Quarternary large mammals from the Apidima Caves (Lakonia, S Peloponnese, Greece)

by

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K e y w o r d s Large mammal fauna (Quaternary Palaeolithic), Apidima caves, (S Peloponnese, Greece)

Summary

The large mammalian remains from the most important Quaternary site in Apidima (South Peloponnese, Greece), have been studied in the present paper. Two Middle Pleistocene hominid skulls, associated with many fossilized animal bones, as well as bone and lithic artefacts, underline the importance of this prehistoric site. The study of the most representative specimens of the fauna showed the presence of carnivores, mainly felids, mustelids and foxes; herbivores, mainly small bovids and cervids; very large mammals, such as hippopotamids and elephants; as well as micromammals (leporids and rodents) and birds, which lived in the area from the Middle Pleistocene to Holocene. From the study of this fauna the paleoecology and the paleoenvironment of the area are discussed, in conjunction with the Palaeolithic activities of the Man during this period.

Introduction

Historical overview – Geological background of the region

The Apidima complex of six maritime caves is located in Mesa Mani (Lakonia), on a steep coast of the western Mani peninsula, which is the southernmost continental point of the Balkan peninsula, very near to the active Hellenic subduction zone. Tectonic events, in conjunction with the eustatic sea level fluctuations of the Quaternary, developed a series of interactive speleoenvironments such as Apidima (BASSIAKOS, 1993). The Neogene is represented by Late Pliocene marine deposits, which are yellowish marls (RONDO-YANNI et al., 1995, VERGINIS et al., 1975). Quaternary terrestrial deposits are represented, in some places, by very cohesive cemented breccias, sometimes with fossils; and scree and talus cones compacted during the Mindel, Riss and Würm. North of Apidima, the site of Kalamakia, where excavations are still in progress, has yielded few elephant and rhino remains, as well as remains of caprids and cervids (considered as hominid food), dating to 80-40x10³ years BP (LUMEY de & DARLAS, 1994). In the south, the presence of Dama and Elephas and the absence of carnivore and dwarf forms (BARTSIOKAS, 1998) as well as of many other large mammalian fossil remains, found mainly in cohesive cemented breccia, indicates the "bridges" joining the Cythera island with the continent, so the partition of the island from the Peloponnese mainland happened during the Late Pleistocene (MANOLESSOS, 1955).

The Apidima caves are karstic formations within the Middle Triassic-Late Eocene limestone (Plattenkalk) of depth 500m, from 4 to 24m above sea level, in a vertical zone of depth 20m (Fig.1). The development of the caves is due to the vertical strikes of the limestone, while the horizontal opening is made by the sea according to the geological observations made by RONDOYANNI et al. (1995). In the very thick and cohesive breccia up to 23m above sea level, two Middle Pleistocene hominid skulls were found in cave A, 4m above sea level. These finds give major importance to the Apidima site (PITSIOS, 1979, 1996, COUTSELINIS et al., 1991).

About 20.000 bones, bone fragments and teeth have been collected by Prof. Dr. Theodore PITSIOS and his team since 1978, during four field seasons of systematic excavations from the four caves (A, B, C and D) and they are now stored in the Museum of Anthropology (Athens University). Among the rich macro- and micro- mammal and bird material, a skeleton of a buried woman (+18m), numerous bone and lithic artefacts, fire traces and food remains were found (PITSIOS, 1979, 1983, 1985a,b, PITSIOS & LIEBHABER, 1995). The ESR dating of the travertine calcite and the fossilized

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Figure 1: Map of Greece with the locality (left) and the Apidima maritime caves (above): a) Ground plan 5 m above sea level b, c) vertical sections of the caves (drawings from PITSIOS, 1985b, PITSIOS & LIEBHABER, 1995) (o.s.l.: old sea level) skeletal remains gave ages for two samples $25-45 \times 10^3$ and $20-30 \times 10^3$ years BP (LIRITZIS & MANIATIS, 1995, BASSIAKOS, 1993).

Systematic Palaeontology

Introduction

The paleontological study is mainly based on the determinable, well preserved and most representative large mammal material, as the statistical study of the bone fragments is given by LAX (1995). The study took place in the Museum of Anthropology of Athens University, where this material is stored, during the years 1991–97.

Taxonomy

Order CARNIVORA Bowdich, 1821 Superfamily FELOIDEA SIMPSON, 1931 Family Felidae GRAY, 1821 Subfamily Felinae PIVETEAU, 1961 Genus **Panthera** OKEN, 1816

Panthera pardus (LINNAEUS, 1758) (Plate 1, Figs. 1–8, Text-figs. 2, 5, Table 1)

Material Maxilla fr. dex, I³ LAO-B-346 sin, C^s LAO-B-091 dex, C^s fr. LAO-B-409 dex, I₃ LAO-B-383a dex, dC_iLAO-B-175c dex, P₄ LAO-B-159e sin, 2 femur prox. LAO-C-729 dex, 697+700d sin, radius LAO-B-388c +389 sin, radius prox. LAO-C-649c, tibia LAO-C-722 sin, 2 patellae LAO-C-814 sin, LAO-B-390 dex, astragalus LAO-C-641 dex, navicularis LAO-B-389b sin, McV LAO-B-389a dex, PhI LAO-B-410a, PhII LAO-B-348e. Description Anterior part of a maxilla, with the alveoli of C^s, P², P³ and the P⁴ antero-external root are preserved. The dimensions are: L* P²alveoli=5.2, BP²alveoli =4.5, LP³alveoli=16.6, BP³alveoli=8.5 mm. A slightly worn I³ is robust, with a well developed labial tubercle and longitudinal crest. A C^s is slightly worn, with well distinguished longitudinal flutes. Half a fragment of a C^s, preserved in cohesive breccia, is very robust. A slightly worn milk canine has dimensions very close to those of recent leopard (dC^s: LxB=6.5x5.4mm, I.P.H* coll. Regalia, Tab. 1). A P₄ lacks only a small posterior part of the protoconid; the anterior accessory cuspid is well developed and the talonid is wide. Of two femurs, the proximal part with the caput are preserved; and of two radii, one is complete, while the other preserves the proximal part and most of the diaphysis. A tibia is almost complete and robust. Two patellae, an astragalus, a navicular, a fifth metacarpal, a first and a second phalanx of a medial metapodial, are very well preserved and covered with calcite. The Ph2 was found in Cave B in association with caprid and fox remains (Fig. 2)

_													
•	see abbrevia	tions	C*	_	I.	·	P4		I3	dCi			
I	_ *		14.0	(16.5)		8.0	16	.5	6.2	2 6.	6		
F	3		11.0	13.0		6.2	8.	.7	4.5	5 5.	7		
H	H		63.0	-	2	6.5	26.	.5					
I	Icrown	(2	.5.0)				11.	.0					
Г			RADI	US	TIB	IA	Mc V	/	PhI	Ph II			
Ī		1	79.0		(23	0.0)	52.	2	44.2	2 28.	0		
I	OTprox.		23.0	25.4	(4	9.5)	13.	.7	16.	5 13.	5		
[]	DAPprox.		16.2	18.2	(4	0.5)	12.	.9	12.8	3 13.	2		
I	OTdia.		17.0	(18.2)		19.0	7.	.8	11.2	2 min8.	1		
I	DAPdia.		10.5		2	22.2	8.	2	8.9	} 8 .	1		
I	OTdistal		35.5			36.4	12.	.3	13.0) 12.	8		
1	OAPdistal		21. 2			24.8	12.	5	9.7	7 10.	4		
I	DTd.art.		24.5		2	26.7	12.	.0			ļ		
I	DAPd.art.		17.2			21.5	12.	.5					
ASTRAGA	LUS	P	ATEL	LAE		N	AVICL	JLAI	RIS	FEI	Л	JR.	
L	38.4	L	34.	5	33.0	L			16.5	DTprox.		54.7	
DT	32.5	DT	27.	0	24.5	DT			23.0	D caput		25.5	27
DAP	24.5	DAP	14.	6	14.0	DAI	P		18.4				
DTcaput	21.8	Hart.	24.	0	22.0								
DTcollum	17.4	DTart.	26.	7	24.2								
DTtrochlea	22.5												

Table 1. Panthera pardus-Apidima: Measurements of teeth and postcranial skeleton, in mm

