AND CONCLUSION

The F- and DS-sites are comparable in their small antelopes, cf. *Leptobos* and *Equus*. Other elements, present in only one of the two sites are also present in Greek localities such as Vólax, Sésklo and Dafneró (KOUFOS *et al.*, 1991; ATHANASSIOU, 1996; KOSTOPOULOS, 1996; KOUFOS & KOSTOPOULOS, 1997), as well as Valea Grâunceanului and Fintîna lui Mițilan in Romania (RADULESCO & SAMSON, 1991), St.Vallier and Senèze in France (SCHAUB, 1923, 1944, VIRET, 1954) and Villarroya and La Puebla de Valverde in Spain (HEINTZ, 1978; ARRIBAS HERRERA & BERNAD GARCÍA, 1994).

A taxon present in the F- and E-sites that is known from all of the Pliocene is *Nyctereutes*. This genus was disappeared in Europe after the first occurrence of the wolf, at the end of the Pliocene (Senèze Faunal Unit, MNQ18). Taxa ranging from the Late Pliocene to the Pleistocene include *Mitilanotherium*, *Dama rhenana* and *Gazellospira*. Typically Late Pliocene taxa include *Gazella bouvrinae* and *Gazella borbonica*. In Western Europe, *Gazella* went extinct before the end of the Pliocene (and is not present in Senèze anymore), but in SE Europe, the genus has lived on longer, until the very end of the Pliocene, showing marked diversity of forms. The co-occurrence of *Mammuthus* and *Anancus* in the same formation points to a similar age; MN17, or (less likely) upper MN16. The *Equus* cf. *stenonis* morphology gives more precise biochronological clues; it indicates a lower MN17 (MNQ17) age, as it is similar to the samples of Sésklo, Dafneró and Vólax but rather unlike the smaller and more slender, stratigraphically younger forms of Gerakaroú, Líbakos etc., dated in MNQ18–MNQ19 (KOUFOS & KOSTOPOULOS, 1997). A detailed study of the gazelles and canid might also lead to a precise estimation of the age. At this stage, a dating of the F-Site in lower MN17 seems very likely, which roughly corresponds to the time range between some 2.5 Ma and about 2.0 Ma (disappearance of *Nyctereutes*, entry of *Canis*). The DS-Site is probably of similar age, but more material is needed for detailed biochronology.

The E-site, with *Nyctereutes*, a bovid and a sabre-toothed cat, differs from the F-site and DS-site in its horse being more robust. DERMITZAKIS *et al.* (1991) suggested, based on the robust horse, a Late Pleistocene age for this site, although they stated that it is in contradiction with the reference of the astragalus to a stenorid horse. The reinterpretation of the canid from the E-Site as *Nyctereutes*, suggests that a Late Pliocene age is more realistic.

The U-Site, with only a *Mammuthus meridionalis* molar, is in the range Late Pliocene – early Middle Pleistocene (about 2.7–0.7 Ma). *Anancus arvernensis*, the only taxon from the H-Site, ranged from the latest Miocene to the latest Pliocene (about 7 to 1.8 Ma). *Testudo* sp. from the T-Site is of little help in biostratigraphy.

Some of the localities are thus of a Late Pliocene age (plausibly lower MN17), while others have poor fauna, that does not exclude a Late Pliocene age (2.7–1.8 Ma).

The presence of a giraffid and the presence of at least four bovid species suggest relatively dry or open landscape, as does the fauna of some of the Greek localities mentioned above. The absence of suids (e.g. *Sus strozzi*) and large deer (e.g. *Eucladoceros*), that are known from other localities of a similar age, might also suggest an open or dry landscape, though we have to bear the small sample size in mind.

Table 15: Faunal content of the excavated sites at Väterá.

