# Large mammals except cave-bears from the Loutra Almopias Cave, Late Pleistocene, Macedonia, Greece

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**Abstract**

Excavations in the Loutra Almopias cave yielded a large amount of different vertebrate taxa assigned to two different time horizons. Here we describe the carnivores, with the exception of the cave bear, and herbivores found in the cave. Special focus lies on the mustelids, not evaluated previously, and the comparison of leopard, hyena and chamois. The composition of the mustelids in the isolated chamber Ia confirms its chronological assignment into the Late Glacial, while most of the larger mammals, such as *Crocuta, Panthera* and *Rupicapra*, fit into the time before the Last Glacial Maximum (LGM).

**Zusammenfassung**

Die Grabungen in der Loutra Almopias Höhle ergaben eine große Anzahl an unterschiedlichen Vertebraten, die zwei verschiedenen Zeithorizonten zugeordnet werden. Wir beschreiben hier die Carnivora, mit Ausnahme des Höhlenbären, und die Herbivoren aus der Höhle. Der Schwerpunkt liegt auf den bis jetzt unbearbeiteten Musteliden, sowie auf dem morphologischen Vergleich der Hyäne, des Leoparden und der Gämse. Die Zusammensetzung der Musteliden aus der isolierten Kammer Ia bestätigt die zeitliche Einstufung in das Spätglazial, während die meisten Großsäuger, wie *Crocuta*, *Panthera* und *Rupicapra*, in die Zeit vor dem letzten Vereisungshöhepunkt im Glazcial (LGM) zu stellen sind.

**Key words:** Carnivora, Artiodactyla, Almopias cave, Late Pleistocene, Greece

## 1. Introduction

The cave is situated in the Almopia Speleopark in Macedonia (Greece), which holds a group of caves of scientific interest. It is embedded in Maastrichian limestone. During the Quaternary, the intramontane basin of Almopia experienced extensive karstification, thus leading to the formation of the cave (Lazaridis, 2005).

Scientific investigations took place from 1990 to 2012 and yielded more than 20.000 specimens, most of them belong to the cave bear, making it the richest Pleistocene fossil cave in Greece. The cave is structured into different chambers. LAC Ia, the smallest chamber, is less than a square meter, difficult to access and completely separated from the others.

Sedimentation in the cave changed between warm and humid intervals with calcareous crusts and tufas and colder sections with clastic sediments (Tsoukala et al., 2006).

Dating the material proved difficult since most of the bones had too few or no collagen at all. Only one femur of *Ursus* (GrN-7573) revealed a reliable radiocarbon result of 37.880 +370/-360 (cal 42.361±378) years before present (a BP). Sediments and sinter (dated with various methods such as OSL, LUM, U/Th and C14) fill the time gap with results from 29.900 to 11.500 a BP. The micromammals from LAC Ia yielded an age between 11.230 ± 110 (VERA-0060) and 12.350 ± 40 (VERA-5631) a BP. A charcoal remain from LAC Ic is dated around 5.000 a BP (Zacharias et al., 2008). Therefore most of the animal remains from the cave come from the Middle Weichselian (OIS 3) with the exception of smaller mammals from LAC Ia, which are placed into the Late Glacial (Tsoukala et al., 2006).

Descriptions of the Pleistocene material from Loutra Almopias were made by Tsoukala et al. (2001), Tsoukala & Rabeder (2005) and Tsoukala et al. (2006) with overviews of the setting, excavation and the main findings. In this work, the focus lies on the description of all non-ursid and non-micromammal material with a special focus on the carnivores and artiodactyls. It includes a detailed evaluation of the distribution of these taxa in the different parts of the cave.

***Abbreviations***

PIUW – Department of Palaeontology Vienna

LAC – Loutra Almopias cave

MIN – minimum number of individuals

LAC I, Ia, Ib, Ic, II and III refer to the chambers, where the specimens were found. For a detailed description of the chambers see Tsoukala et al., 2006.

***Measurements***

Capital letters are used for upper teeth (e.g. M – upper molars, P – upper premolars) small letters are used for lower teeth (e.g. m – lower molars, p – lower premolars)

DO – smallest depth of the ulna at the olecranon

Dpa – smallest depth above the processus anconaeus

Hcrown – crown height of the canine, measured from the enamel band

Hroot – root height of the canine, measured from the enamel band

L ant.-post – length measured anterior-posterior

Wp – maximal width proximally

Dp – maximal depth proximally

Wd – maximal width distally

Dd – maximal depth distally

mL – maximal length

mW – maximal width

mL art – maximal length of the articulation

mW art – maximal width of the articulationm

H – maximal height

sD – smallest diaphyses width

BT - width of trochlea

WoP – width over processus anconeus

nt-post – long bones measured anteroposterior

## 2. Methods

Measurements were taken with a calliper up to 0.1mm and follow VON DEN DRIESCH (1976). Measurements given in tables are in millimetre. Measurements were only taken on dental and/or postcranial material of taxonomic value. If only few elements per taxa are present, the measurements are given in the list of the material; otherwise, separate tables are provided. Photos and plates were made by Rudolf Gold (PIUW).

## 3. Systematic description

Order: Carnivora (Bowdwich, 1821)

Family: Mustelidae (Fischer, 1817)

Subfamily: Mustelinae (Fischer, 1817)

The subfamily includes a variety of carnivores with different food and hunting preferences ranging from the largest mustelid, the wolverine to the smallest, the least weasel and from the African honey badger to the South American Eira.

Today the mustelid fauna in Greece consists of *Meles meles* (badger), *Martes martes* (pine marten), *Martes foina* (stone marten), *Vormela peregusna* (marbled polecat), *Mustela lutreola* (European mink), *Mustela putorius* (European polecat), *Mustela erminea* (ermine) and *Mustela nivalis* (least weasel). Recorded from some Greek islands is *Lutra lutra* (European otter) (Massetti, 1995). In the Loutra Almopias caves four of the nine extant known species could be identified.

Genus: *Mustela* (Linnaeus, 1758)

Members of the genus *Mustela* live in Europe, Asia, North and South America and Africa. It was introduced to Australia by men. In Europe during the Pleistocene, the following taxa have been known so far: *M. nivalis* (least weasel), *M. erminea* (stoat), *M. eversmanni* (steppe pole cat), *M. lutreola* (European mink) and *M. putorius* (European polecat) (Spitzenberger, 2001).

*Mustela nivalis* (Linnaeus, 1758)

Material (all from chamber Ia): LAC 1292 right maxilla fragment with Csup and P2; LAC 10503 left P4; LAC 1290a left mandible fragment with p2-p4 (Plate 1, Fig. 1a & b); LAC 3850 left mandible fragment with m1 broken; LAC 3851 right mandible fragment with alveoli of p3-p4, m1, alveoli of m2; LAC 3852 right dp4; LAC 10524 left mandible fragment with broken p3, p4-m1; LAC 10520 I fragment; LAC 2910 left m1. Measurements of 1290a, 10524 see Table 1.

The smallest of the mustelids is represented by a number of single teeth, permanent and milk teeth, by a right lower mandible fragment with p2-p3 and a right upper maxilla fragment with I2, Csup, root fragment of P2 and P3. Only *M. nivalis* is of that size and it was the smallest predator in the Loutra Almopias caves, only found in chamber Ia.

*Mustela* (*Putorius*) *putorius* (Linnaeus, 1758)

Material (all from chamber Ia): LAC 10518 maxilla fragment with a right I1 and left I1-2, alveolus for I3; LAC 4269 right maxilla fragment with Csup, P1-P4 and M1 (Plate 1, Fig. 4); LAC 2905 left

Csup.; LAC 2904 and LAC 4265 right Csup.; LAC 3839 right P3; LAC 2906 left mandible with root of broken canine, p2–p4, m1-m2; LAC 4268 left mandible fragment with root of broken canine, p2, p3, distal part of p4, m1 and m2 (Plate 1, Fig 3a-c); LAC 3833 left cinf and LAC 2911 right cinf. Measurements of LAC 4269, 2906, and 4268 see Table 1.