*Abbrevations: (In material the letters A, B, C and D after LAO indicate the cave, where the specimen has been found). I: Incisor, dC: deciduous canine, C: Canine, P: Premolar, M: Molar, Cr: Cranium, Mx: Maxilla, Md, md: Mandible, diast.: diastema, pr: protocone, hy: hypocone, pa: paracone, me: metacone, prd: protoconid, hyd: hypoconid, pad: paraconid, med: metaconid, end: endoconid, cg.: cingulum, a.c.: accessory cuspid, pas: parastyle, mes: metastyle, mcl: metaconulus, trd: trigonid, tld: talonid, tl: taloni, cons.: constriction, int.: internal, ext.: external, prox., pr.: proximal, dis., d.: distal, a.: anterior, p: posterior, s: superior, i: inferior, L: Length, B: Breadth, H: Height, D: Diameter, DT: Diameter transversal, DAP: Diameter anteroposterior, Id: Infradental, a.s.: articular surface, dia.:diaphysis, Mc: Metacarpal, Mt: Metatarsal, Mp: Metapodial, Ph: Phalanx, art.: articulation, cond.: condylus, inc. sem.: incisura

semilunaris, pro. ang .: processus angularis, sym .: symphysis. IPH: Institut Paleontologie Humaine, Paris

D i s c u s s i o n The Apidima leopard is robust like the one from Arago Cave (France), more so than the modern specimens at the collections in Vienna University and in Institut Paleontologie Humaine, Paris and less so than those from Vraona Cave (Attiki, Greece) (NAGEL, 1995, 1999) and Jaurens (France) (Fig. 5) of Würm III age (BALLESIO, 1980), while the protoconid angle of the P₄ Apidima specimen is 75° and 80° for the Jaurens specimen. Leopard specimens from Lezetxiki Cave (Spain) is also much more robust (ALTUNA, 1972), but not those from Stranska Skala (Brno) (HEMMER, 1971, THENIUS, 1972).

The leopard is particularly ubiquitous, widely distributed and eurythermic animal, which flourished in Europa, in the coldest phases of the Würm. Its prey consists of medium-sized herbivores, such as deer (KURTEN, 1968, ARGANT A. & J., 1990, ARGANT, 1991), which are most abundant in the Apidima palaeofauna. In Greece, Pleistocene leopards have been identified at very few sites, such as Vraona cave (NAGEL, 1995), where Latest Pleistocene Felis (Lynx) lynx and Felis silvestris coexist with the leopard (SYMEONIDIS et al., 1980). Leopard is also found in Dyros associated with hippopotamus of age 25-30x103 years BP (BASSIAKOS,

1993) and recently Loutraki Almopia caves of about the same age. From the Middle Pleistocene of Arago (Tautavel) felid coexistence (leopard, lynx and wild cat) is also recorded by CREGUT (1976).

> Genus Felis LINNAEUS, 1758 *Lynx* Kerr, 1792 Felis (Lynx) lynx (LINNAEUS, 1758) (Plate 1, fig. 9, Text-figs. 3, 5, table 2)

Material: 2C^sLAO-D-087 dex, LAO-B-412b sin, humerus LAO-C-713c dex, calcaneus LAO-C-646 sin Description Of the upper canines one is an unworn, germ, with hollow root, of a rather small juvenile (L*C^s=6.5, BC^s=5.1, HC^scrown=13.8 mm) (Fig. 3, 2). The dimensions are similar with those of the Stranska Skala lynx (THENIUS, 1972) and that of L' Escale (BONIFAY, 1971) (Fig. 5). Of the post-cranial skeleton a calcite-covered humerus and calcaneus are rather small (of L. pardina size, maybe female). Of the former, the distal diaphysis with the upper part of the foramen supracondylicum is preserved. The oldest known L. lynx are of Eemian age and their widest distribution was reached during the Würm (KURTEN, 1965,



Figure 2: Panthera pardus:-Apidima. 1) Maxilla fr. LAO-B-371a sin, a) palatinal, b) basal, 2) $I^3LAO-B-346 sin, a)$ lateral, b) lingual, 3) C^s LAO-B-091 dex. a) labial, b) lingual, c) posterior, 4) P₄ LAO-B-159e sin, lingual, femur prox. 5) LAO-C-729 dex and 6) 697+700d sin, anterior, 7) radius LAO-B-388c+389 sin a) anterior, b) posterior, 8) tibia LAO-C-722 sin, a) anterior, b) distal, patellae 9) LAO-C-814 sin and 10) LAO-B-390 dex, plantar, 11) astragalus LAO-C-641 dex, 12) McV LAO-B-389a dex, a) dorsal, b) plantar, 13) PhI LAO-B-410a, 14) PhII LAO-B-348e, dorsal.



Figure 3: Felis (Lynx) lynx-Apidima: C^s 1) LAO-D-087 dex, 2) LAO-B-412b sin, a) lingual, b) labial, 3) humerus distal LAO-C-713c dex, a) anterior, b) posterior, 4) calcaneus LAO-C-646 sin, a) anterior, b) lateral

1968). The fossil specimens are similar to Recent ones, which shows that there was no reduction in size after the Pleistocene. The paleoenvironment seem to be forest (preferably coniferous) (KURTEN, 1965, 1968) and its food mainly hares and wild goats, both abundant in the Apidima site.

 Table 2. Felis (Lynx) lynx-Apidima: Measurements of tooth and post-cranial skeleton, in mm.

(C ^s	Cal	caneus	Humerus				
L	9.7	L	40.2	DT distal	23.0			
В	8.0	DAP	14.0	DTd.art.	18.0			
Н	43.0	DT	18.0	DT trochlea max	10.0			
Hcrown	16.0	DAPd.art.	9.1	min	8.0			
		DTd.art.	10.6					

Genus *Felis* LINNAEUS, 1758 *Felis silvestris* SCHREBER, 1777 (Text-figs. 4, 5, Table 3)

M at e r i a l Mandible fr. with C_i and P_3 LAO-C-558b sin, M_1 LAO-C-589 sin.

D e s c r i p t i o n The anterior part of a calcite covered mandible includes the crown of an unworn and not well-risen canine, high and slender with 2 buccal longitudinal flutes. The premolar is half-risen and robust and there are also the P_4 alveoli. The dimensions show a more robust wild cat than that from Portel (France, Late Pleistocene) and Arago (Middle Pleistocene) (Fig. 5). The long and large lower carnassial is unworn, with a posterior longitudinal crest (Fig. 4). Its dimensions are close to the maximum for the fossil specimens given by KURTEN (1965). In cave C, a humerus, radius and ulna LAO-C-765b dex, all of the same, rather small individual, and a radius prox. LAO-C-797a dex, are surface findings and seem to belong to a recent cat.

The Pleistocene wild cat is very large (KURTEN, 1965a), although of a remarkable size, is difficult to identify, especially on this fragmentary material but size alone may be sufficient to distinguish wild cat from the domestic form, which are both present in the Apidima



Figure 4: *Felis silvestris*-Apidima: 1) Mandible fr. with C_i and P_3 LAO-C-558b sin, lateral, 2) M_1 LAO-C-589 sin, a)lingual, b)labial

cave C. The teeth of the wild cat, especially the lower carnassial, are much larger than that of the Europe fossil wild cat (KURTEN, 1965). The stable diet consists mainly of small rodents, abundant in the Apidima site. It is mainly a woodland animal preferring mixed forest (KURTEN, 1968).

Table 3. Felis silvestris-Apidima: Measurements of mandible, teeth and post-cranial skeleton, in mm

Mandit	ole	C		P ₃	M ₁
Hmddiast.	10.7	L	5.9	(6.0)	9.6
$Hmd(P_3, P_4)$	10.2	В	4.3	(3.2)	4.3
Dmax.sym.	15.4	Hcro	wn 10.5		13.0
Dmin.sym.	6.0				

Superfamily CANOIDEA SIMPSON, 1931 Family Canidae GRAY, 1821 Genus Vulpes (LINNAEUS, 1758) Vulpes vulpes (LINNAEUS, 1758) (Plate 1, figs. 10, 11, Text-figs. 6, 7, Table 4)

M a t e r i a l : Maxilla fr. LAO-C-715b dex, $2C^{s}$ LAO-C-610 dex and 641b sin, P⁴ LAO-C-727a dex, P⁴ fr. 571b dex, $2M^{1}$ LAO-C-746c (maxilla fr. with the C^s, P¹ alveoli and P²) and LAO-C-787d dex, M¹ fr. LAO-D-681a dex,



Figure 5: Ratio-diagram comparing the dimensions of various teeth and elements of the post-cranial skeleton of felids: 1. LC^s, 2. BC^s, 3. LI³, 4. BI³, 5. LC_i, 6. BC_i, femur: 7. DTprox., radius: 8. L, 9. DTprox., 10. DTdia, 11. DTdistal, tibia: 12. DTdistal, astragalus: 13. L, 14. DT, 15 DAP, 16. DTcollum, 17. DTcaput, calcaneus: 18. L, 19. DT, 20. DAP, navicularis: 21. L, 22. DT, 23. DAP, patella: 24. L, 25. B, McV: 26. L, 27. DTprox., 28. DTdia., 29. DTdistal, PhI: 30. L, 31. DTprox., 32. DTdia., 33. DTdistal. Standard *F. (L.) lynx* -recent, IPH coll. Regalia. (LAO: Apidima, IPH: Institut Paleontologie Humaine-Paris, Jaurens (BALLESIO, 1980), L'Escale (BONIFAY, 1971), Stranska Skala (THENIUS, 1972), Vraona, Attiki (NAGEL, 1995).