	F	E	H	DS	T	U
Reptilia						
<i>Testudo</i> sp.					+	
<i>Chelonia</i> indet.	+					
Aves						
Aves indet.	+			+		
Primates						
<i>Paradolichopithecus arvernensis</i>	+					
Carnivora						
<i>Nyctereutes megamastoides</i>	+	cf.				
<i>Meles thoralis</i>	+					
Mustelidae indet.	+					
Felidae indet.					+	
Machairodontinae indet.		+				
Carnivora indet.	+				+	
Proboscidea						
<i>Anancus arvernensis</i>	cf.		+			
<i>Mammuthus meridionalis</i>					cf.	cf.
Perissodactyla						
<i>Equus stenonis</i>	cf.					
<i>Equus</i> sp.		+			+	
<i>Stephanorhinus etruscus</i>					cf.	
Artiodactyla						
<i>Dama rhenana</i>	cf.					
Cervidae indet.					+	
<i>Mitilanotherium inexpectatum</i>	cf.					
<i>Gazella borbonica</i>	aff.				aff.	
<i>Gazella bouvrinae</i>	cf.					
Antilopinae Type A	+					
Antilopinae Type D	+				+	
<i>Gazellospira torticornis</i>	cf.					
<i>Leptobos</i> sp.	cf.				cf.	
Bovidae indet.		+				

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J.P. BRINKERINK prepared the specimens. S. VAN DER GEER made the photographs.

ABSTRACT

A preliminary description of the fossil vertebrates from six sites in the surroundings of Vaterá on Lesbos is given. Characteristic elements from the richest site are: a giant turtle, *Paradolichopithecus arvernensis*, *Nyctereutes megamastoides*, *Meles thoralis*, cf. *Anancus arvernensis*, *Equus* cf. *stenonis*, *Dama* cf. *rhenana*, *Mitilanotherium* cf. *inexpectatum*, *Gazella* cf. *bouvrainae*, *Gazella* aff. *borbonica* and *Gazellospira* cf. *torticornis*. The other sites yielded poorer, but otherwise similar faunas, with in addition: cf. *Mammuthus meridionalis*, *Stephanorhinus* cf. *etruscus* and better material of *Anancus arvernensis*. These faunas are considered to be Late Pliocene in age and comparable with the faunas of Vólax, Dafneró and Sésκλο (Greece).

ΠΕΡΙΛΗΨΗ

Στην παρούσα εργασία δίδεται μία προκαταρκτική περιγραφή των απολιθωμένων Θηλαστικών, τα οποία βρέθηκαν σε έξι θέσεις της περιοχής των Βατερών (Ν. Λέσβος). Χαρακτηριστικά πανθικά στοιχεία της πλουσιότερης θέσεως είναι: μία γιγαντιαία χελώνα, *Paradolichopithecus arvernensis*, *Nyctereutes megamastoides*, *Meles thoralis*, cf. *Anancus arvernensis*, *Equus* cf. *stenonis*, *Dama* cf. *rhenana*, *Mitilanotherium* cf. *inexpectatum*, *Gazella* cf. *bouvrainae*, *Gazella* aff. *borbonica* και *Gazellospira* cf. *torticornis*. Οι άλλες θέσεις έδωσαν φτωχότερες, αλλά γενικά όμοιες, πανίδες, με επιπρόσθετα στοιχεία τα cf. *Mammuthus meridionalis*, *Stephanorhinus* cf. *etruscus*, καθώς και καλύτερο υλικό του *Anancus arvernensis*. Οι περιγραφόμενες πανίδες θεωρούνται ανωπλειοκαινικής ηλικίας και είναι συγκρίσιμες με αυτές του Βόλακα, του Δαφνερού και του Σέσκλου.

REFERENCES

- ALBERDI, M.-T., CERDEÑO, E., LÓPEZ-MARTÍNEZ, N., MORALES, J. & M.D. SORIA (1997). La fauna villafranquiense de el Rincón-1 (Albacete, Castilla – La Mancha). *Estudios Geológicos*, 53: 69-93.
- ARRIBAS HERRERA, A. & J. BERNAD GARCÍA (1994). Catálogo de Mamíferos pliocenos del yacimiento de Villarroja (La Rioja), en la colección del Museo Geominero. *Boletín Geológico y Minero*, 105 (3): 14-26.

