Disponible en ligne sur ScienceDirect
www.sciencedirect.com

Elsevier Masson France
EM|consulte
www.em-consulte.com

GEOBIOS

Geobios 43 (2010) 389–402

Original article

New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University☆

Nouvelle analyse des Carnivores pléistocènes dans la Grotte de Petralona (Macédoine, Grèce) dans les collections de l'Université Aristote de Thessalonique

Gennady F. Baryshnikov [a], Evangelia Tsoukala [b,*]

[a] *Zoological Institute, Russian Academy of Science, Universitetskaya nab., 1, 199034 Saint Petersburg, Russia*
[b] *Aristotle University (AUTH), Geology School, 54124 Thessaloniki, Greece*

Received 23 June 2009; accepted 26 January 2010
Available online 31 May 2010

Abstract

New taxonomic study of the ''old collection'' of Carnivora from Petralona Cave, associated to the well-known hominid skull, housed in the Geology School of the Thessaloniki Aristotle University since 1960, revealed 11 species (*Canis arnensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Ursus deningeri*, *U. spelaeus*, *U. arctos*, *Pliocrocuta perrieri*, *Pachycrocuta brevirostris*, *Crocuta crocuta*, *Panthera leo spelaea*, and *Felis silvestris*), which are described in detail. The species composition is typical of the eastern part of the European Mediterranean and may be divided into three biostratigraphic assemblages: early Middle Pleistocene, late Middle Pleistocene and Late Pleistocene.

Keywords: Carnivora; Petralona Cave; Greece; Middle Pleistocene; Late Pleistocene

Résumé

Une révision taxonomique des Carnivores de l'« ancienne collection » de la Grotte de Petralona, qui sont associés au célèbre crâne d'hominidé et conservés depuis 1960 à l'Institut de Géologie de l'Université Aristote de Thessalonique, montre la présence de 11 espèces qui sont étudiées en détail : *Canis arnensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Ursus deningeri*, *U. spelaeus*, *U. arctos*, *Pliocrocuta perrieri, Pachycrocuta brevirostris, Crocuta crocuta*, *Panthera leo spelaea* et *Felis silvestris*. Cet assemblage d'espèces est caractéristique de la partie orientale de l'Europe méditerranéenne. Il peut être subdivisé en trois ensembles biostratigraphiques : Pléistocène moyen ancien, Pléistocène moyen récent et Pléistocène supérieur.

Mots clés : Carnivores ; Grotte de Petralona ; Grèce ; Pléistocène moyen ; Pléistocène supérieur

1. Introduction

Petralona cave developed in Mesozoic (Jurassic) limestone, with rich decoration of reddish speleothemes (showing cave); it has yielded thousands of fossils. It is located very close to Triglia village, the municipal center of this area, in the northwest part of the Chalkidiki Prefecture (Macedonia, N. Greece), SE of and about 50 km from Thessaloniki (Fig. 1). Sediments of Petralona Cave are divided into several stratigraphic levels (Kurtén and Poulianos, 1977, 1981). Their age does not exceed 800,000 years, since Brunhes/Matuyama palaeomagnetic boundary was not found (Papamarinopoulos et al., 1987; M. Taieb, pers. comm.).

The Pleistocene mammalian fauna of Petralona Cave, which is famous owing to finding the preneanderthal hominid skull (Stringer et al., 1979), has been repeatedly studied since 1960. The associated herbivore fauna consists of: *Equus petralo-*

☆ Corresponding editor: Gilles Escarguel.
* Corresponding author.
E-mail address: lilits@geo.auth.gr (E. Tsoukala).