* see abbre- viations	C ^s	P ⁴	1		M ²	
L*	7.4	15.6	9.8	10.3	-	6.0
В	4.9	7.0	13.5	2.5	11.3	8.0
н	31.0					
Hcrown	17.0					

		P	P 1	P ₂	P	3	P4		N	ſı		M ₂	M ₃	dCi	D	4
L		4.4	4.4	9.0	9.5	10.3	11.0	16.0	15.7	16.2	14.4	7.2	4.0	3.5	10.8	10.6
В		2.7	3.1	3.4	3.8	3.8	4.3	6.0	6.5	6.5	5.5	5.2	3.7	2.5	4.0	4.0
н		9.8	9.7					14.2		17.7				16.8		
Her	own				7.0					9.0	9.0					
								M	IANDI	3LE						
LI	[1-cond	d.	1	109.0	LP _i al	v.		35.2	DTcon	d.	1	.4.7	HmdP3a.			13.8
L	Ciaco	ond.	1	07.5	LM _i a	alv.	2	26.2	Hcond			7.3	HmdM ₁ a.			16.2
	C _i pco	ond.	1	100.5	LP ₁ -N	∕l₃ alv.	6	51.2	Hmdd	iast.	1	1.6	HmdM ₁ p.		16.5	17.0
D	max s	ym.		28.0	Dmin	sym.	1	10.0					Hramus(p	oro.angcond.)		18.0

	RADIUS	TIBIA	C.	CALCANEUS				
L		130.0	L	30.5				
DTprox.		20.8	DT	11.4				
DAPprox.		22.3	DAP	12.0				
DTdia.		8.5						
DAPdia.		8.3						
DTdistal	14.5	15.0	1					
DAPdistal	8.2	10. 2	1					
DTd.art.	12.0	11.0						
DAPd.art.	7.2	9.5						

Table 4. Vulpes vulpes-Apidima: Measurements of teeth, mandible and post-cranial skeleton, in mm



Figure 6: *Vulpes vulpes*-Apidima: 1) C^s LAO-C-610 dex, a)lingual, b)labial, 2) P⁴ LAO-C-727a dex, a) labial, b) lingual, c)occlusal, 3) M¹ LAO-C-746c a) labial, b) occlusal, mandible frs. 4) with P₃, M₁ LAO-C-543 dex, lateral and 5) with M₁, M₂ LAO-B-352c-353 dex, a) lateral, b) M₁ lingual, c)occlusal, 6) P₂ LAO-C-559c sin, lingual, 7) P₃ LAO-B-358c dex, labial, 8) P₄ LAO-C-589 sin, a) labial, b) lingual, 2M₁ 9) LAO-A-033 dex, lingual and 10) LAO-C-641b sin, a) labial, b) lingual, 11) dC₁ LAO-D-82z sin, a) lingual, b) anterior, 12) D₄ 88d sin, a) lingual, b) occlusal, 13) radius distal LAO-B-393b sin and 14) tibia LAO-B-402a+404 sin, anterior, 15) calcaneus LAO-B-348e dex, medial.

 M^2 LAO-C-813d dex, 2mandible frs. with P_3 , M_1 LAO-C-543 dex and with M_1 - M_2 LAO-B-352c-353 dex, C_1 fr. LAO-C-539b dex, P_1 and M_3 LAO-C-786b dex, P_1 LAO-C-669c dex, P_2 LAO-C-559c sin, P_3 LAO-B-358c dex, $2P_3$ fr. LAO-D-239f and LAO-C-584a dex, P_4 LAO-C-589 sin, P_4 fr. LAO-C-501b dex, $2M_1$ LAO-A-033 dex and LAO-C-641b sin, d C_1 LAO-D-82z sin, $2D_4$ LAO-D-86h and 88d sin, femur fr. LAO-C-813d, radius distal LAO-B-393b sin, tibia LAO-B-402a+404 sin, calcaneus LAO-B-348e dex.

Description A maxilla fragment with molar alveoli is preserved. Of two C^s one is robust, while the other is completely worn. An upper carnassial, of height 3.5mm, has anteriorly a weak crest and cingulum, while the protocone is pronounced anteriorly. The M^1 are relatively robust, and an external cingulum is well developed. The molar M^1LAO -C-746c is associated with a maxilla fragment. Of two mandible fragments, one lacks the processus coronoideus, and contains the P₃ and M₁, while the other is small fragment with the first two, almost unworn, molars (Fig.6). Two small isolated and slightly worn teeth, P_1 and M_3 , are each other, probably of the same individual. An anterior half of P_3 and posterior half of a P_3 and of a P_4 are preserved, with breadths 3.2, 3.4 and 4.5mm respectively. A lower carnassial lacks the exterior half of the trigonid, while the talonid has developed tubercles. Of a long, slightly worn P₄ there is a short but distinguishable cingulum, on the hidenmost part. Long premolars characterize the Apidima fox (Fig. 7). The slightly worn lower carnassials lack an accessory cuspid between the well-developed metaconid and hypoconid, which is present on those of the recent species. A lower milk canine is slender, with a well-distinguished cuspid at

		(C° _		C	- -	MANDIBLE		М	1	P ₂	HU	MERUS		ULNA
	n	X	min	max										n=2-3	
L	4	4.80	4.5	5.0	5.5	5.0	LmdcondCi alv.	53.0	L	11.0	4.5	L	73.8		
в	4	3.80	3.6	3.9	3.0	3.5	Lmdcondli alv.	54.0	В	4.5	2.9	DTprox.	14.0		7.5art.
н	3	20.23	19.2	21.0	17.6	18.0	LI1-M2 alv.	38.0	Hcrown	5.3		DAPprox.	15.0		
Harown	3	9.87	9.4	10.2	8.0	9.8	LP1-M2 alv.	30.8	Ltr	7.2		DTdia.	5.5		
							LC _i -M ₂ alv.	35.0	Ltld	3.8		DAPdia.	6.0		
							LP _i alv.	16.5	Btl⁴	3.3		DTdistal	15.97	(15.6-16.3)	
							LM; alv.	14.8				DAPdistal	9.33	(8.7-10.3)	7.5
							DTcond.	9.4	Bcjalv	4.5	4.6	DTtrochlea	11.1	(11.0-11.2)	
							Hcond.	3.7				DTcaput	10.0		
							Dsym. max	14.5				·			
							min	8.2							

Table 5. Martes foina-Apidima: Measurements of mandible, teeth and post-cranial skeleton, in mm



Figure 7: Ratio-diagram comparing the dimensions of various teeth and elements of the post-cranial skeleton of foxes. 1. LC^s, 2. BC^s, 3. LP⁴, 4. BP⁴, 5. LM¹, 6. BM¹, 7. LI₁-cond., 8. LC₁a.-cond., 9. LC₁p.-cond., 10. DTcond., 11. Hcond., 12. Hmddiast., 13. HmdP₃a. 14. HmdM₁a., 15. Hramus (pro.ang.-cond.), 16. LP₂, 17. LP₃, 18. LM₁, 19. BM₁, 20. LM₂, 21. LD₄, Radius: 22. DTdistal, 23. DAPdistal, Tibia: 24. L, 25. DTprox., 26. DAPprox., 27. DTdia. 28. DTdistal, Calcaneus: 29. L, 30. DT, 31. DAP. Standard: *Vulpes vulpes* -recent, IPH coll. Regalia (Jaurens after BALLESIO, 1979)

the base of the crown. A milk carnassial has a very developed metaconid and hypoconid, while the talonid is tricuspid. Only distal part of a slender radius is preserved. A complete, well-fossilized, tibia and calcaneus were found in cave B, in association with the leopard.