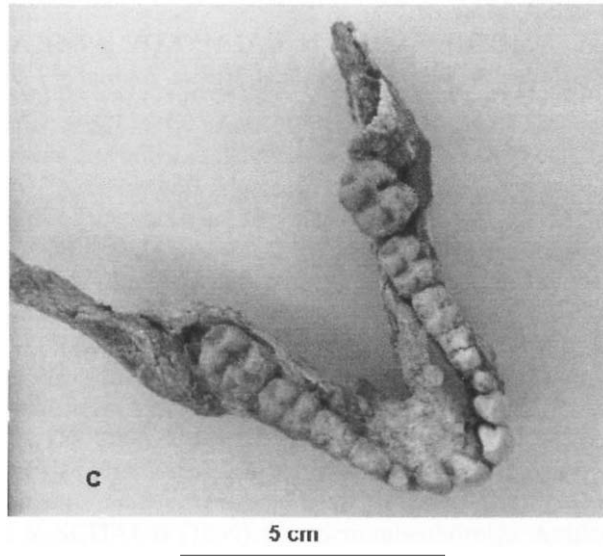
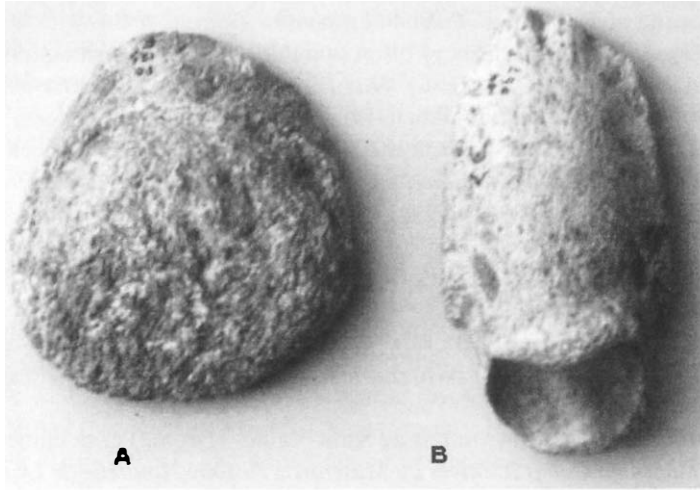
- ATHANASSIOU, A. (1996). *Contribution to the study of the fossil mammals of Thessaly*. PhD thesis, University of Athens, Athens (in Greek).
- ATHANASSIOU, A. (2001). New data on the *Equus stenonis* from the Late Pliocene locality of Séslo (Thessaly, Greece). *Geodiversitas*, 23 (3): 439-469.
- ATHANASSIOU, A. (this volume). A new gazelle species (Artiodactyla, Bovidae) from the Late Pliocene of Greece.
- AZZAROLI, A. (1953). The deer of the Weybourn Crag and Forest Bed of Norfolk. *Bulletin of the British Museum (Natural History)*, 2 (1): 1-96.
- AZZAROLI, A. (1992). The cervid genus *Pseudodama* n. g. in the Villafranchian of Tuscany. *Palaeontographia Italica*, LXXI: 5-16.
- BOEUF, O. (1983). *Le site villafranchien de Chilhac (Haute-Loire, France). Etude paléontologique et biochronologique*. Thèse, Université de Paris VII, Paris.
- DE GIULI, C. (1972). On the type form of *Equus stenonis* COCCHI. *Palaeontographia Italica*, LXVIII: 35-49.
- DELSON, E. (1975). Evolutionary history of the Cercopithecidae. In SZALAY, F.S. (Ed.). *Approaches to Primate Paleobiology*. Volume 5: Contributions to Primatology. Karger, Basel.
- DERMITZAKIS, M.D., EISENMANN, V. & S.F. GALOUKAS (1991). The presence of Pleistocene Mammals in Lesvos Island (E. Aegean). *Bulletin of the Geological Society of Greece*, XXV (2): 405-421.
- DMITRIEVA, E.L. (1977). *Neogene Antelopes from Mongolia and adjacent regions*. Nauka, Moskva.
- DUVERNOIS, M.P. (1990). Les *Leptobos* (Mammalia, Artiodactyla) du Villafranchien d'Europe occidentale. Systématique, évolution, biostratigraphie, paléoécologie. *Documents des Laboratoires de Géologie Lyon*, 113: 1-213.
- DUVERNOIS, M.P. & C. GUÉRIN (1989). Les Bovidae (Mammalia) du Villafranchien supérieur d'Europe occidentale. *Géobios*, 22 (3): 339-379.
- EISENMANN, V. (1979). Les métapodes d'*Equus sensu lato* (Mammalia, Perissodactyla). *Géobios*, 12 (6): 863-886.
- EISENMANN, V. (this volume). The primitive horses of the VATERÁ formation (Lesbos, Greece).
- GENTRY, A.W. (1978). Bovidae. In MAGLIO, V.J. & H.B.S. COOKE (Eds.). *Evolution of African Mammals*. Harvard University Press, Cambridge.
- GERAADS, D. (1986). Les ruminants du Pléistocène d'Oubeidiyeh (Israel). In TCHERNOV, E. & C. GUÉRIN (Eds.). *Les mammifères du Pléistocène inférieur de la vallée du Jourdain à Ougédiyeh. Mémoires et Travaux du Centre de Recherches Français de Jérusalem*, 5.
- GUÉRIN, C. (1980). Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie Lyon*, 79 (1-3): 1-1184.
- GROMOVA, V. (1949). Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisani form. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 17 (1): 1-373.
- HEINTZ, E. (1969). Le dimorphisme sexuel des appendices frontaux chez *Gazella deperdita* GERVAIS (Bovidae, Artiodactyla, Mammalia) et sa signification phylogénique. *Mammalia*, 33 (4): 626-629.
- HEINTZ, E. (1975). *Gazella borbonica* (Bovidae, Mammalia) et l'âge pliocène du gisement de Las Higuieruelas (Alcolea de Calatrava, Ciudad Real, Espagne). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 78 (3): 219-224.
- HEINTZ, E. (1978). La faune villafranchienne de La Puebla de Valverde, Teruel, Espagne. Composition qualitative et quantitative. *Géologie Méditerranéenne*, V (2): 277-280.