The maxilla fragment (LAC 4269) is broken mesially in front of the I2, the alveolus for I3 still present. The tooth row from Csup to M1 is quite well preserved. Only the tip of the upper canine is broken; the paracone on the P4 is slightly worn. This mustelid material in this size group is either *M. putorius* or *M. eversmanni* but in the latter the protocone on the P4 is slightly larger and more rounded.

The left mandible (LAC 2906) is broken mesially, with the alveolus of i3 still visible; the canine is broken with its root still in place, and the ramus ascendens is damaged. The other left mandible (LAC 4268) is as well only preserved from the alveolus of the i3 to the m2, the ramus ascendens broken. Its canine is broken but the root still present. The mandible was broken at the position of the p4 and the anterior part of p3 is missing. The m1 is very small and the metaconid missing on the carnassial, which is typical for *M. putorius*. Therefore the material is assigned to *M. putorius*.

All specimens were found in the isolated chamber Ia The polecat is not present in Greece today.

Genus: *Martes* (Pinel, 1792)

Members of the genus *Martes* live today in the northern deciduous forests of Europe, Asia and North America. In Europe, during the Pleistocene, the following taxa have been known so far: *M. foina* (stone marten), *M. martes* (pine marten), *M. zibellina* (sable). They are carnivorous to omnivorous and not as specialized on meat as their smaller relatives from the *Mustela*-group (Grupe & Krüger, 1990).

*Martes foina* (Erxleben, 1777)

Material: LAC 6938 left M1 (I); LAC 10480 left M1 (III); LAC 14481 right P4 (Ib); LAC 2892 left mandible fragment with alveolus for cinf and p2-p3, p4 broken (Ia); LAC 3829 left mandible with cinf, alveolus of p1, p2-m1 (Ia) (Plate 1 Fig 2a&b). Measurements see Table 1.

The occlusal surface of both M1 is well preserved and roots are missing. The buccal shape of the M1 with a more pronounced paracone and metacone allows an assignment to *M. foina*. The P4 is slightly worn and the protocone is missing but the shelf in front of the paracone is very small so the protocone was probably very closely attached, as typical in *M. foina*. On the mandible (LAC 3829) the protoconid and paraconid of the m1 are already worn, as well as the hypoconid. Otherwise only the tips of the remaining teeth show signs of wear. On the m1 the metaconid is closed attached to the protoconid and the paraconid is also extended lingually, as known from *M. foina*.

The material was found in the chamber Ia as well as in the main chambers of the Loutra Almopias cave. The migration of *M. foina* into Europe seems to have started from Asia and it probably arrived

during the Latest Pleistocene (Anderson, 1970 in Buskirk et al., 1994 in Spitzenberger, 2001).

*Martes martes* (Erxleben, 1777)

Material: LAC 7481 left M1, 6.9 x 9.6 mm (III) (Plate 1, Fig. 7); The upper molar is buccal less grooved as typical for *M. martes*, therefore the assignment. LAC 3830 is a right mandible fragment with cinf to p3 (Ia). The M1 was found in the main part of the Loutra Almopias cave in chamber III and the mandible in Ia. The pine marten today is found in most parts of Europe with decent vegetation. Therefore, it is not distributed in the arid areas such as south of the Pyrenees, the Pindos mountains and southern Ukraine (www.arkive.org, retrieved 08.2017).

*Martes* sp.

Since remains of the pine marten and the beech marten, which are of similar size, co-occurred in the Loutra Almopias cave area, it was not possible to distinguish the material, when no diagnostic features were present. Therefore the following material is only assigned to the genus *Martes*: LAC 3831 right Csup. (Ia); LAC 3832 right cinf. (Ia); LAC 2878 (left mandible fragment with alveoli for m1-m2 (Ic); LAC 3821 right tibia fragment (Ia); LAC 3822 left tibia fragment (Ia); LAC 3823 left radius fragment (Ia). Measurements see Table 1.

Genus: *Meles (*Linnaeus, 1758)

The badger is a wide spread animal in the holarctic area. A study on the mitochondrial DNA (Del Cerra et al. 2010) concluded four different phylogeographic groups (European, Continental Asia, Southwest Asian and North-East Asian). They suggest an independent evolution of these types since the Pliocene. For the last glacial part, they see no indication that the European, as well as the Russian regions, were recolonised by the Southwest Asian badgers, except maybe the Crete island population which is more closely related to the Southwest-Asian type. Baryshnikov (2009) commented on these results, that there is not enough morphological evidence for a separation on a species level. Therefore we refer to the European badger here as *Meles meles*.

Subfamily: Melinae (Linnaeus, 1758)

Genus: *Meles* (Linnaeus, 1758)

*Meles meles* (Linnaeus, 1758)

Material: LAC 7409 left maxilla fragment with P3-M1(III) (Plate 1, Fig. 5); LAC 204 left i3 (II); LAC 8704 right i3 (III). Measurements see Table 1.

The badger is not very common in the Almopias cave but the specimens were found in the main part of the

cave in chamber III. Only one maxilla fragment and three single teeth were preserved. The maxilla fragment consists of the P2 to P4 and the alveoli of M1, parts missing on the lingual-posterior side. The teeth are not very worn. Part of the alveolus of the canine is preserved but there is not enough space between it and the P2. Therefore no P1 was present on this specimen. This tooth is missing in about 50% of the extant badgers (Baryshnikov, 2009)

The P4 resembles that of a recent badger in morphology and size and does not differ in its size range from other Late Pleistocene badgers. Baryshnikov (2009) described the extensive sample from Kudaro cave and Binagady, Caucasus. The ones from Kudaro are slightly larger while the material from Binagady is about the same size as the material from Loutra Almopias. With the small sample, no information about sexual dimorphism or possible differences on a subspecies level can be given.

Mustelidae indet.

Several specimens belong to mustelids but cannot be identified further. Among them are phalanges of small to very small size, tooth fragments and tooth germs.

Family: Canidae *(*Fisher von Waldheim, 1817)

Genus: *Canis* (Linnaeus, 1758)

*Canis lupus* (Linnaeus, 1758)

Material: LAC 13701 right P4 fragment (mL = 23,8 mm, mW = 11,8 mm) (I) (Table 2, Plate 1, Fig 10); LAC 3912 caput femori (Ic); LAC 2888 right metacarpal 5 (Ia); LAC 3931, 3932 and LAC 3933 first phalanges (Ia).

The paracone and the metacone blade on the P4 are very worn, the protocone and its root are broken. Further damaged are the buccal and posterior side, as well as parts below the paracone. The tooth is rather worn but the overall morphology is that of a canid carnassial, too small for a lion or hyena and not slender enough for a leopard. It is far too worn to give any indication whether it may have belonged to a male or female wolf. The postcranial material is fragmentary with only one complete metacarpal 5. Metrically, the phalanges found in LAC Ia, are very small, even dog-size.

*Canis lupus*, the wolf, was distributed in the Mediterranean area until the end of the Sub-Atlantic (Sablin & Khlopachev, 2002, Sommer & Benecke, 2005). It retreated later on further north.