0016-6995/$ – see front matter © 2010 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.geobios.2010.01.003

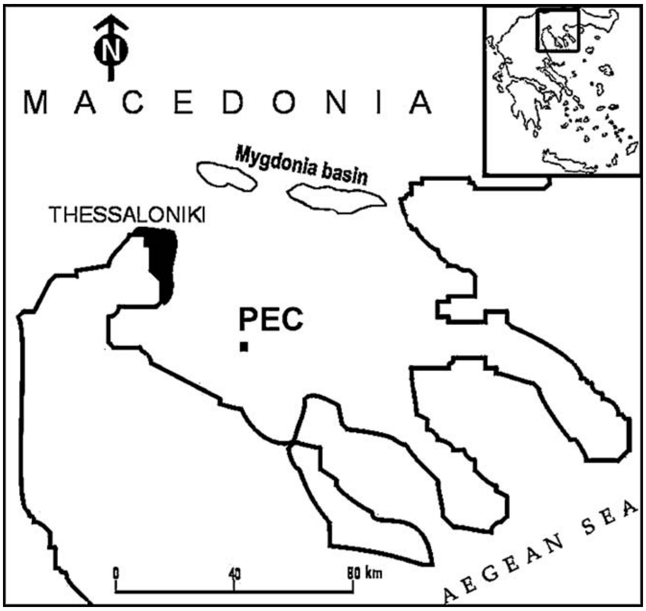

Fig. 1. Map of Greece showing the location of Petralona Cave (PEC).

niensis Tsoukala, 1989; *Equus* sp. (caballoid group); *Dicerorhinus hemitoechus* (Falconer, 1968); *Bos primigenius* Bojanus, 1827; *Bison priscus* Bojanus, 1827; *Capra ibex macedonica* Sickenberg, 1971; *Pliotragus macedonica* Crégut and Tsoukala, 2005; *Praemegaceros* sp.; *Cervus elaphus* Linnaeus, 1758; *Dama dama* (Linnaeus, 1758); *Sus scrofa* ssp. (Kanellis, 1962; Sickenberg, 1964, 1971; Tsoukala, 1989, 1991; Crégut-Bonnoure and Tsoukala, 2005; Pappa et al., 2005; Koufos and Tsoukala, 2007).

The present communication deals with the reexamination of the ''old collection'' (PEC) of Carnivora that is kept in the Geology School of the Thessaloniki Aristotle University. This collection has been provisionally identified by Tsoukala (1989, 1991). Additional material, studied by Sickenberg (1964, 1971) and housed for many years in Hannover (Germany), was returned in Thessaloniki Paleontological Museum and is also included in this study. For comparison, we used fossil material from different Pleistocene localities of Europe and Caucasus. In addition, our results were compared to those obtained earlier for the Carnivora remains from Petralona Cave (Kurtén and Poulianos, 1977, 1981), which comprise the ''new collection'' stored in the Petralona museum.

In the course of the study, we examined collections from following depositories: UCBL, Université Claude Bernard, Lyon 1, Villeurbanne, France; LGQM, Laboratoire de Géologie du Quaternaire, Marseille-Luminy, France; MHNL, Muséum d'Histoire Naturelle, Lyon, France; MNHUB, Museum für Naturkunde, Humbold-Universität zu Berlin, Germany; NHM, Natural History Museum, London, United Kingdom; MNHM, Muséum National d'Histoire Naturelle, Paris, France; NMM, Naturhistorisches Museum, Mainz, Germany; NSMW, Naturwissenschaftliche Sammlung, Museum Wiesbaden, Germany; PEC, School of Geology, Aristotle University, Thessaloniki, Greece; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

2. Systematic Paleontology

Family: CANIDAE Fischer von Waldheim, 1817

Canid remains from Petralona Cave were assigned to *Canis lupus mosbachensis*, *Vulpes praeglacialis*, *Cuon priscus* Thenius, 1954 (Kurtén and Poulianos, 1977, 1981), and *Canis lupus mosbachensis*, *Xenocyon* cf. *lycaonoides* and *Vulpes vulpes* (Tsoukala, 1989, 1991).