- KOSTOPOULOS, D.S. (1996). *The Plio-Pleistocene artiodactyls of Macedonia (Greece); systematics, palaeoecology, biochronology, biostratigraphy*. PhD Thesis, University of Thessaloniki (in Greek).
- KOSTOPOULOS, S.D. & A.S. ATHANASSIOU (1997). Les gazelles du Pliocène moyen-terminal de la Grèce continentale (Macédoine, Thessalie). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 205 (3): 413-430.
- KOUFOS, G.D. (1992). Early Pleistocene Equids from Mygdonia basin (Macedonia, Greece). *Palaeontographia Italica*, LXXIX: 167-199.
- KOUFOS, G.D. & D.S. KOSTOPOULOS (1993). A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Western Macedonia (Greece). *Bulletin of the Geological Society of Greece*, XXVIII (3): 131-143.
- KOUFOS, G.D. & D.S. KOSTOPOULOS (1997). Biochronology and succession of the Plio-Pleistocene macromammalian localities of Greece. *Biochrom '97*, Montpellier, 1997. *Mémoires Travaux E.P.H.E. Inst. Montpellier*, 21: 619-634.
- KOUFOS, G.D., KOSTOPOULOS, D.S. & K.K. KOLIADIMOU (1991). Un nouveau gisement de mammifères dans le Villafranchien de Macédoine occidentale (Grèce). *Comptes Rendus de l'Académie des Sciences*, 313: 831-836.
- KOUFOS, G.D. & T. VLACHOU (1997). *Equus stenonis* from the middle Villafranchian locality of Volax (Macedonia, Greece). *Geodiversitas*, 19 (3): 641-657.
- MADE, J. VAN DER (1996). The genus *Dama* at the dawn of the Quaternary. *INQUASEQS '96 The Dawn of the Quaternary, palaeoenvironment, stratigraphy and climate. Abstracts*: 62.
- MADE, J. VAN DER (1999a). Ungulates from Atapuerca-TD6. *Journal of Human Evolution*, 37: 389-413.
- MADE, J. VAN DER (1999b). On *Euraxis*, on the rules of the ICZN, on methodology. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1999 (11): 676-678.
- MADE, J. VAN DER & S.T. HUSSAIN (1994). Horn cores of *Sivoreas* (Bovidae) from the Miocene of Pakistan and utility of their torsion as a taxonomic tool. *Geobios*, 27 (1): 103-113.
- MARIN, M. (1987). *Equus stenonis granatensis* en el Pleistoceno inferior de Venta Micena (Granada, España). *Paleontología i Evolució*, Mem. Esp. 1: 255-282.
- MEULEN, A.J. VANDER & T. VAN KOLFSCHOTEN (1986). Review of the Late Turolian to Early Biharian mammal faunas from Greece and Turkey. *Memorie della Società Geologica Italiana*, XXXI: 201-211.
- PFEIFER, T. (1997). *Dama (Pseudodama) reichenau* (KAHLKE, 1996) (Artiodactyla, Cervidae, Cervini) aus den Mosbach Sanden (Wiesbaden-Biebrich). *Mainzer Naturwissenschaftliches Archiv*, 35: 31-59.
- PFEIFER, T. (1999). Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometa-carpaler Hirsche des Pleistozäns. Phylogenetische Rekonstruktion – Metrische Analyse. *Courier Forschungsinstitut Senckenberg*, 211: 1-218.
- PILGRIM, G.E. & S. SCHAUB (1939). Die Schraubenhörnige Antilope des europäischen Oberpliocäns und ihre systematische Stellung. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, 62 (3): 1-30, pls. 1-3.
- PRAT, F. (1980). Les Equidés villafranchiens en France, genre *Equus*. *Cahiers du Quaternaire*, 2: 1-290.
- RADULESCO, C. & P. SAMSON (1991). Traces d'activité humaine à la limite Pliocène/Pléistocène dans le Bassin Dacique (Roumanie). In E. BONIFAY & V. VANDERMEERSCH (Eds.). *Les Premiers Européens*. Éditions du C.T.H.S., Paris.
- SAMSON, P. & C. RADULESCO (1966). Sur la présence des girafidés dans le Villafranchien supérieur de Roumanie. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 10: 588-594.