Genus: *Vulpes (*Frisch, 1775)

*Vulpes vulpes* (Linnaeus, 1758)

Material: Upper dentition; LAC 7646 right I3 (III); LAC 3825 right Csup (Ia); LAC 3647 right P4

fragment (Ia); LAC 2900 left M1 buccal side only (Ia); LAC 5719 left M2 (I); Lower dentition; LAC 4267 and LAC 2901 refitted, juvenile left mandible fragment with p4 in crypt, m1-m2 and m3 in crypt (Ia) (Plate 1, Fig. 6a&b); LAC 3826 left mandible fragment with alveoli for cinf to m1 (Ia); LAC 3835 left i3 (Ia); LAC 1291 right i3 (Ia); LAC 4939 left i2 (II); LAC 2893 left cinf (Ia); LAC 3827 left p2 (Ia); LAC 4266 right p2 (Ia); LAC 3828 left p4 (Ia); LAC 2897 right m1 both roots damaged (Ia); LAC 2896 left m1 posterior root broken (Ia). Postcranial elements: LAC 3820 right humerus fragment, only distal part preserved (Ia); Measurements see Table 2.

Two left mandible fragments, LAC 2901 and LAC 4267, belong together. The symphysis fits together perfectly. The p4 is still in crypt as well as the m3. The m2 is not fully erupted; m2 as well as m1 are not worn. The individual was of semi-adult age. LAC 2896 and LAC 2897, one left and right m1 probably belong to a second individual and they are equally unworn. The postcranial material is very fragmented. Apart from a distal fragment of a right humerus, only a broken part of a phalange and the proximal part of a metapodial could be identified. Metrically as well as morphologically, the material fits into the *Vulpes* range. All the material came from the chamber Ia. It consists at least of two individuals.

Family: Felidae (Gray, 1821)

*Felis silvestris* aff. *catus* (Linnaeus, 1758)

Material: LAC 1292c (Ia) left upper carnassial fragment.

The P4 fragment consists of the buccal part of the paracone and the metastyle blade. The lingual and anterior part is missing, as well as the anterior root. The tooth was found in LAC Ia, a chamber of the cave where mainly remains of Holocene smaller animals were found. The specimen is of very small size and probably also of Holocene age, thus the affiliation to the domestic cat rather than the feral one.

Genus: *Panthera (*Oken, 1816)

*Panthera pardus* (Linnaeus, 1758)

Material: LAC 13268 right cranium fragment with P3 (Ic) (Plate 2, Fig. 1a&b), LAC 9980 right Csup (Ic), LAC 3978 left m1 (Ic) (Table 1, Plate 1, Fig. 8a & b), LAC 13530 left radius proximal fragment (Ic), LAC 13284 left radius (Ic), LAC 11779 left ulna proximal fragment (Ic), LAC 8385 left ulna proximal fragment (I), LAC 12102 left trapezium (Ic), LAC 14918 left tarsale 3 and cuniforme (Ic), LAC 3913 right proximal part metatarsal 3 fragment (Ic) LAC 4170 left first digit (II), LAC 2628, 5813 second digits (Ic, I).

The most of the leopard specimens were found in LAC Ic. Only the complete ulna (LAC 8385) and the intermediate phalange (LAC 5813) was recovered from chamber I; the posterior phalange (LAC

4170) from champer II. Since two left radius and ulna fragments were found, the material seems to belong to two individuals (MNI = 2). A metrical comparison (Fig. 1) of the m1 and P3 indicates leopards of average size.

Fossil remains from the Pleistocene leopard are scarce. Nevertheless, material is known in the entire of Europe (e.g. Fischer, 2000, Pacher & Rabeder, 2016). While it probably co-existed with a similar large felid, *Panthera onca gombaszögensis*, during the Middle Pleistocene (Hemmer, 1971, Hemmer et al., 2010, Fischer, 2000). The leopard is the only felid of this size in the Late Pleistocene (Wolsan, 1993, Sommer & Benecke, 2005) and the Holocene (De Grossi Mazzorin, 1995, Žuravlev, 1999) in Europe.

| ***Pantera pardus*** | specimen | mL | mW |
|---|---|---|---|
| LAC 3978 sin | m1 | 19.2 | 8.5 |
| LAC 13268 max frag dext | M1* | 3,1 | 6,9 |
| | P4* | 23,3 | 12,6 |
| | P3 | 17.4 | 8.5 |
| | P2* | 6,3 | 4,4 |
| | Csup* | 15,7 | 13,8 |
| | I3* | 8,5 | 6,2 |
| | I2* | 6,8 | 3,1 |

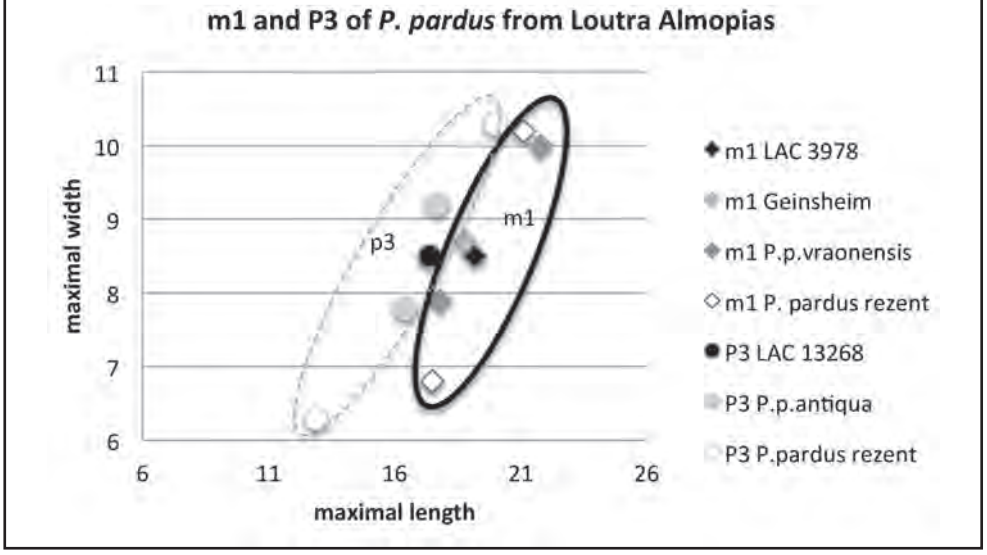


Fig. 1: Scatter diagram of m1 and P3 of *Panthera pardus* from Loutra Almopias caves in comparison (Schmid, 1940, Nagel, 1999, Del Campana, 1954, Koenigswald et al., 2006).

Several fossil subspecies have been described from Europe: *P. p. sickenbergi* (Schütt, 1969) and *P. p. lunellensis* (Bonifay, 1971) from the Middle Pleistocene, *P. p. antiqua* (Del Campana, 1954), and *P. p. vraonensis* (Nagel, 1999) from the Late Pleistocene. Genetic investigations of the fossil leopards will be necessary to confirm or refute the taxonomic value of these subspecies. We therefore, refer the material from Almopias cave to *Panthera pardus* (Fig. 1).

The specimens fit morphologically as well as metrically into the *P. pardus* group. The upper canine is with a minimum height of 62 mm of average to larger size; the fossil and extant leopards range from 50 to 80 mm (Schmid, 1940) The same is true for the upper P3 (Plate 2, Fig. 1). The postcranial material, specially radius and ulna, range metrically more on the upper end of the scale and may indicate that one of the individuals was a male. Since only one incomplete metapodial was found, a comparison with the material from Vraona (*P. p. vraonensis*) is not possible (Del Campana 1954, Nagel, 1999, Schmid, 1940).