The Apidima fox has similar dimensions with that from Jaurens (BALLESIO, 1979). The comparison of the dimensions with those from Portel (Late Pleistocene), Arago and Lazaret (Middle Pleistocene) (France) is shown on the ratio-diagram (Fig. 7). In Greece, Middle Pleistocene V. vulpes has been identified at Megalopolis (SICKENBERG, 1976) and Petralona cave (TSOUKALA, 1989), while Late Pleistocene species have been recorded in Vraona cave, Attiki (SYMEONIDIS et al., 1980) and Agios Georgios cave (Kilkis, TSOU- KALA, 1992a). In Apidima, its presence is consistent with the presence of abundant rodent, leporid and bird remains (KURTEN, 1968).

> Family Mustelidae FISCHER, 1817 Genus *Meles* LINNAEUS, 1758 *Meles meles* LINNAEUS, 1758 (Text-fig. 8)

M a t e r i a l C^s LAO-C-278b dex, C_i LAO-C-443c dex, M₁ LAO-C-628d sin, ulna distal LAO-B-367b sin. D e s c r i p t i o n : A C^s is very worn, with robust root (LC^s=7.0, BC^s=5.4 mm). Of a slender, short-crowned C_i, the base of the intensely curved crown is of oval transversal section (LC_i =5.9, BC_i =4.9 mm). A little-worn lower carnassial lacks small postero-lingual part (LM₁=16.3, BM₁=7.3, Ltr^d=8.6, Btr^d=6.4 mm). Of the



Figure 8: *Meles meles*-Apidima: 1) C^sLAO-C-278b dex, labial, 2) C₁LAO-C-443c dex, a) labial, b)lingual, 3) M₁ LAO-C-628d sin, a) labial, b) occlusal, 4) ulna distal fr. LAO-B-367b sin, a) anterior, b) lateral

post-cranial skeleton, an ulna preserves the robust distal part (Fig. 8).

The badgers although inhabited in the Early Middle Pleistocene of Europe, they are similar to modern species (KURTEN, 1965). Apidima badger seem to be less robust (sexual dimorphism is also considered), as this from Portel (Late Pleistocene), Arago and Lazaret (Middle Pleistocene).

Genus Martes PINEL, 1792

Martes foina (ERXLEBEN) (Text-fig. 9, Table 5)

Material 4C^s LAO-C-755b dex, 811b, 765 and

568c sin, 2 mandible frs. with M_1 LAO-C-483 dex and with P_2 LAO-C-779b dex, C_1 LAO-C-735a dex and 254i sin, humerus LAO-C-808a sin, 2 humerus distal LAO-C-483b sin and LAO-C-772 dex, 2 ulnae LAO-C-778a sin and LAO-C-483b

Description: Four C^s are slightly worn or unworn, of circular transversal section at the base of the crown, with well developed root. Of two mandible fragments, one preserves condylus, all alveoli and lower carnassial, while the other preserves an anterior part of corpus, with premolar alveoli and P₂ (Fig. 9). The anterior and posterior mental foramina are rather close each other, while in pine marten they are farther apart, and this character, according to Janossy (ANDERSON, 1970), is useful in separating the two species. The unworn carnassial has a rather long trigonid, but not broad talonid, with well-developed hypoconid, hypoconulid and metaconid. The height of the mandible corpus, in front of the P_2 , is 9.0mm. Of three humeri, bearing foramen supracondylicum, one is complete, while the other two lack the proximal epiphysis. Of two ulnae, one lacks only the tuber olecrani, while the other lacks the distal part, therefore seem to be of a juvenile (DTprox.art.=6.8mm). These post-cranial bones seem to belong to a recent marten.

Beach or stone marten, occuring in mixed forests and on rocky hill sides, has a Middle East or south-west Asia origin and a more southern and eastern distribution than *Martes martes*. Although it is absent from their fossil record, it is found on Crete and Rhodes islands (may be due to man), but not on other Mediter-



Figure 9: Martes foina-Apidima: C^s 1) LAO-C-755b dex, 2) 811b, 3)765 lingual and 4) 568c sin, a) lingual, b) labial, mandible frs. with M_1 5) LAO-C-483 dex a, d) lingual, b) labial, c, e) occlusal, with P_2 6)LAO-C-779b dex, labial, 7)C, LAO-C-735a dex, 8) 254i sin, lingual, 9) humerus LAO-C-808a sin, posterior, humerus distal 10) LAO-C-483b sin, a) posterior, b) anterior, 11) LAO-C-772dex, 12) ulna LAO-C-483b sin, lateral.

ranean islands, nor in N. Africa and Arabia (ANDERSON, 1970). In Greece, Late Pleistocene mustelids have been identified at Vraona cave, Attiki (*Meles meles, Martes* sp., *Mustela* cf. *putorius* (SYMEONIDIS, et al., 1980), and *Mustela putorius robusta* at Agios Georgios cave, Kilkis (TSOUKALA, 1992a).

Order ARTIODACTYLA OWEN, 1848 Suborder RUMINANTIA SCOPOLI, 1777 Family Bovidae GRAY, 1821 Subfamily Caprinae GILL, 1872 Genus *Capra* LINNAEUS, 1758

Capra ibex LINNAEUS, 1758

(Plate 1, Figs. 12, 13, Plate 2, Figs. 1–4, Text-figs. 10, 11, Table 6)

Material: Skull fr. with horn LAO-B-163a, horn frs LAO-B-78, 78d, 80, 137, 6maxilla frs with P²-M³ LAO-C-285a, with P³-M³ LAO-D-26a sin, with P³-M² LAO-B-174a/b, with P4-M3 LAO-D-24 dex, with P2-P4 LAO-B-190, with M², M³ LAO-74, P³ LAO-B-414b, P⁴ LAO-70a, 3M1 LAO-C-269b and 622c, LAO-B-158e, 9M² LAO-B-148, 358d, 362c, 426c, LAO-C-251, 653a, 656, 814a dex, LAO-D-821a, $M^{1,2}$ and $M_{1,2}$ LAO-A-19, 34, 44a, LAO-B-70, 77, 166a, 166c, 408b, 413b, 414b, 415a, 417c, 418a, 11M³ LAO-A-07, 08a, 15 dex, LAO-B-139, 364, 393a sin, 410c, 416c, 426, LAO-C-655, 666 dex, 12mandible frs with P2-M3 LAO-C-728 sin, 2with P_3 - M_3 LAO-B-74, 179 sin, with P_4 - M_3 LAO-D-18a sin and 79e dex, , with M₁,M₂ LAO-B-30, with M₂,M₂ LAO-B-382 sin, with M, LAO-C-497, with D₃-M₃ LAO-B-167c, with D₂-M₁ LAO-C-509, 2with D₄-M₁ LAO-B-151, 417, with D₃-D₄ LAO-A-41, with D₄ LAO-B-375,377, mandible fr. juv. LAO-B-361, 361a, I LAO-A-105, LAO-B-80, 165e, 357c,d, 416c, LAO-C-579a, 585a, 640c, 653a, 786b, 2P2 LAO-B-375b, LAO-C-267, P3 LAO-A-120 sin, 6P, LAO-A-34c, 101c, LAO-B-70, 156n, 168, 176b, 5M, LAO-B-28a, 159f, 171c, 362c, LA0-C-622c, 2 M, M, LAO-B-161e, 360, 3M, LAO-C-695b, 699c, 703b, 5M, LAO-B-189b, 347a, 392, 426e, LAO-C-703b, 5D, LAO-B-77, 78, 80, 347a, 419a, pelvis fr. LAO-B-65, humerus distal LAO-C-64 3b dex, 2radius frs LAO-B-387a (and ulna) dex, 92, 4astragali LAO-D-681b, LAO-B-75, 348e, 363 dex, 2cuboscaphoidea frs LAO-B-74a, 139a, McIII+IV LAO-B-385 dex, MtIII+IV fr. juv. LAO-B-425, Mp distal LAO-A-55a, 2PhI LAO-B-156g and LAO-D-232b, 3PhII LAO-B-344b 346a, 416, PhIII LAO-B-153d. Description A juvenile skull fragment, with part of a horn (its dimensions at the base, are: Dmaxxmin = 25x21 mm), as well as few horn fragments are preserved (Fig.10.1, 2, pl.1.12). A maxilla fragment includes all cheek-teeth, which are slender and thin enamelled (P² and M³ especially), indicating a not robust, but young individual. Molars vary little to deeply worn. A M³ has intense metastyle; some morphological differences with that from Petralona are indicated on Fig.10. Some mandibles are robust, and may belong to the same individual. Apidima ibex is less robust than the Petralona ibex. Concerning P², P⁴ and M1 of the former are notably smaller than the latter, the large M₃ of which, has the talonid angle more open. Of the post-cranial skeleton, a cuboscaphoideum is robust (DT=37mm); a distal, calcite-covered humerus bears trace of carnivore gnawing; and a radioulna lacks the olecranon. A complete metacarpal is calcite-covered, the dimensions of which indicate a female (Fig.10, pl.1.13). Of two PhI, one is well fossilized and robust, while the other seems recent. A PhII bears a big hole posteriorly, probably trace of carnivore gnawing (86h). Of two astragali, one is rather small, while the other is robust. Caprid bones from Cave B, have been found in breccia, highly fossilized, while there are recent bones of Capra hircus. This species is descended from the wild goat C. aegagrus ERXLEBEN, which is distributed from Greek islands and Asia Minor eastward to India (KURTEN, 1965).