- SCHAUB, S. (1923). Neue und wenig bekannte Cavicornier von Senèze. *Eclogae Geologicae Helvetiae*, XVIII (2): 281-290.
- SCHAUB, S. (1944). Die oberpliocäne Säugetierfauna von Senèze (Haute-Loire) und ihre verbreitungsgeschichtliche Stellung. *Eclogae Geologicae Helvetiae*, 36 (2): 270-289.
- SHARAPOV, S. (1974). *Sogdianotherium* – a new genus of the family Giraffidae from the Upper Pliocene of Tadjikistan. *Paleontologicheskii Zhurnal*, 4: 86-91.
- SHER, A. (1997). An Early Quaternary bison population from Untermassfeld: *Bison menneri* sp. nov. In KAHLKE, R.D. (Ed.). *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*. Teil 1. Dr. Rudolf Habelt, Bonn.
- SICKENBERG, O. (1967). Die Unterpleistozäne Fauna von Wolaks (Griech. - Mazedonien) I. eine neue Giraffe (*Macedonitherium martinii* nov. gen. nov. spec.) aus dem Untern Pleistozän von Griechenland. *Annales Géologiques des Pays Helléniques*, XVIII: 314-330, pls. 45-46.
- SPAAN, A. (1992). A revision of the deer from Tegelen (province of Limburg, The Netherlands). *Scripta Geologica*, 98: 1-85.
- STEENSMA, K.J. (1988). *Plio-/Pleistozäne Großsäugetiere (Mammalia) aus dem Becken von Kastoria/Grevena, südlich von Neapolis – NW-Griechenland*. PhD thesis Univeristy of Clausthal: 315 pp.
- VIRET, J. (1954). Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères Villafranchiens. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, IV: 1-200.
- VISLOBOKOVA, I.A. (1988). Family Cervidae. In NIKIFOROVA K.V. & E.A. VANGENGHEIM (Eds.). *Late Pliocene – Early Pleistocene biostratigraphy of Tadzhikistan*. Akademia Nauk SSSR, Moscow.
- VISLOBOKOVA, I.A., DMITRIEVA, E. & N. KALMYKOV (1995). Artiodactyls from the Late Pliocene of Udunga, western Trans-Baikal, Russia. *Journal of Vertebrate Paleontology*, 15 (1): 146-159.