Suborder Feloidea (Simpson, 1931)

Family: Hyaenidae (Gray, 1869)

Genus: *Crocuta* (Kaup, 1828)

*Crocuta crocuta spelaea* (Goldfuss, 1832)

Material (Plate 1, Fig. 9, Plate 2, Figs. 2-5, 8a & b), all from chamber Ib; exceptions are mentioned in brackets. LAC 9150 left upper canine; LAC 6629 right first incisor; LAC 11788 left first incisor; LAC 6862 left second incisor; LAC 11823 right third incisor (I); LAC 8475 right p4 (I); LAC 7097 right lower canine. Vertebrae: LAC 9500 cervical v.; LAC 6129, 6679, 6838, 12379, 11454 thoracic v.; LAC 7107, 8427, 9293, 11310 lumbal v.; LAC 6284 right pelvis fragment; LAC 11287 left acetabulum; LAC 9172 left humerus; LAC 11060 left femur; left caput femori LAC 11235 left and 11334 right; LAC 6282 left radius; LAC 7225 right radius; LAC 13675 right ulna fragment proximal with diaphysis; LAC 9283 right tibia; LAC 8177 left patella; LAC 8263 right scapholunatum; LAC left 9504 left pyramidal; LAC 6681 right capitulum; LAC 7171 left hamatum; LAC 8179a left calcaneus; LAC 6680, 7034 left and LAC 7185 right naviculars ; LAC 7712 right tarsal 3; LAC 9365 left metacarpal 2; LAC 6274 right metacarpal 3; LAC 9002 left and 7047 right metacarpals 4; LAC 13638 right and 12632 left metacarpals 5; LAC 9003 left metatarsal 2; LAC 6285 left metatarsal 3; LAC 9007 right and LAC 6050 left metatarsals 4; LAC 4313, 6134, 6310, 6815, 6839, 7045, 7048, 7106, 9530 phalanges 1, LAC 8825, 14898 (subadult, Ic) phalange 1; LAC 10130 phalange 2 (Ic); LAC 6291, 8072, 11582 phalanges 3, LAC 7953b, 8042 two coprolites. Re-measured or new material see Table 3; otherwise see Tsoukala et al. 2006.

The cave hyena is present with more than 60 specimens, including cranial and postcranial material. From the skull, only part of the cranium is preserved. No jaws were found, only single teeth. The bones show no signs of gnaw marks. Most of the vertebrae lack on one or both sides the epiphyses. Four metapodials fit together and seem to be from one individual (LAC 9365, 6274, 7047, 13638) (Plate 2, Fig. 8a & b). One metatarsal is slightly pathological, being thicker and more rugose in the diaphysis. Left and right limb bones as well as carpal and tarsal bones are of similar size. The minimum individual number is therefore only two. Judging from the state of the bones, it was probably one semi-adult and one adult individual; the latter older or maybe sick.

One major factor to separate *Crocuta* into a fossil and an extant form was size. The fourth premolar has a total length of 22.7mm and a width of 14.4mm. Extant ones range from 19 to 23mm and 10 to 12mm; fossil ones can go up to 25mm and 15mm. Tibias from fossil hyenas are about 200mm to 210mm long (Engelbrecht, 2011), the one from Loutra reaches 193mm. So the material from Loutra Almopias is in general larger than the extant hyenas but average in size when compared to fossil ones.

Almost all the material came from chamber LAC Ib, only two teeth were found in the adjacent chamber I and III, potentially transported there by water or other animals (Fig. 2).

The cave hyena is a well-known member of the Late Pleistocene fauna and the only hyaenid species in the Late Pleistocene in Eurasia. Investigations regarding the genome, place the Eurasian population within the extant one, granting it a subspecies status. The latest occurrence in Europa is up to 30,000 maybe 25,000 years before present (Hofreiter & Stuart, 2009, Rohland et al., 2005, Sheng et al., 2014).

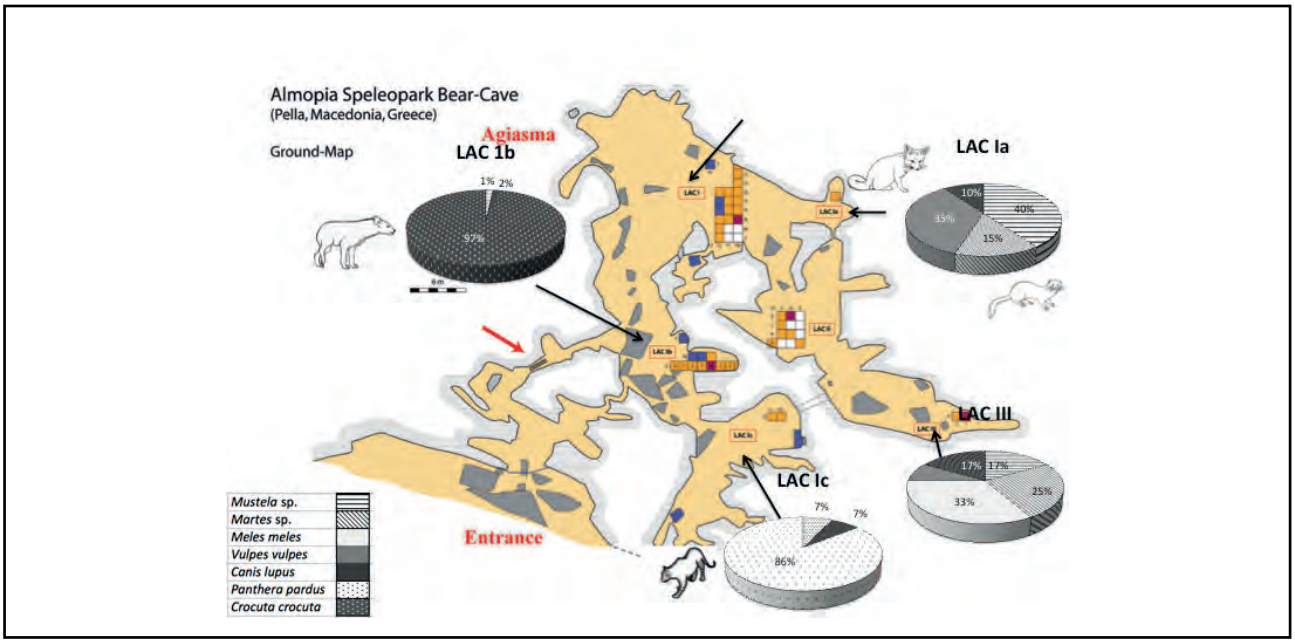


Fig. 2: Carnivore distribution in the Loutra Almopias caves

Order: Artiodactyla

Family: Bovidae (Gray, 1821)

Subfamily: (Caprinae Gill, 1872)

Genus: *Capra* (Linnaeus, 1758)

*Capra ibex (*Linnaeus, 1758)

Material: LAC 6840 (Ib) right 3, 4. upper premolar; LAC 1820 (II) and 6536 (I) two i1,2; LAC 9303 & 9308 left (Ib) radius; LAC 1833 left (II) capitatotrapezoid (same individual with LAC 905)*; LAC 14940 (I) astragalus prox. right; LAC 8826 (Ib); cuneiform right; LAC 905 left (II) Mc 3+4 (same male individual with LAC 1833); LAC 6790 right (III) Mt3+4, female juvenile; LAC 13818 (I) Mp3+4 distal; LAC 6340, 6341 (Ib) 2 first Phalange (same individual?); LAC 11268 (Ic) Ph1; LAC 5590, 5591, 5595, 5596, 3090 Ph 1 (Ia).

*Ibex* remains are found in all chambers of the cave implying a rather heterogenous fossil history of the assemblage further strengthen by their differing preservation quality. None of the remains shows traces of carnivore activity. *Ibex* went extinct in Greece during the Holocene (Geskos, 2013).

Genus: *Rupicapra (*Blainville, 1816)
*Rupicapra rupicapra* (Linnaeus, 1758)
Material: LAC 8796 phalange 2 (Ib) 2; LAC 10095 phalange 2(Ic); LAC 11800 astragalus (Ic).
The three bones attributed to *Rupicapra rupicapra* are the first evidence of this species in the Pleistocene of Greece (Tsoukala, 1992a). A comparison of the remains with material from the collection of the Institute of Palaeontology, Vienna confirms the determination (Plate 2, Figs. 6 & 7).
The remains come from chamber Ib and Ic but their chronological age is unknown. Especially the astragalus shows clear traces of bone abrasion due to transport.
Today, the subspecies *R. rupicapra balcanica* is an endangered taxa in Greece. It survived in dispersed small populations like those in the Pindos and Rhodope mountains, Sterea Ellada or Mount Olympus (Papaioannou & Kati, 2007).