Family Cervidae GOLDFUSS, 1820 Genus *Megaloceros* BROOKES, 1828

Megaloceros sp. (Text-fig. 12, Table 7)

M a t e r i a l : Maxilla frs. with P³-M¹ LAO-C-629 sin, M² LAO-C-798d, 800d sin, mandible fr. LAO-C-647a with P₃-M₃ 647 sin, M₂ LAO-C-308e sin, P₄ LAO-C-803a sin.

D e s c r i p t i o n : A maxilla fragment is calcite-covered, with thick-enamelled worn teeth. A large M^2 has very thick (1.4mm) enamel and an intense cingulum between lobes, but less strong than of this from the Petralona *Premegaceros* sp. (Fig. 12). The mandible is very fragmentary, while the teeth are very robust and well preserved. The P₃ is very robust, the M₁ is worn, the M₂ has a small cingulum between lobes and the M₃ is middle worn (crown-height 23mm), with very intense cingulums between lobes and postero-lingual of talonid.

The giant deer is widely distributed in Europe and northern Asia, occurred in the Holsteinian and Eemian interglacials and also in "cold stages", therefore it doesn't indicate particular stage(s) (LISTER, 1986). In Macedonia (N. Greece), among other sites (TSOUKALA, 1992b), the giant deer has been recorded in Agios Georgios cave, Kilkis (BASSIAKOS & TSOUKALA, 1996) and in Drama (KOUFOS, 1981), of Late to Latest Pleistocene age.

Genus *Cervus* LINNAEUS, 1758 *Cervus elaphus* LINNAEUS, 1758 (Plate 2, Fig. 1, Text-fig. 12, Table 7)

M a t e r i a l 4 Antler frs. LAO-C-311, 529, 518 and 782, 6maxilla frs. with P²-M³ LAO-D-27 dex, with M²-M³ LAO-C-585 dex, with D²-M¹ LAO-D-242 dex, LAO-C-286b dex and 309d sin and with D² LAO-C-327d, 2C^s LAO-C-254, 290a, 2P² LAO-B-159c sin, LAO-D-90 dex,



Figure 10: Artiodactyla-Apidima: *Capra ibex*, 1)horn frs. a) LAO- B- 80, b)LAO-B-79, 2) M³ a) LAO-B-364sin, palatinal, b) LAO -C-703b, c) Petralona PEC 326 dex, labial (for comparison), 3)astragalus LAO-B-363 dex, a) anterior, b) posterior 4) McIII+IV LAO-B-385 dex, *Dama dama* 5) Mc distal fr. LAO-B-087a.

TEETH	n	x	min	max	Sn-1	v			n)	(min	ma	x	Sm-1	v
LP ^z	1	7.8	1	1				LP ₂	3	6.	33	6.0	7.	0		
BP ²	1	4.8	1					BP ₂	3	4.	70	4.0	5.	5		
	5	9.24	8.2	10.0	0.81	9.1		LP ₃	4	8.	65	8.4	<u>9</u> .	<u>0</u>		
BP ³	5	8.84		9.0	0.69	7.7	8	BP ₃	4	6.	73	6.1	7.	7	~ ~~	
	6	9.26	/.0	11.0	1.65	17.8			9	10.	15	9.0	11.	3	0.72	/.05
	1 ₽	10.53	9.0	11.5 46 E	1 0.80	0.4			40	44	28	10.2	16	4	4 70	12 40
		12 94	10.5	14 5	1.00				19	14 Q	21 55	7 5		a l	0.52	6 13
	24	18 45	17.0	22.0	1.30	7.0	ดีไม่	M	22	17	98	15.0	20	š	134	7.45
BM ²	24	14.61	12.0	17.2	1.31	8.9	5	BM2	22	10.	66	9.0	14.	5	1.44	13.52
LM ³	13	23.52	20.0	26.0	1.64	7.0	i õ	LM ₃	12	26.	97	24.2	30.	0	1.59	5.91
BM ³	17	13.70	11.5	15.5	0.98	7.1	18 1	BM ₃	12	10.:	29	9.5	11.	8	0.62	6.08
LD ²	1	8.5	i				- 11	LD ₂	1	5.	00					
BD ²	1	6.0						BD ₂	1	3.	80		1			
	1	12.3					<u> </u>		4	9.2	20	8.3	10.			
		9.0				1	- 1 :		3	0.4 17	87 45	0.0	20.	2	4 94	7 52
		0.5							11	7	40 22	6.0	20.	n l	0.76	10 59
1 M ¹	1	14.0					_ '					0.0	J 3 .	Ŭ	0.70	10.00
BM ¹	i	11.0														
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Hmd(dia	st.)	14	4.5	LM		66.0) 6	54.0	LP ²	-M ³		61	.0		•	1
Hmd(M ₁)_ົ	20	8.2	-												
	HU	MERUS					RADI	JS		1	Г	CŨ	BOSCA	PHOID	DEUM	
DTdistal			37.5		DTpr	OX.		40.0	35.5	1		L			18.5)	
DTd.art.			36.5		DAP	Drox.	1	18.0	17.3			DT		`	27.0	
DAPd.ar	t.		21.5		· · ·							DAP			22.0	
	AST	RAGALI	JS	= ı	Mc	III+IV	_	I	Phi	-		Phil		Î	PhII	
Llat.	<u> </u>	28.2	37.2 3	<u>4.0</u>	L	T	129.0	46.0	36.	3	28.0	28.0	30.5	н	<u> </u>	(20.0)
Lmed.		25.8	•••••		DTprox.		30.5	16.2	12	5	16.0	14.3	17.0	Hart.		17.0
DTprox		16.8			DAPpro	<u>ر</u> ا	21.0	18.5	14	3	15.5	14.5	17.2	DTar	t I	12.5
DTdistal		18.3	25.4 2	22.2	DTdia		21.2	12.6	9	8	11.2	10.0	12.0		-	
DAPlat		14.7			DAPdia		15.0	15.6	11	7	13.0	11.2	14.0			
DAPmed		16.0	21.2 1	9.2	DTdistal		34.0		1					1		
				··	DAPdist	al	20.0	I	1							
	1				DTtroch	ea	15.8							1	1	

Table 6. Capra ibex-Apidima: Measurements of teeth and post-cranial skeleton in mm



Figure 11: Ratio diagram comparing the dimensions of teeth and metacarpal of the Pleistocene Capra

P³LAO-D-90a dex, 2M¹LAO-C-708a and 636 dex, M^{1,2} LAO-D-239f sin, 5M² LAO-C-280i, 627, 677a, 707 dex, 655 sin, M^s fr. LAO-B-143a, D² LAO-C-809d, D³LAO-C-305h dex, 2mandible frs with D₂-M₁LAO-C-309c sin, mandible fr. and P₄, M₁ LAO-C-286c, I₁LAO-B-78, 159d, 165e, 367b, LAO-C-308g, 553, 633, 644d, 779a, 813c, P₄ LAO-C-801b, M, LAO-C-264, 2M, LAO-D-227d dex, LAO-C-727b, M₃ LAO-D-86d dex, M₃ fr. LAO-D-197b dex, D₃ LAO-C-811b, 2D, LAO-C-691a, 785, atlas LAO-C-244, epistrophaeus LAO-C-780, cervical LAO-C-602, 2pelvis fr. LAO-D-80, 242b sin, humerus distal LAO-C-546, patella LAO-C-445a, scaphoid and pyramidal LAO-C-321c dex, semilunar LAO-C-325d sin, 6astragali LAO-C-306b, 445a, 531, 590a dex, LAO-D-231, 237c, calcaneus LAO-242a dex, 2cuboscaphoidea LAO-C-282d and LAO-C-451a, 4Mp frs LAO-C-307, 309f, 311a, 588, 4PhI LAO-C-445a, 498, 582a,

LAO-D-237, 3PhII LAO-C-763f, 813e, LAO-D-86h, 2PhIII LAO-C-533a, 757.