PLATES

PLATE I



Chelonia gen. et sp. indet.

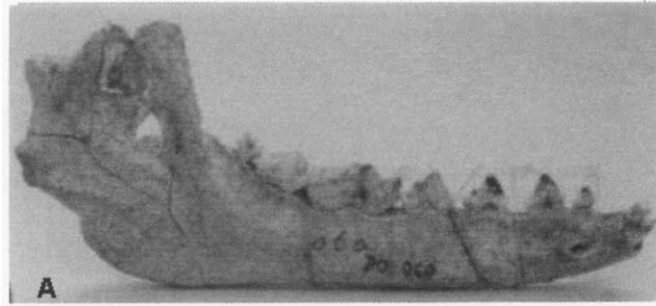
A: Osteoderm (PO 071 F)

B: Phalanx III (PO 067 F)

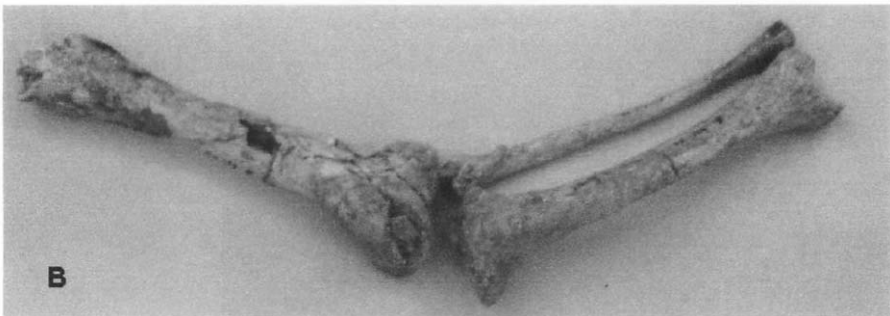
Paradolichopithecus arvemensis (DEPÉRET, 1929)

C: Mandibula (PO I 14 F)

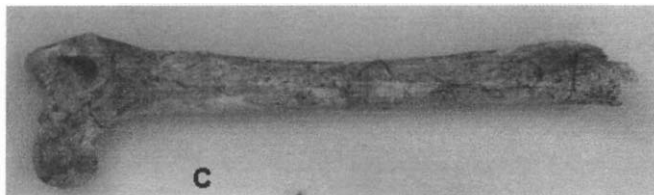
PLATE II



5 cm



5 cm



5 cm

Nyctereutes megamastoides (POMEL, 1843)

A: Mandibula (PO 060 F)

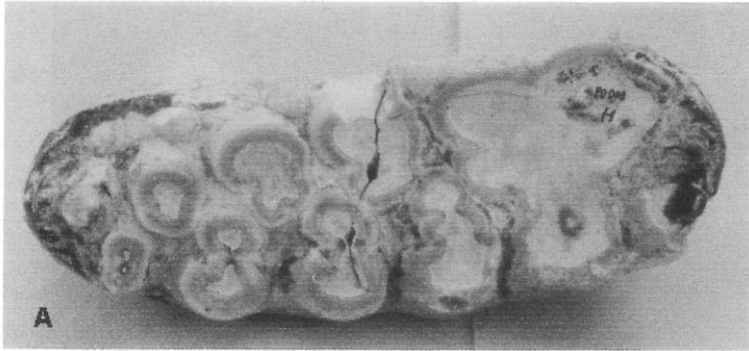
Mustelidae gen. et sp. indet.