Family: Cervidae (Gray 1821)

Genus: *Cervus* (Linnaeus, 1758)

*Cervus elaphus* (Linnaeus, 1758)

Material. LAC 11425 phalange 2; LAC 9992 phalange 3 (Ic); LAC 15500 phalange 2 (I), LAC 6680 left semilunar bone (Ib).

The red deer is represented by two middle phalanges and a distal phalange. Phalanges LAC 11425 and 9992 are from the same individual. They show no trace of carnivore activity. Two middle pha-

langes come from chamber Ia and might therefore represent Late Glacial/Holocene remains of the red deer in the Loutra Almopias cave.

Genus: *Dama (*Frisch, 1775)

*Dama dama* (Linnaeus, 1758)

Material: LAC 13122 Antler frag. (Ic); LAC 6338 left (I) and LAC 4302 (Ib) left scapula fragments; LAC 10096 metapodial trochlea (Ib).

While the fallow deer is today native in Eurasia, the occurrence in the Mediterranean area, especially in Greece during the Last Glacial is discussed (e.g. Massetti, 2012). Since the age determination of the material is not clear, no further information on this topic can be added.

Subfamily: Bovinae (Gill, 1872)

Genus: *Bos (*Linnaeus, 1758)

*Bos primigenius (*Bojanus, 1827)

Material: LAC 9319 proximal phalange (Ib), LAC 5597 phalange 1 prox. epiphysis fragment (Ia).

This extinct species is a typical element of the European Late Pleistocene and is known till the Holocene when it was domesticated into cattle breeds. The specimen shows clear traces of gastric acids, typical for a bone that passed the digestive system of a carnivore (Andrews & Cook, 1990). It was found in LAC Ib where most of the *Crocuta* remains come from. The proximal epiphyseal fragment from a large bovid comes from chamber Ia and shows a different porous preservation. Its age assignment is unclear.

## 4. Discussion and Conclusion:

The Mediterranean as well as the Balkan area have been important refugia for larger mammals during colder periods and only recently more attention has been given to migration tendencies of the small carnivores as well (Sommer & Benecke, 2005, Sommer & Nadachowski , 2006, Miracle & Brajkovic, 2010). Therefore the assignment of the various groups of carnivores from the Loutra Almopias cave to the different chambers and so to different time events was of importance. It was only a short-term hyena cave since the hyena findings are from two individuals only and only two coprolites were found mostly in chamber Ib. The remains from the leopard, maybe two individuals, were mainly found in chamber Ic and almost no other carnivore remains were retrieved from chamber I, since it was mostly used by cave bears, judging from the number of bones found there. The isolated chamber Ia was the main site where specimens of mustelids were deposited (Fig. 2). Therefore it is very unlikely, that all

these carnivores used the cave at the same time.

The single phalange from *B. primigenius* shows traces of hyena activity. Bones of other herbivores are rare and bear no traces of bite marks, while several unidentified long bone fragments show green bone fractures and partly gnawing activity.

The lion, reported in Tsoukala et al. (2006) had to be reassigned to *Ursus*. *Panthera pardus* remains were found from two individuals. The wolf is only represented by one carnassial. Given the large amount of cave bear bones found in Loutra Almopias, this cave system was inhabited by cave bears, with the hyena and other carnivores as occasional guests.

The smaller carnivores include *M. nivalis*, *M.* (*Putorius*) *putorius, M. foina, M. martes* and *M. meles*. With the exception of *Putorius*, all taxa are present in Greece today as well, at least in the Northern part in the Rhodope mountains. Regarding their size, they all are in the extant size range. The least weasel (*nivalis*) seems to be more often found in the Late Glacial than in the time before or after while *Putorius* has rarely been found in Late Glacial sites in Europe but the species is mentioned from Spain and Italy (Altuna, 1972, Tozzi, 1971 in Sommer & Benecke, 2005). This is the first record from Greece from the Late Glacial, whereas the giant polecat *Mustela putorius* has been recorded in the Late Pleistocene hyenid den of Agios Georgios Cave (Kilkis) (Tsoukala, 1992b). *Martes* and *Meles* are at least once recorded in one fossil Greek site (Julien, 1973 in Sommer & Benecke, 2005). All these faunal elements prefer a temperate to cool environment with bushy and rocky areas; *M. foina* is not known from the northern parts of Europe.

Since this material seems to come mainly from the isolated chamber Ia, dated into the Late Glacial, these remains probably are from a cooler phase, maybe Dryas II. This part of the cave was probably used by smaller carnivores, mustelids. Therefore, this area was also used as a glacial refuge for taxa such as the badger, the marten and the European polecat. The fact that *M. nivalis* was also present indicates somewhat lower temperature than today.

Middle-sized carnivores such as the red fox (*V. vulpes*) and the arctic fox (*Alopex lagopus*) existed sympatrically during the Pleni-Glacial and in some areas even during the Late-Glacial in Greece, but only the red fox is known from the fossil record so far. *V. vulpes* has a very large range of habitats and is not specialised in its diet (Sommer & Benecke, 2005).

*C. crocuta* and *P. pardus* are typical elements of the Late Pleistocene. Genetic analyses indicate a close relationship of the fossil *Crocuta* with the extant ones (Barnett et al., 2009, Rohland et al., 2005). The size of these taxa from Loutra Arideas does not even exceed the values of the extant ones.

Ecologically, hyenas and leopards today inhabit subtropical semi-arid deserts to dry forests. Although they are not very dependent on water, they are not able to live in deserts (Honer et al., 2008, Varela et al., 2010). In the Late Pleistocene, hyenas seem to be present in Europe during drier conditions (Nagel et al., 2017). Clearly, these larger carnivores came from a different time span than the mustelids from chamber Ia.

Among the herbivores chamois is the most important finding. It is the first record of this species in Greece and it is a typical form for mountainous areas. *C. ibex*, *C. elaphus* and *D. dama* were probably food remains of the occasional large predator seeking shelter in the cave.

## 5. Acknowledgments

We are thankful to Rudolf Gold (photographer Department of Palaeontology, University Vienna) for the photos and the compilation of the plates. We are grateful to Dr. Vangelis Vlachos (Aristotle University, Thessaloniki) for the co-ordination of information during the research progress. We thank the Austrian Academy of Sciences, Commission of Quaternary Research, for their long term financial support of the excavations as well as the local authorities for the partial financial support.

## 6. References

Altuna, J. (1972). Fauna de mamiferos de los yacimientos prehistóricos de Guipuzoa. - Munibe **24**(1/4): 1-464.

Anderson, E. (1970). Quarternary evolution of the genus *Martes* (Carnivora, Mustelidae). - Acta zool. Fenn. **130**: 1-32.

Andrews, P. & Cook, J. (1990). Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with analysis of the Pleistocene cave faunas from Westbury-dib Mendip, Somerset, UK. University Chicago Press, 231pp.

Barnett, R. Shapiro, B., Barnes, I. A., Ho, S. Y., Burger, J., Yamaguchi, N., Higham, T. F. G., Wheeler, T., Rosendahl, W., Sher, A., Sotnikova, M., Kuznetsova, T., Baryshnikov, G., Martin, L. D., Harington, R., Burns, J. & Cooper, A. (2009). Phylogeography of lions *(Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. - Molecular Ecology **18**: 1668-1677.

Baryshnikov, G., (2009). Pleistocene Mustelidae (Carnivora) from Paleolithic site in Kudaro Caves in the Caucasus. Russian Journal Theriology **8**(2): 75-95.

Bonifay, E. (1971). Carnivores quaternaires du sud-est de la France. - Mémoires Museum national histoire naturelle Paris **21**(2): 43-377.