D e s c r i p t i o n : Of four small antler fragments one is tine, tine-tip and two almost circular at the base (D = 13.0 mm, 23.5 x 26.5 and 15.0 x 16.0mm). Among the upper teeth, the molars are more or less worn, with intense cingulum, in some cases antero-palatinal, or/ and between the two lobes. Of very worn milk teeth, there is a strong cingulum on D² and a very intense and high anteriorly on D³ and a weak one between the two lobes of D⁴. A mandible with milk teeth is probably of the same individual with the maxilla LAO-D-309d. Lower milk teeth are very thin enamelled. A M₂ has a small external cingulum between the lobes, a M_{1.2} has no cingulum, with wrinkled enamel and well developed metastylid. Its occlusal length is 32.0 mm.

	Γ	Megal	Megaloceros sp. Cervus elaphus						Dama dama							
	n	х	min	max	n	x	min	max	S _{n-1}	v	n	x	min	max	Sn-1	v
LP BP LP BP LP BP LP BP LM BM LM BM LM BM BM BM BM BM BM BM BM BM BM BM BM BM	1 1 1 1 1 1 1 1	20.8 21.6 18.0 21.7 25.5 25.0 22.5 28.5 27.5 (27.3)			4 4 2 3 1 1 1 1 5 5 1 1	16.20 16.72 17.30 19.50 18.20 21.30 24.20 24.80 26.76 24.82 26.40 25.00	15.5 15.0 17.0 18.5 26.0 22.1	16.5 19.2 17.6 20.0 27.5 26.0	0.60 1.56	2.25 6.29	88556613136676	13.81 12.59 13.04 15.40 12.57 16.90 18.90 18.42 21.65 21.26 20.45 19.65	12.2 12.0 11.9 13.9 15.5 16.5 16.5 19.8 19.8 19.8 19.8 19.5	15.8 13.6 14.1 16.5 13.3 18.0 21.6 20.8 23.0 22.0 22.5 20.8	11.35 0.54 0.83 1.07 0.71 0.88 1.76 1.29 0.46 1.04 1.10 0.91	8.22 4.27 6.36 7.00 5.66 5.21 9.18 6.96 2.20 4.90 5.39 4.66
LD ² BD ² LD ³ BD ³ LD ⁴ BD ⁴ LD ² -M ³ LD ² -D ⁴		(21.5)			6 6 4 3 3 1	17.85 11.17 21.83 16.87 21.70 18.87 126.50	17.0 10.6 20.7 16.0 20.6 18.5	19.2 12.7 22.5 17.5 22.4 19.1	0.83 0.50 0.78 0.71	4.64 4.48 3.57 3.20	7 7 8 8 8 8 8 1 2	12.74 8.74 14.62 12.37 15.08 15.68 90.0 43.15	12.4 8.20 13.0 10.4 15.2 14.2	13.6 9.0 15.0 13.4 16.4 17.4	0.46 0.29 0.71 0.92 0.38 1.08	3.62 3.36 4.88 7.44 2.42 6.92
LP-2 LP-2 LP-3 BP-4 LP-4 BP-4 LM-4 BM-2 LM-2 BD-2 BD-2 LD-4 BD-4 LD-2 BD-4 LD-2 BD-4 LD-2 BD-4 LD-2 BD-4 LD-2 BD-4 LD-2 BD-4 LD-2 BD-4 BD-4 BD-4 BD-4 BD-4 BD-4 BD-4 BD-4	1 1 2 2 1 1 2 2 1 1 1 2 2 1 1	19.50 12.20 21.65 12.55 24.50 15.50 29.75 16.90 38.70 18.50	21.2 12.4 28.8 16.0	22.1 12.7 30.7 17.8	2244 1 1 1 2 1 3 3	18.20 9.75 22.55 14.17 34.0 13.0 6.6 18.1 9.0 29.67 12.67	17.0 9.5 19.2 12.8 18.0 29.0 12.0	19.4 10.0 25.5 15.7 18.2 30.0 12.7			2255555533331122441111	9.35 6.20 12.86 7.58 13.64 8.86 16.94 11.48 18.90 12.10 24.17 11.73 8.2 5.0 12.80 6.25 20.15 9.00 95.00 33.2 60.0 41.8	8.7 5.6 12.5 6.5 12.5 8.5 14.7 11.0 18.0 11.8 23.0 11.0 12.3 6.1 19.0 7.0	10.0 6.8 13.5 8.6 15.2 9.3 18.3 12.2 19.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12	0.49 0.90 1.03 0.41 1.55 0.57	3.87 11.88 7.59 4.63 9.20 5.02

н	JMERUS			D. dama								
C. elaphus		D. dama	Ph I			Ph III			McIII+IV			
DTdistal DAPdistal DTd.art. D tr.max. D tr.min. D tr.creat D cond.	68.0 62.0 64.0 45.0 32.0 35.2 31.0	41.0 37.8 36.5 28.0 17.8 23.7	L DTprox. DAPprox. DTdia. DTdistal DAPdistal	41.0 15.5 18.0 12.5 14.0 14.0	L H DT Hart. DTart.	27.7 20.2 12.0 14.0 10.5	37.0 20.5 13.5 17.0	DTdia. DAPdia. DTdistal DAPdistal	(22.7) (23.3) (39.6) (25.1)	49.5 32.5		
PATELLA	_											
Lart. DTart.	37.5 25.0											

ASTRAGALUS D. dama (n=2) 55 32.7-38.4 C. elaphus 58.07 55.5-610 35.55 L DT 4 4442243 36.00 34.5-37.0 24.00 23.0-20.0 DAP 31.62 30.0-34.0 21.20 20.0-22.2 58.07 55.5-61.0 38.0 Llat. 53.30 50.6-56.0 36.5 Lmed. 32.30 32.0-35.4 23.0 DTprox. 34.5-37.0 29.3-34.0 24.4 21.5 22.0 36.00 DTdistal 31.27 31.37 DAPlat. 30.0-33.0 DAPmed 4 CALCANEUS CUBOSCAPHOIDEA 32.0 42.5 L DT DAP DTtuber DAPtuber 111.0 35.0 22.0 27.2 24.5 29.0 L DT DAP 44.4 39.8 (36.5) 25.5 (34.2) DTart(as) 37.3 32.0 DTart.(as.) DAPart.(as.) Hart.(cub.) 20.0 25.0 23.0 Bart.(cub.) 10.0 SCAPHOID PYRAMIDAL SEMILUNAR L 26.6 30.0 24.5 18.5 27.5 DT 18.7 23.5 DAP 33.0 30.5



Figure 12: Ratio-diagram comparing dimensions of teeth of cervids from LAO (Apidima), PEC (Petralona, TSOUKALA, 1989), Megalopolis (MELENTIS, 1965), Camiac, Combe Grenal (GUADELLI, 1987), coll. Reilhac, Museum Nationale Histoire Naturelle-Paris. 1. LP², 2. BP², 3. LP³, 4. BP³, 5. LP⁴, 6. BP⁴, 7. LM¹, 8. BM¹, 9. LM², 10. BM², 11. LM³, 12. BM³, 13. LP₂, 14. BP₂, 15. LP₃, 16. BP₃, 17. LP₄, 18. BP₄, 19. LM₁. 20. BM₁, 21. LM², 22. BM², 23. LM³, 24. BM³. Standard: *D. dama*, recent, Rome (LEONARDI & PETRONIO, 1976).