B: Femur (PO 143 F), tibia (PO 144 F), fibula (PO 145 F)

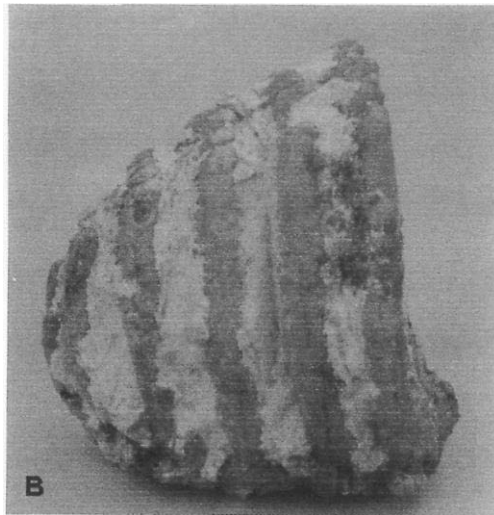
Carnivora gen. et sp. indet.

C: Femur (PO 153 F)

PLATE III



5 cm



5 cm

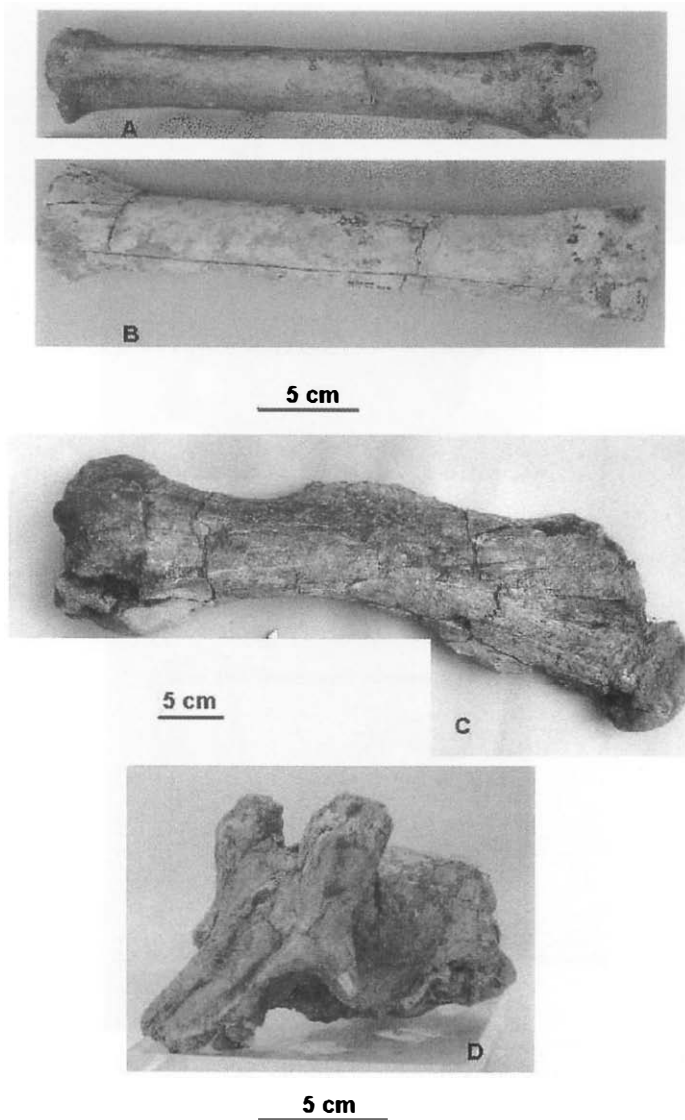
Anancus arvernensis (CROIZET & JOBERT, 1828)

A: Molar (PO 008 H)

cf. *Mammuthus meridionalis* (NESTL, 1825)

B: Molar fragment (PO 515 U)

PLATE IV



Equus cf. stenonis COCCHI, 1867

A: Metatarsale III (PO 110 F)

Equus sp.