Buskirk, S. W. , Harstad, A. S., Raphael, M. G. & Powell, R. A. (1994): Martens, Sables, and Fishers – Biology and conservation. – 484 pp.; Comstock Publ., Ithaca London.

De Grossi Mazzorin, J. (1995). La fauna rinvenuta nell'area della Meta Sudans nel quadro evolutivo degli animali domestici in Italia. Padusa Quaderni **1**: 309-318.

Del Campana, D. (1954). Carnivori quaternari della tecchia e della caverna di Equi nelle Alpi Apuane

(Mustelidi, Canidi, Felidi). Palaeontographica Italica **44**: 1-43.

Del Cerra, I., Marmi, J., Ferrando, A., Chashchin, P., Taberlet, P. & Bosch, M. (2010). Nuclear and mitochondrial phylogenies provide evidence for four species of Eurasian badgers (Carnivora). - Zoologica Scripta **39**: 415-425.

Engelbrecht, A. (2011). Intraspecific variation between *Crocuta crocuta crocuta* and *Crocuta crocuta spelaea* from Central Europe. - Master Thesis at the University of Vienna, 208 pp.

Fischer, K. (2000). Ein Leoparden-Fund, *Panthera pardus* (L., 1758), aus dem jungpleistozänen Rixdorfer Horizont von Berlin und die Verbreitung des Leoparden im Pleistozän Europas. Mitteilungen Museum Naturkunde Berlin, Geowissenschaften, **3**: 221-227.

Geskos, A. (2013). Past and present distribution of the genus *Capra* in Greece. Acta Theriologica **58**(1): 1-11.

Grupe, G. & Krüger, H. H. (1990). Feeding ecology of the stone and pine marten revealed by element analysis of their skeletons. Science Total Environment **90**: 227-240.

Hemmer, H. (1971). Zur Kenntnis pleistozäner mitteleuropäischer Leoparden (*Panthera pardus).* Neues Jahrbuch Geologie Paläontologie, Abhandlungen . **138**(1): 15-36.

Hemmer, H., Kahlke, R. D. & Vekua, A. K. (2010). *Panthera onca georgica* ssp. Nov. from the Early Pleistocene of Dmanisi (Republic of Georgia) and the phylogeography of jaguars (Mammalia, Carnivora, Felidae). - Neues Jahrbuch Geologie Paläontologie, Abhandlungen **257**(1): 115-127.

Hofreiter, M. & Stuart J. (2009). Ecological Change, Range Fluctuation and Population Dynamics during the Pleistocene. Current Biology **19**: R584-R594.

Honer, O., Holekamp, K. E. & Mills, G. (2008). «*Crocuta crocuta* ». IUCN Red List of Threatened Species. Version 2017. International Union of Conservation of Nature. Retrieved 04 August 2017.

Koenigswald von, W., Nagel, D. & Menger, F. (2006). Ein jungpleistozäner Leopardenkiefer von Geinsheim (nördliche Oberrheinebene, Deutschland) und die stratigraphishe und ökologische Verbreitung von *Panthera pardus*. Neues Jahrbuch für Geologie und Paläontologie 5: 277-297.

Lazaridis, G. (2005). Speleological research in the Loutra Arideas area (Macedonia, Greece). Abhandlungen der Naturhistorischen gesellschaft Nürnberg **43**: 155-162.

Massetti, M. (1995). Quaternary biogeography of the Mustelidae family on the Mediterranean islands. *Hystrix*, the Italian Journal of Mammalogy **7**(1-2): 17-34.

Massetti, M. (2012). Atlas of the terrestrial mammals of the Ionian and Aegean Islands. De Gruyter: 302.

Miracle, P.T. & Brajkovic, D. (2010). The palaeoecological significance of the Pleistocene mammalian fauna from Veternica Cave, Croatia. Revision of the Lagomorpha, Canidae, Mustelidae and Felidae. Geologica Croatica **63**(2): 207-224.

Nagel, D. (1999). *Panthera pardus vraonensis* n. ssp., a new leopard from the Pleistocene of Vraona/Greece. Neues Jahrbuch Geologisch Paläontologische Mitteilungen **3**: 129-150.

Nagel, D., Kavcik-Graumann, N. & Rabeder G. (2017). Subtropical steppe inhabitans in the Late Pleistocene cave faunas of Eastern Middle Europe. In: Abstract volume 23rd ICBS, Slovakia.

Pacher, M. & G. Rabeder (2016). The leopard (*Panthera pardus*), the rare hunter of the Alpine area during the Late Pleistocene. Cranium **33**(1): 42-50.

Papaioannou, H. I. & Kati I. V. (2007). Current status of the Balkan chamois (*Rupicapra rupicapra balcanica*) in Greece: Implications for conservation.- Belgian Journal Zoology, **137**(1): 33-39

Rohland, N., Pollack, J. L., Nagel, D., Beauval, C., Airvaux, J., Pääbo, S. & Hofreiter, M. (2005). The population History of Extant and Extinct Hyenas.- Molecular Biology & Evololution **22**(12): 2435-2443.

Sablin, M. V. & Khlopachev, G. (2002). The Earliest Ice Age Dogs: Evidence from Eliseevichi.- Current Anthropology **43**(5): 795-799.

Schmid, E. (1940). Variationsstatistische Untersuchungen am Gebiß pleistozäner und rezenter Leoparden und anderer Feliden. - Z. Säugetierkd. **15**: 1-179.

Schütt, G. (1969). *Panthera pardus sickenbergi* aus den Maurer Sanden. - Neues Jahrbuch Geologische und Paläontologische Mitteilungen **1969**: 299-310.

Sheng, G.-L., Soubrier, J., Liu, J.-Y., Werdelin, L., Llamas, B., Thomason, V. A., Tuke, J., Wu, L.-J., Hou, X.-D., Chen, Q.-J., Lai, X.-L. & Cooper, A. (2014). Pleistocene Chinese cave hyenas and the recent Eurasian history of the spotted hyena, *Crocuta crocuta*.- Molecular Ecology **23**: 522-533.

Sommer, R. & Benecke, N. (2005). Late-Pleistocene and early Holocene history of canid fauna of Europe (Canidae).- Mammalian Biology – Zeitschrift für Säugetierkunde **70**(4): 227-241.

Sommer, R. S. & Nadachowski, A. (2006). Glacial refugia of mammals in Europe: evidence from fossil records. Mammal Review **36**: 251-265.

Spitzenberger, F. (2001). Die Säugetierfauna Österreichs. – 895 pp.; Grüne Reihe des Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Tsoukala, E. (1992a). Quaternary Faunas of Greece.- Courier Forschungsinstitut Senckenberg **153**: 79-92.

Tsoukala, E. (1992b). The Pleistocene large mammals from the Agios Georgios Cave, Kilkis (Macedonia, N. Greece).- Geobios **25**(3): 415-433.

Tsoukala, E., Rabeder, G. & Verginis, S. (2001). *Ursus spelaeus* and Late Pleistocene associated faunal remains from Loutraki (Pella, Macedonia, Greece). Excavations of 1999. - Cadernos. Laboratoria Xeolóxica de Laxe **26**: 441-446.

Tsoukala, E. & Rabeder, G. (2005). Cave bears and Late Pleistocene associated faunal remains from Loutra Arideas (Pella, Macedonia, Greece). 15 years of research. Naturhistorische Gesellschaft Nürnberg, **45**: 225-236.