Canis arnensis Del Campana, 1913
Figs. 2–4

Material: 3 maxilla frs.: with P4-M1, PEC 100 sin, with M1, M2 PEC 101 sin and with M1 PEC 101 sin; M1 PEC 103 dex; 12 mandible frs. with: p4 PEC 110 dex, m2 PEC 119 dex, p4 fr., m1 PEC 1607 sin, p2-m3 PEC 1608 sin, p3-m3 PEC 1609 sin, p2-m1 PEC 1610 dex, p4-m3 PEC 1611 dex, p2-m1 PEC 1612 dex, p2, m1, m2 PEC 1613 dex, p2-m1 fr. PEC 1614 sin, c1 fr., p4-m2 PEC 1615 sin, p3-m1 PEC 1616 dex; 6m1: PEC 104-107 dex, PEC 108, 117 sin; canines: 3C1 EC 111, 112, 115 sin and 3c1 PEC 113, 114 dex, 116 sin; ulna prox. + dia. PEC 120 sin.

Remarks: A small representative of the genus *Canis,* which had been found in Petralona Cave, was identified as *C. lupus mosbachensis* Soergel, 1928 (Kurtén and Poulianos, 1977, 1981; Tsoukala, 1989, 1991). This small wolf, sometimes assigned to *C. etruscus* F. Major, 1877, is also known from other Middle Pleistocene sites in the southern Europe and Caucasus (Bonifay, 1971; Baryshnikov, 1986). *C. accitanus* from Plio-Pleistocene boundary deposits in Spain is considered to be the smallest *Canis* of the earliest Pleistocene of Europe (Garrido and Arribas, 2008).

Rook and Torre (1996) have demonstrated that these finds from the latest Early and Middle Pleistocene of European Mediterranean, including Petralona Cave, are referred to the coyote-like canid *C. arnensis* Del Campana, 1913, whereas *C. mosbachensis* is confined to the northern part of Europe. In addition, presence of *C. arnensis* in the latest Pliocene-earliest Pleistocene Greek localities (Gerakarou, Mygdonia, Alikes) has been established (Koufos, 1987; Kostopoulos et al., 2002).

The small fossil dog from Petralona Cave has dental characters of the genus *Canis*: M1 with robust hypocone (Fig. 2(a)), m1 with distinct metaconid and pronouncedly developed entoconid, m2 with metaconid, and m3 present (Figs. 2(b–f) and 3(a, b)).

The comparison of the upper tooth row P4-M1 (PEC 100; Fig. 2(a)) from Petralona Cave with that of *C. mosbachensis* from Westbury-sub-Mendip in Great Britain revealed that the P4 of PEC 100 is shorter, whereas M1 is longer and wider than these teeth in *C. mosbachensis* (Table S1). The latter species is also distinguishable by some characters of the lower dentition (Tables S2–S4). In Petralona Cave material, the premolars are shorter and thicker as compared with those of *C. mosbachensis* from Mosbach in Germany and Westbury in England. In addition, the length and width of m1 from Petralona Cave are, on the average, smaller than these parameters in m1 of *C. mosbachensis* (Table S4).

Tooth measurements of the specimens of the small dog from Petralona Cave correspond to those of *C. arnensis* (Kurtén,