B: Metatarsale III (PO 005 E)

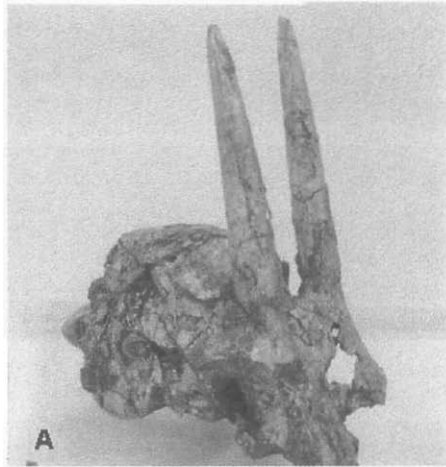
Stephanorhinus cf. etruscus (FALCONER, 1859)

C: Femur (PO 570 DS)

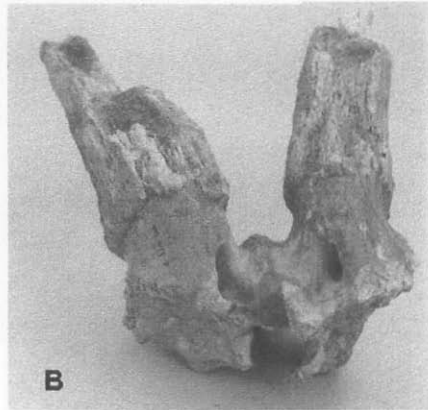
Dama cf. rhenana (DUBOIS, 1904)

D: Cranium (PO 134 F)

PLATE V



5 cm

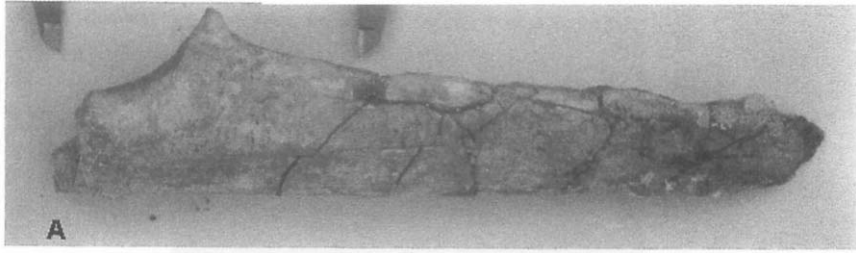


5 cm

Antilopinae gen. et sp. indet. (Type D)
A: Cranium (PO 614 F)

Antilopinae gen. et sp. indet. (Type A)
B: Frontlet (PO 077 F)

PLATE VI



5 cm



5
cm

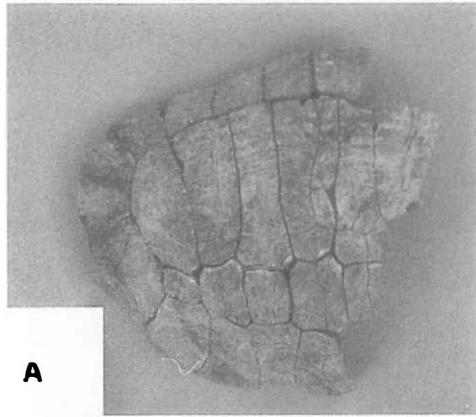
Felidae gen. et sp. indet.

A: Ulna (PO 561 DS)

cf. *Leptobos* sp.

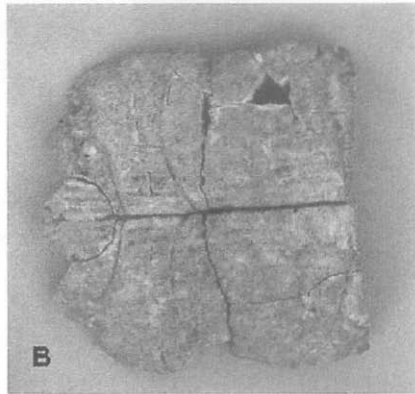
B: Metacarpale III-IV (PO 608 DS)

PLATE VII



A

5 cm



B

5 cm

Testudo sp.

A: Carapax (PO 098 T)

B: Plastron (PO 098 T)