Tsoukala, E., Chatzopoulou, K., Rabeder, G., Pappa, S., Nagel, D. & Withalm, G. (2006). Paleontological and stratigraphical research in Loutra Arideas Bear Cave (Almopia Speleopark, Pella,

Macedonia, Greece) .- Scientific Annals, School of Geology Aristotle University of Thessaloniki **98**: 41-67.
Varela, S., Lobo, J. M., Rodriguez, P. & Batra, P. (2010). Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time. - Quaternary Science Review **29**: 2017-2035.
Von den Driesch, A. (1976). Das Vermessen von Tierknochen aus vor- und frühgeschichtlichen Siedlungen.- 114pp.; Institut für Paläoanatomie und Domestikationsforschung Tiermedizin München.
Wolsan, M. (1993). Evolution des carnivores quarternaires en Europe centrale dans leur contexte stratigraphique et paleoclimatique.- L'Anthropologie Paris **97**: 203-222.
Zacharias, N., Kabouroglou, E., Bassiakos, Y. & Michael, C.T. (2008). Dating and analysis of speleosediments from Aridaia at Macedonia, Greece. - Radiation Measurements **43**: 791-796.
Žuravlev, O. P. (1999). Säugetierfauna und Umwelt am Südlichen Bug während der Antike Archäologie in Eurasien **6**: 389-407.

Internet Sources

http://www.arkive.org/pine-marten/martes-martes (retrieved 08.2017).

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| *Mustela nivalis* | specimen | ml | mW |
|---|---|---|---|
| LAC 1290a | p2 | 1.3 | 0.9 |
| mandible fragment sin | p3 | 1.9 | 0.9 |
| | p4 | 2.6 | 1.2 |
| LAC 10524 sin | p3 | broken | |
| mandible fragment | p4 | 1.9 | 0.9 |
| | m1 | 4.8 | 1.4 |

| *Mustela* (*P.*) *putorius* | | ml | mW |
|---|---|---|---|
| LAC 4269 | I3* | 3.3 | 2.1 |
| maxillar fragment dext | Csup | 4.1 | 4.2 |
| | P2 | 2.8 | 1.9 |
| | P3 | 4.5 | 2.5 |
| | P4 | 8.1 | 4.3 |
| | M1 | 3.2 | 6.2 |
| LAC 2906 | i3* | 1.1 | 1.2 |
| manidible fragment sin | cinf | 4.5 | 3.8 |
| | p2 | 2.5 | 1.5 |
| | p3 | 4.6 | 2.0 |
| | p4 | 4.8 | 2.7 |
| | m1 | 8.8 | 5.5 |
| | m2 | 2.6 | 2.1 |
| | p2-m2 | 20.4 | |
| | H below m1 | 8.1 | |
| LAC 4268 | cinf | 4.7 | 3.7 |
| mandible fragment sin | p2 | 2.4 | 2.2 |
| | p3 | 4.0 | 2.5 |
| | p4 | broken | |
| | m1 | 8.8 | 3.3 |
| | m2 | 2.4 | 1.8 |
| | H below m1 | 9.1 | |

| *Martes foina* | | ml | mW |
|---|---|---|---|
| LAC 6938 | M1 | 5.3 | 7.6 |
| LAC 10480 | M1 | 5.2 | 7.7 |
| LAC 14481 | P4 | 9.2 | broken |
| LAC 2892 | p1 | 4,5 | 2,7 |
| mandible fragment sin | p2 | 5,7 | 2,8 |
| | p3 | broken | |
| LAC 3829 | cinf | 3.9 | 3.4 |
| | p1* | 1.3 | 1.5 |
| | p2 | 4.2 | 2.6 |
| | p3 | 5.3 | 2.6 |
| | p4 | 6.0 | 2.8 |
| | m1 | 9.4 | 4.2 |

| *Meles meles* | | ml | mW |
|---|---|---|---|
| LAC 7409 | P2 | 4.4 | 3.1 |
| maxillar fragment sin | P3 | 5.7 | 3.8 |
| | P4 | 8.6 | 7.9 |
| LAC 7646 | I3 | 4.6 | 3.3 |

Tab. 1: Measurements of the Late Pleistocene mustelid remains from Loutra Almopias (Greece). Measurements in mm and as defined in VON DEN DRIESCH (1976); * = measurements taken at the alveoli.

| *Canis lupus* | specimen | mL | mW |
|---|---|---|---|
| LAC 13701 | P4 fragment | 23.8 | 11.8 |
| LAC 3933 | phalange 1 | 35.4 | SD 7.2 |
| LAC 3931 | | 34.8 | SD 6.7 |
| | | | |
| *Vulpes vulpes* | specimen | mL | mW |
| LAC 7646 dext | I3 | 3.7 | 3.0 |
| LAC 3825 dext | Csup | 5.6 | 3.9 |
| LAC 2900 sin | M1 | 9.9 | broken |
| LAC 5719 sin | M2 | 5.6 | 8.4 |
| LAC 2893 sin | cinf | - | 4.0 |
| LAC 2897 dext | m1 | 15.5 | 5.9 |
| LAC 2896 sin | m1 | 15.7 | 5.6 |
| LAC 3827 sin | p2 | 8.0 | 3.2 |
| LAC 4266 dext | p2 | 8.1 | 3.0 |
| LAC 3828 sin | p4 | 8.8 | 4.0 |
| LAC 3826 md sin | p1 | (4.0) | |
| alveoli only | p2 | (7.3) | |
| | p3 | (9.3) | |
| | p4 | (9.9) | |
| LAC 2901+4267 md sin | p4 in crypt | | |
| refitted | m1 | 16.5 | 6.0 |
| | m2 | 7.6 | 5.1 |
| | m3 | in crypt | |

Tab. 2: Measurements of the Late Pleistocene canid remains from Loutra Almopias (Greece). Measurements in mm and as de ined in VON DEN DRIESCH (1976); * = measurements taken at the alveoli.

| *Panthera pardus* | specimen | mL | mW | mH |
|---|---|---|---|---|
| LAC 13268 mx frag. dext. | M1* | 3.1 | 6.9 | |
| | P4* | 23.3 | 12.6 | |
| *measured at the alveolus | P3 | 17.4 | 8.5 | |
| () minmal | P2* | 6.3 | 4.4 | |
| | Csup* | 15.7 | 13.8 | |
| | I3* | 8.5 | 6.2 | |
| | I2* | 6.8 | 3.1 | |
| LAC 9980 dext | Csup | 13.5 | 10.7 | (61.9) |
| LAC 3978 sin | m1 | 19.2 | 8.5 | |
| Postcranial remains | | mL | Lp | Wp |
| LAC 13284 sin | radius | 196 | 24.7 | 16.6 |
| LAC 13530 sin | radius frag. | - | 24.6 | 18.4 |
| | | mL | DPa | DO |
| LAC 8385b sin | ulna | | 35.3 | 30.5 |
| LAC 18779 sin | ulna | | (30.4) | (30.1) |
| | | | Lp | Wp |
| LAC 3913 dext | metatarsale 3 | | 16.0 | 11.5 |
| LAC 4170 dext | phalange 1 | | 35.5 | |
| LAC 2628 | phalange 2 | | 30.2 | |
| LAC 5813 | phalange 2 | | 30.Mai | |

| *Crocuta crocuta* | specimen | mL | mW | mH |
|---|---|---|---|---|
| LAC 9150 sin | Csup | 15.2 | 13.0 | 63.3 |
| LAC 6629 dext. | I1 | 7.4 | 5.2 | |
| LAC 11788 sin | I1 | 7.1 | 5.4 | |
| LAC 6862 sin | I2 | 8.7 | 6.5 | |
| LAC 11823 dext | I3 | 8,9 | 8.0 | |
| LAC 7097 dext | Cinf | 15.7 | 12.9 | 63.5 |
| LAC 8475 dext | p4 | 22.7 | 14.4 | worn |
| Postcranial remains | | mL | Wp | Wd |
| LAC 9172 sin | humerus | - | - | 59.3 x 44.5 |
| LAC 13675 dext. | ulna | - | | |
| LAC 6282 sin | radius | 224.8 | - | 43.7 x 27.3 |
| LAC 7225 dext. | radius | 227.3 | 36.6 x 20.6 | 42.4 x 26.2 |
| LAC 11060 sin | femur | 236.0 | (59.7 x 25.4) | (40.3 x 30.3) |
| LAC 9283 detx. | tibia | 193.3 | - x 57.1 | 34.2 x 26.1 |
| LAC 8179 sin | calcaneus | 61.5 | 27.7 (mW) | |
| LAC 9365 sin | Mc 2 | 79.61 | 15.6 x 19.0 | 16.6 x 16.6 |
| LAC 7047 dext. | Mc 4 | 82.26 | 11.9 x 20.2 | 14.1 x 14.1 |
| LAC 9002 sin | Mc 4 | 82.43 | 10.9 x 18.0 | 13.7 x 17.7 |
| LAC 12632 sin | Mc 5 | 68.83 | 12.2 x 18.6 | 12.7 x 13.1 |
| LAC 13638 dext. | Mc 5 | 68.73 | 12.4 x 18.9 | 12.9 x 13.4 |