A robust D_{A} has a very intense and high cingulum between lobes, as well as lingual, anterior and posterior well developed cingulums. Of atlas, the breadth of the anterior articulation is 45 mm; of the posterior one 39.5mm, while its maximum height is 51.5mm and the caudal height of corpus is 23.5 mm. Most of the post cranial bones are calcite covered. Of pelvis, the acetabulum has dimensions: Dmax = 49 and Dmin =43 mm. Only a distal part of humerus is well preserved, which indicates a robust individual. Of six astragali, one was found on the surface, outside of cave D, while among the others, found in cave C, one is poorly preserved, but robust (L = 52 mm). A calcaneus is slender but high, and lacks the anterior articulation for malleolus. The sustentaculum tali is long but not high, with a posterior projection. The body is +/- constant anteroposteriorly, the articulation for astragalus +/-rectangular and there is a quite deep sulcus posterior of tuber. The cuboscaphoidea, patella and PhI (one of a juvenile) are well preserved, while the distal part of a metacarpal is poorly preserved, with cutting and rolling marks. In addition to recent specimens, many more tooth and bone fragments, mainly from Cave C (LAO 309) have been identified as cervid remains (the minimum number of individuals of which is 5).

Genus Dama FRISCH, 1775 Dama dama (LINNAEUS, 1758) (Plate 1, Text figs. 10–12, Table 7)

14 Maxilla frs. with P²-M³ LAO-C-Material 520b sin, with P²-M³ (M³ 705b)and 2M^{1,2} 706d, with P²-M¹ 771, with P³-M³ 527, with P⁴-M³ 520c sin, with P^4-M^2 634 dex, with D^2-M^2 576a dex, with D^2-D^4 , with D^2 , D^3 579a dex, with D^3 - M^2 644d, with D^4 - M^2 and P4 dex, LAO-C-700b, with D2-D4 and 2M1 LAO-C-726a and 708a, with D³, D⁴ 643d, 505 sin, P² and P³ LAO-C-529b, 4P² LAO-C-573c and two 588b dex & sin, LAO-B-139d, P3 LAO-B-184d, P4 LAO-A-17c sin, P⁴ and M¹LAO-C-653a, M¹LAO-C-558h, 2M²LAO-C-655 and 709 sin, M^{1,2} LAO-C-700b, 2M³ LAO-A-34, LAO-C-638a sin, 2D² LAO-C-544c, 701a, 13mandible frs with P₂-M₂ LAO-C-565 dex, with P₃-M₂ LAO-B-171a, with P_4 -M₃ LAO-C-593 sin, with P_3 -M₁ 672, with M_1 - M_3 579, 2with D_4 - M_2 577 and 639 dex, 2with M_{3} 568, 572a dex, 2with D_{2} - D_{4} 549, 306 sin, with D_{3} , D_{4} 594a dex, with D, LAO-C-557c, I LAO-C-280f, 554a, 571b, 622c, 633, 644d, 4P, LAO-C-614b, 744c, 810d, 814a, dex, 3P₃ LAO-C-698b, 725e, 746c, P₄ LAO-A-101c dex, 2M, LAO-C-547b, 701a, M, LAO-C-649c dex, 2D₄ LAO-B-162d, LAO-C-531b, 2 pelvis frs LAO-C-580, 618, 2 humeri distal LAO-C-703c sin, 2 astragali LAO-C-562, 717 dex, 3cuboscaphoidea LAO-

C-633, 700d, 810c sin, astragalus-calcaneus-cuboscaphoid. juv.LAO-C-644, 644a, Mc dis.LAO-B-87a, Mp fr. LAO- A-05, 4PhI LAO-C-488b, 531a, 626, 805d, 2PhII LAO-C-605, 643f, 6PhIII LAO-C-533a, 603, 610a, 622, 622c, 633a.

Description: The teeth vary in worn stage and have very plicated and thin enamel and, in some cases, a very high and strong cingulum between lobes, as well as closed fossets. On some molars (M1LAO-B-22, M3 LAO-C-638a etc.) there is a well developed and high (7.4 mm) cingulum between lobes. Mandible fragments are preserved in consolidated breccia. The lower molars have small external cingulums, the M, have anterior and between lobes intense cingulums, while the M₄ have small or no cingulums between lobes. At the base of a D_{4} there are two external cingulums between the lobes. Of the post-cranial skeleton, only pelvis acetabulums (D = 33 and 37 mm), two distal humeri (one is of a juvenile bearing trace of carnivore gnawing), astragali, calcaneus and cuboscaphoideum, mainly of juveniles, a distal metapodial (DTdistal = 29 mm) (Fig. 10.5, Pl. 1.14) and phalanges are well preserved and most representative. It is rather smaller in size than the fallow deer from Petralona cave (Fig. 12).

The fallow deer comes from Eemian (KURTEN, 1968), it is known during historical times, among other Mediterranean sites, in Crete island, while today very few representatives are living in Rhodes island. Late Pleistocene representatives are referred in Kythera island (MANOLESSOS, 1955) and Vraona cave, Attiki (RABEDER, 1995).

> Suborder SUIFORMES JAECKEL, 1911 Family Hippopotamidae GRAY, 1821 Genus *Hippopotamus* LINNAEUS, 1758

Hippopotamus amphibius antiquus DESMAREST, 1822 (Text-fig. 13, Table 8)

Material C^sLAO -A-117 sin and Ph II LAO-B-175.

Description A fragment of upper canine is partly calcite-covered and poorly preserved, while the very well preserved second phalanx, corresponds to the second or fifth anterior metapodial, according to the index Ia = (DAPpr.art./DTpr.art. x100) = 66.87.

Cs		PhII		
L	8.4	L	33.5	
В	25.3	DT prox.	34.3	
		DAP prox.	21.8	
		DT pr.art.	31.7	
		DAP pr.art.	21.2	
		DAP d.art.	20.0	

Table 8. *Hippopotamus amphibius antiquus*-Apidima: Measurements of the upper canine and the second phalanx, in mm.



Figure 13: Hippopotamus amphibius antiquus-Apidima. Above: C^sLAO -A-117 sin, a. labial, b. distal, c. mesial. (AA; cross section) Below: Ph II LAO 175, a.anterior, b.posterior.

D i s c u s s i o n : The dimensions of the hippopotamid remains found in caves B and A (where the two hominid skulls have been found), are relatively small, therefore may belong to a smaller individual, such as a young female, but not to a dwarf type, although dwarf endemic races of hippopotamids evolved in several Mediterranean islands. The hippopotamids are widely distributed, either in mainland or in the Greek islands (SYMEONIDIS & THEODORU, 1985/86), while only few fossil localities have been recorded in the south-east European and transcaucasian area (KAHLKE, 1987, 1989). On the other hand Hippopotamus amphibius antiquus DESMAREST, 1822, or H. a. incognitus FAURE, 1984, has been identified at many (~350) fossiliferous sites in western Europe (FAURE, 1985). In Peloponnese (S. Greece) this species has been identified at several sites, such as Dyros cave (SYMEONIDIS & THEODOROU, 1985/86); Kleitoria (MELENTIS, 1969); Megalopolis, of Holsteinian age (MELENTIS, 1964, 1965b), in a paleoenvironment with rich vegetation; Marathousa (Megalopolis basin) of Early Biharian (SICKENBERG, 1976), with main associated fauna Mammuthus meridionalis and Praemegaceros verticornis. The paleoenvironment was open landscape with many lakes, low moors, marshy forests in a humid, but not very warm climate. H. ex. aff. amphibius major has been recorded in Elis (THENIUS, 1955) of Astian (Middle Villafranchian) age and in central Macedonia of Villaynian age (Koufos et al., 1989). Hippopotamid remains have been identified also at Thessaly (Pinios river, BOESSNECK, 1965); Aliakmon river (MELENTIS, 1966); Euboia; Kos; Kephallonia; Agios Demetrios-Kato Salmeniko (SYMEONIDIS & THEODOROU, 1985/86); Neapolis (STEENSMA, 1988); Ptolemaida etc.

Order Proboscidea ILLIGER, 1811 Family Elephantidae GRAY, 1821 (Text-fig. 14, Table 9)

Material: Ph II LAO-C-282e

Description A rather short but robust second phalanx is the unique elephant remain. It is much higher posteriorly than anteriorly, while the proximal articular surface is relatively very wide and concave, without medial crest and may belong to *Elephas (Paleoloxodon) antiquus* FALCONER & CAUTLEY (1847).