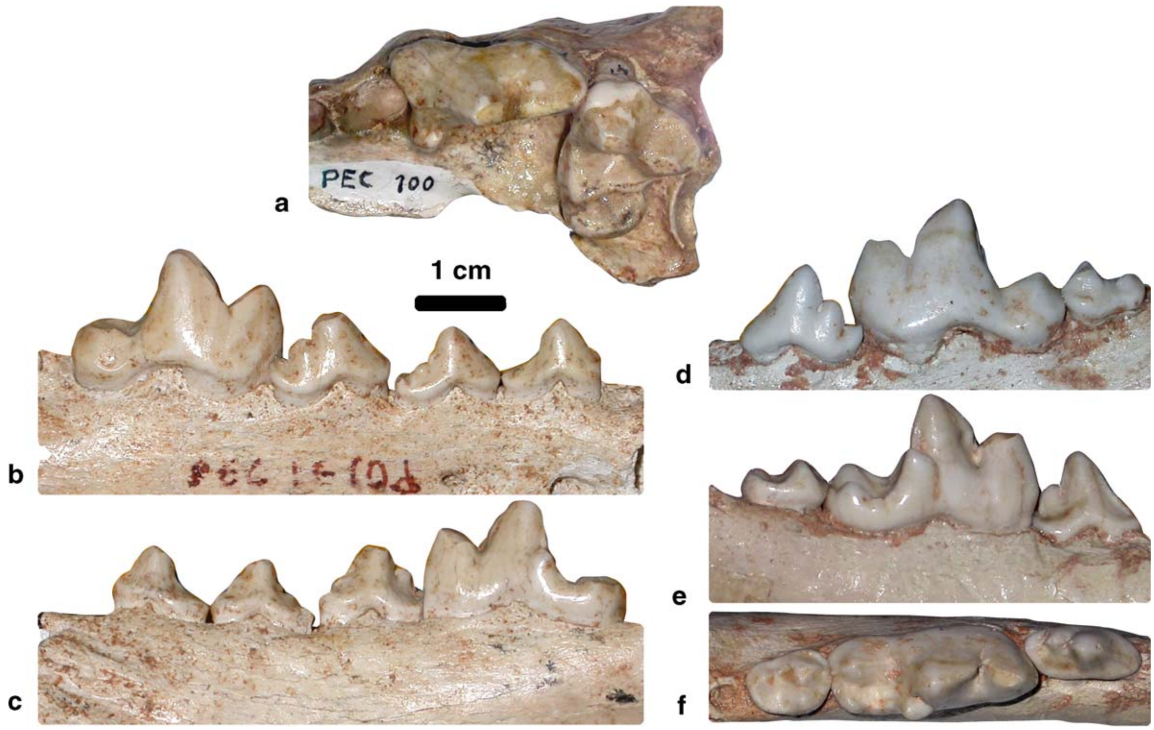

Fig. 2. *Canis arnensis*: upper (**a**) and lower cheek teeth (**b–f**); labial (b, d), lingual (c, e) and occlusal (a, f) views. a, PEC 100, left; b, c, PEC 1610, right; d–f, PEC 1615, left.

1974; Koufos, 1987; Rook and Torre, 1996), which allows its assignment to this species. The analyzed morphometric data also coincide with dimensions of material from Petralona Cave published by Kurtén and Poulianos (1977, 1981). The ratio between the greatest length (m1 talonid length/m1 length) separates the samples of *C. arnensis* from Petralona Cave and *C. mosbachensis* from Mosbach and Westbury in spite of some overlapping (Fig. 4).

The most robust specimen of m1 in the examined material (PEC 117) has greatest length 24.7 mm and width 9.3 mm. With size approaching m1 of *C. mosbachensis*, aforementioned ratio (m1 length/m1 talonid length) is calculated as 31.2%. In the *C. mosbachensis* from Westbury, this index varies from 26.2% to 29.9% for teeth having length from 21.8 mm to 24.0 mm, with only two longer specimens (25.3 mm and 25.4 mm) having this index 32.7% and 33.6%.

The similarity to *C. arnensis* in size and proportion is revealed for two isolated m1 found in the Middle Pleistocene (Acheulean) layer 5 of Kudaro 1 Cave in Caucasus (Table S4). These specimens occupy an intermediate position between the samples of *C. arnensis* and *C. mosbachensis* (Fig. 4). The layer 5 of Kudaro 1 Cave was also found to contain a maxillary fragment, which has

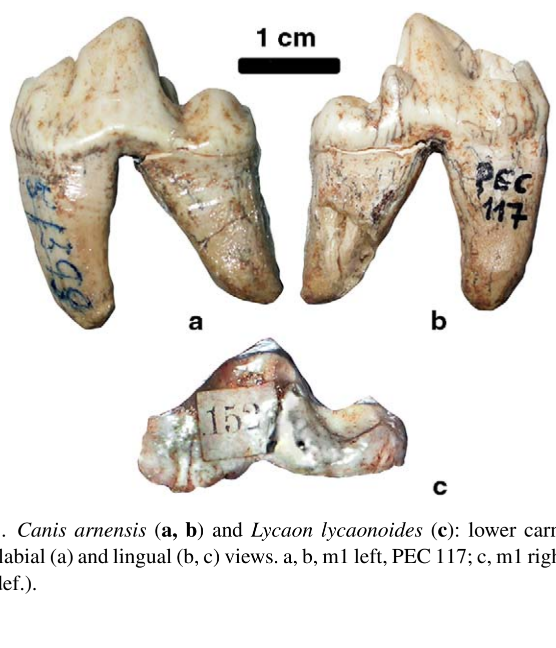

Fig. 3. *Canis arnensis* (**a, b**) and *Lycaon lycaonoides* (**c**): lower carnassials teeth; labial (a) and lingual (b, c) views. a, b, m1 left, PEC 117; c, m1 right, PEC 118 (def.).