Tab. 3: Measurements of the Late Pleistocene felids and *Crocuta crocuta* remains from Loutra Almopias (Greece). Measurements in mm and as defined in VON DEN DRIESCH (1976); * = measurements taken at the alveolie.

**Plate 1**

Fig. 1. *Mustela nivalis* LAC 1290a, left mandible fragment with p2-p4; a – buccal view; b – lingual view.

Fig. 2. *Martes foina* LAC 3829, left mandible fragment with cinf, alveolus of p1, p2-m1; a – buccal view; b – lingual view.

Fig. 3. *Mustela* (*Putorius*) *putorius* LAC 4268, left mandible fragment with root of broken canine, p2, p3, distal part of p4, m1 and m2; a – buccal view; b – lingual view; c – occlusal view.

Fig. 4. *Mustela* (*Putorius*) *putorius* LAC 4269, right maxillar fragment with Csup, P1-P4 and M1; occlusal view.

Fig. 5. *Meles meles* LAC 7409, left maxillar fragment refitted with P3-M1 (alv.); occlusal view.

Fig. 6. *Vulpes vulpes* LAC 2901 and LAC 4267, refitted; left mandible with p4 and m3 still in crypt and m2 not fully erupted; a – buccal view; b – lingual view.

Fig. 7. *Martes martes* LAC 7481, isolated left M1; occlusal view.

Fig. 8. *Panthera pardus* LAC 3978 left m1; a – buccal view; b – lingual view.

Fig. 9. *Crocuta crocuta* LAC 8475 right p4; a – buccal view; b – lingual view.

Fig. 10. *Canis lupus* LAC 13701 right P4 fragment, lingual view.

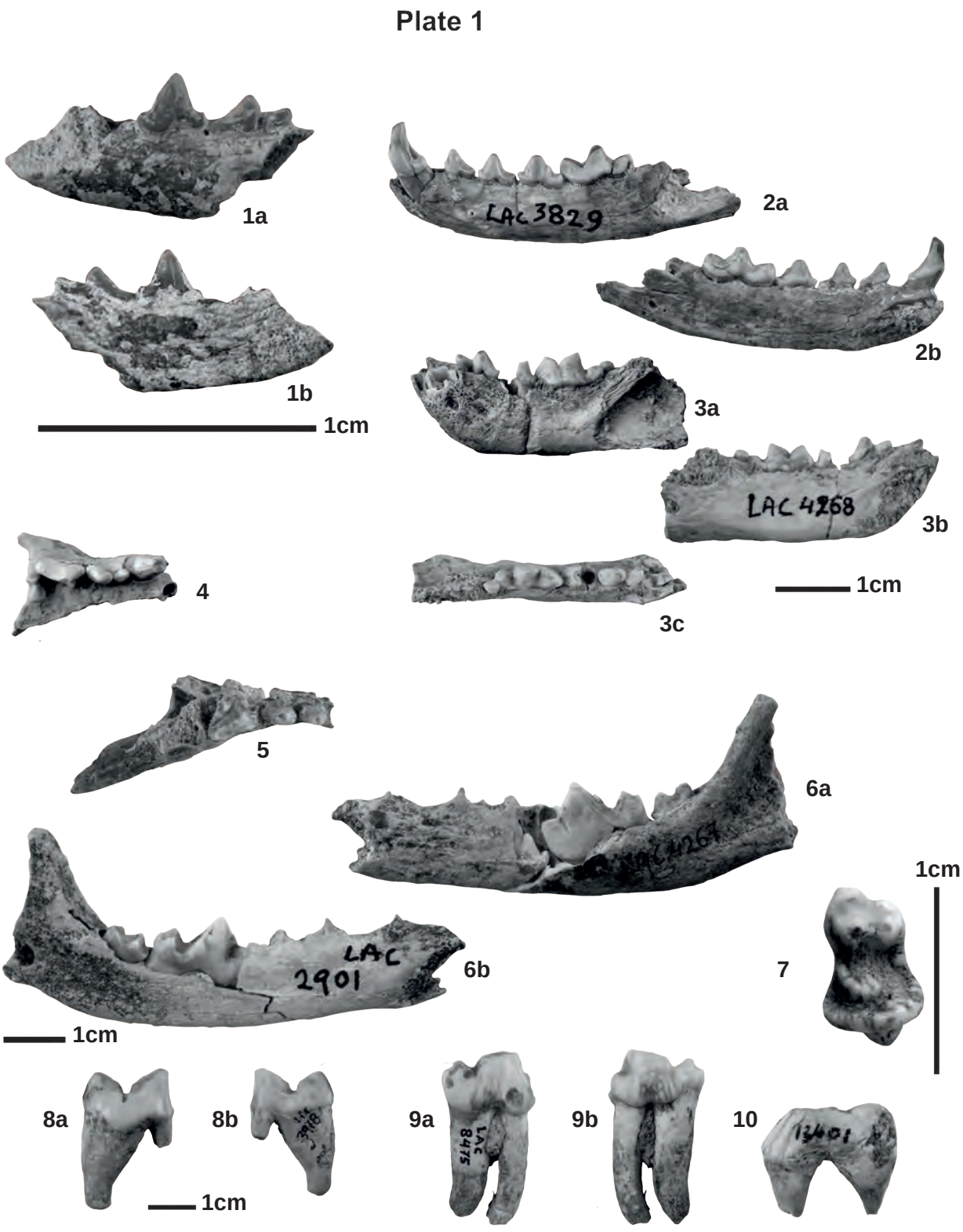
Plate 1
1a
1b
1cm
LAC 3829
2a
2b
3a
LAC 4268
3b
1cm
3c
4
5
6a
LAC
2901
6b
1cm
1cm
7
8a
8b
1cm
9a
LAC
8475
9b
10
13401

**Plate 2**

Fig. 1. *Panthera pardus* LAC 13268 right cranium fragment with P3; a – buccal view; b – lingual view.

Fig. 2. *Crocuta crocuta* LAC 9172 left humerus.

Fig. 3. *Crocuta crocuta* LAC 7225 right radius and LAC 13675 right ulna.

Fig. 4. *Crocuta crocuta* LAC 8179a left calcaneus.

Fig. 5. *Crocuta crocuta* LAC 9283 right tibia.

Fig. 6. Comparison of astragalus of *Rupicapra rupicapra*. 6a - LAC 11800, 6b - PIUW 1882.

Fig. 7. Comparison of middle phalanx of *Rupicapra rupicapra*. 7a - LAC 8796, 7b - PIUW 1773.

Fig. 8. *Crocuta crocuta* LAC 9365 Mc 2, LAC 6274 Mc 3, LAC 7047 Mc4 and LAC 13638 Mc 5; probably from one individual. a – proximal joint facets, b – anterior view.

Scale = 1 cm


Plate 2
1a
1b
2
3
4
5
6 a
6b
7a
7b
8a
8b