Discussion

The rich but very fragmentary material from the Apidima site is not generally preserved in good condition, and is therefore mostly indeterminable. On the other hand the determinations were based on the few but very well preserved specimens. There are well-fossilized specimens, mainly in breccia, as well as recent bones e.g. goats, leporids, birds. There are many burnt and calcite- or salt- covered bones. The action of water is obviously indicated on some specimens, either by the erosion or by the rounding and abrasion of bones and the scattered skeletons.

• Cave C is the most representative in faunal composition, as only hippopotamid remains have not been found up to now. This may have to do with the altitude of the cave (Fig. 1), as the high sea-waves have moved most material (fissure fillings or cone of debris) of the other caves away. The presence of many cervid remains is notable. The presence of many micromammals (rodents), birds (mostly



Figure 14: Elephantidae-Apidima, second phalanx, Ph II, LAO-C-282e, anterior.

Ph II								
1.	Lmax	38.0						
2.	Lant.	30.5						
3.	DT max.	51.0						
4.	DT prox.	50.7						
5.	DAP prox.	32.0	Table 9.					
6.	DT prox.art.	48.5	Measurements of					
7.	DAP prox.art.	29.3	the Apidima					
8.	DT d.art.	41.6	elephant second					
9.	DAP d.art.	20.4	phalanx, in mm					

Taxon / Cave	Α	В	Ċ	D	
Panthera pardus	-	+	+	_	
Felis(Lynx) lynx	-	+	+	+	
Felis silvestris	-	-	+	-	
Vulpes vulpes	+	+	+	+	
Meles meles	-	?	+	_	
Martes foina	_	_	+	_	
Capra ibex	+	+	+	+	
Megaloceros sp.	_	-	+	_	
Cervus elaphus		+	+	+	
Dama dama	+	+	+	?	
Hippopotamus am-					
phibius antiquus	+	+	-	-	
Elephantidae	_	_	+	_	

Table 10. Representation of Quaternary large mammalremains in the four Apidima caves

beaks), leporids and burnt bones is also notable. There are also many turtle bones. Some bones are covered by a brownish-reddish calcite layer. There are a few specimens with probable traces of butchering.

The cave B faunal remains do not include wild cat, marten, giant deer or elephant, while the badger is not well represented. Of the very fragmentary material, mostly indeterminable, some bones are eroded and some are well fossilized, preserved in breccia. The majority of the material is represented by a mixture of caprid and cervid bones and teeth, especially the latter (incisors included). The presence of leopard remains is notable. Surface finds include small felid, fox, goat and deer remains.

The cave D faunal remains include lynx, red fox, wild goat and red deer, while fallow deer is poorly represented. There are bones with carnivore tooth traces, carnivore milk teeth, many birds of galliform size, burnt bones, bones which are rounded or covered with a calcite and/or salty layer, and recent bones, mainly of Caprinae.

The cave A faunal remains include very few representatives, mainly associated with the two hominid skulls, such as the red fox, wild goat, fallow deer and hippopotamus. Some specimens found in breccia on the floor, are eroded, rounded or burnt. The hippopotamus is found in association with rodents, birds and some indeterminable bones in breccia. The material from depths of about 0.70-0.94m consists mainly of artiodactyls, a few burnt bones, and rodents.

Conclusions

A study of the determinable and the most representative large mammal material, among 20.000 teeth, bones and bone fragments from the Apidima caves, has shown the presence of the following species:

Panthera pardus (LINNAEUS, 1758) Felis (Lynx) lynx (LINNAEUS, 1758) Felis silvestris SCHREBER, 1777 Vulpes vulpes (LINNAEUS, 1758) Meles meles LINNAEUS, 1758 Capra ibex LINNAEUS, 1758 Megaloceros sp. Cervus elaphus LINNAEUS, 1758 Dama dama (LINNAEUS, 1758) Hippopotamus amphibius antiquus DESMAREST, 1822 Elephantidae

In addition to these, there are recent specimens which belong to *Felis, Martes, Meles, Capra,* cervids, leporids, rodents and birds.

The presence of fossil and recent bones in this mixed fauna shows that the caves were used during different periods, from Middle Pleistocene to present, and this has to do with the eustatic sea-level fluctuations before today's transgression, which eroded almost all the cave A fillings.

The majority of the finds belongs to herbivoresmainly artiodactyls-which, except for their presence by chance, were the main food of the carnivores mainly felids- that sometimes inhabited the caves. Traces of carnivore gnawing on herbivore bones, especially on juvenile caprid and cervid bones, indicate the food remains of the carnivores.

The juvenile carnivore remains, as well as the food remains, establish them as inhabitants.

The absence of perissodactyl, suid, ursid etc. remains is notable, although a richer fauna could be expected at this, southernmost continental site of Europe, which might have worked as a natural coastal barrier.

The presence of many micromammalian remains, mainly murid and cricetid rodents (mice and voles), as well as insectivores (mostly soricids), birds, reptiles (mostly turtles), and fish (represented by vertebrae) is notable.

The presence of many leporid, rodent and bird remains is consistent with the presence of the foxes and felids.

Some specimens show traces of butchering, and the habitation of man is also established by skeletal remains, artefacts, burials, fire traces etc..

The age of the fossil fauna, according to the stratigraphical distribution of the large mammals (the carnivore distribution was also based on WOLSAN (1993) and cervid distribution on LISTER (1986)), is Middle to upper Middle Pleistocene, and Late Pleistocene.

The climate was temperate, rather mild (not "cold") although in other parts of Europe there were glacial episodes with cold climate. The favourable climatic conditions in combination with the increased land area, because of the lowering of sea-level, helped the immigration and settling of animals and humans. It is an important feature of the Greek Quaternary faunas, that species typical of cold climate (except very few and isolated specimens), are missing up to now. The few extensive studies of Quaternary sites (TSOUKALA, 1992b) do not show faunas typical of cold episodes, such as in rest Europe. Further studies would bring to light valuable conclusions.

The paleoenvironment of the broader area of Mani peninsula, during Pleistocene, was mixed and variable steppe like during sea regression, interrupted by forests (mainly of coniferous trees, wild olivetrees, pistachio and other Mediterranean flora). The mixed forests and rocky hillsides are favourable to certain species such as *Martes foina*. As the Apidima fauna is stratigrafically mixed, careful interpretation is required.

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PLATE 1

Panthera pardus (LINNAEUS, 1758)

- Fig. 1. Maxilla fragment LAO-B-371a sin, occlusal (~1:1)
- Fig. 2. C^sLAO-B-91dex, a) labial, b) lingual, c) posterior (~7.5:10)
- Fig. 3. C^s fragment LAO-B-409dex, labial (~1:1)
- Fig. 4. Radius LAO-B-388c+389sin, a) anterior, b) posterior (~6:10)
- Fig. 5. Navicularis LAO-B-389b sin, a) proximal, b) anterior, c) posterior (~6:10)
- Fig. 6. McV LAO-B-389a dex, a) dorsal, b) plantar, c) medial (~6:10)
- Fig. 7. PhI LAO-B-410a, dorsal (~8:10)
- Fig. 8. PhII LAO-B-348e, dorsal (~1:1)

Felis (Lynx) lynx (LINNAEUS, 1758)

Fig. 9. C^s (~1:1)

Vulpes vulpes (LINNAEUS, 1758)

- Fig. 10. Mandible frag. with M₁, M₂ dex LAO-B-352c,353 dex
 a) labial, b) occlusal, c) M₁ lingual (~1:1)
- Fig. 11. Tibia LAO-C-402a+404 sin (~7:10)

Capra ibex (LINNAEUS, 1758)

- Fig. 12. Horn fr. LAO-B-79 (~7:10)
- Fig. 13. Metacarpal (Mc III+IV) LAO-B-385 sin (~7:10)

Dama dama (LINNAEUS, 1758)

Fig. 14. Metacarpal distal, LAO-B-87a, anterior (~7:10)

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PLATE 1



PLATE 2

Capra ibex (LINNAEUS, 1758)

Fig. 1. Maxilla frag. with P⁴-M³ LAO-C-24 dex

Fig. 2. Maxilla frag. with P³-M³LAO-C-26a sin

Fig. 3. Mandible frag. with P_4 - M_3 LAO-D-18a sin

Fig. 4. Mandible frag. with P_4 - M_3 LAO-D-79e dex

Cervus elaphus (LINNAEUS, 1758)

Fig. 5. Maxilla frag. with P²-M³ LAO-C-27dex. a) labial, b) occlusal.

All Figures ~7.5:10

TSOUKALA, E., Quaternary large mammals ...

PLATE 2