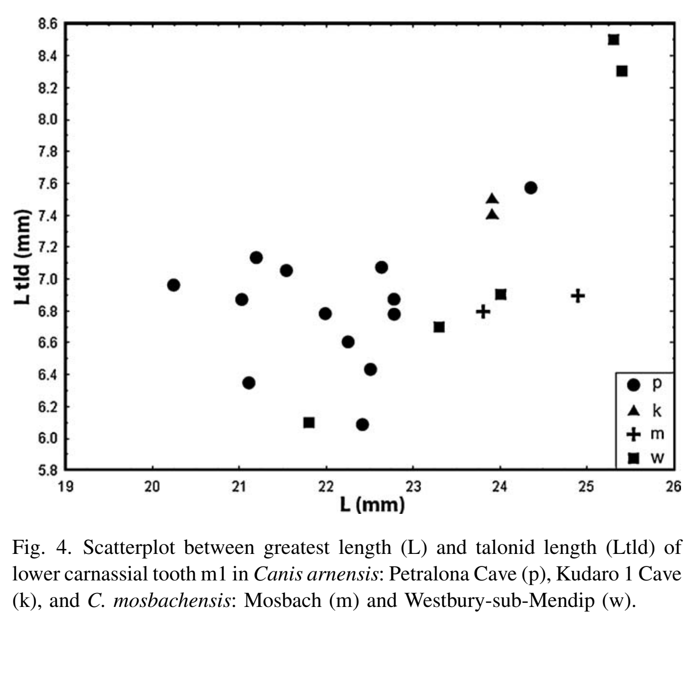

Fig. 4. Scatterplot between greatest length (L) and talonid length (Ltld) of lower carnassial tooth m1 in *Canis arnensis*: Petralona Cave (p), Kudaro 1 Cave (k), and *C. mosbachensis*: Mosbach (m) and Westbury-sub-Mendip (w).

been determined as *Canis* ex gr. *latrans* Say, 1823 (Baryshnikov, 1986). These upper teeth are markedly smaller than those of *C. arnensis* (Table S1). The length of the upper carnassial tooth P4 of the Caucasian canid is similar to *C. accitanus*, the tooth being, however, markedly wider. In the size ratio between P4 and M2 as well as in the premolar proportions, *Canis* ex gr. *latrans* resembles *C. lepophagus* Johnston, 1938 and *C. latrans* from North America (Kurtén, 1974). Presumably, the Caucasian find demonstrates penetration of another species of coyote-like canids to the eastern Mediterranean.

Lycaon lycaonoides (Kretzoi, 1938)
Fig. 3(c)
Material: m1 fr. PEC 118 dex.
Remarks: This species is represented by a fragment of a lower carnassial tooth m1 (PEC 118), which has been previously determined as *Xenocyon* cf. *lycaonoides* (Tsoukala, 1989). Protoconid is very robust, whereas metaconid is reduced and tightly adjoin to protoconid. Talonid is large and almost entirely occupied by the lingually shifted hypoconid. Entoconid is not developed, a small crest being situated at its position, which is extended to the posterior margin of tooth crown (Fig. 3(c)). Measurements of m1 (mm): total width 11.9, length of talonid 7.45, width of talonid 10.0. PEC 118 reveals features characteristic of a hyper carnivore canids, which were repeatedly originated in the different lineages of the family. Recently, the finds of hyper carnivore canids from the Late Pliocene and Early Pleistocene of Eurasia, which were variously identified (*Canis antonii*, *C. falconeri*, *Xenocyon lycaonoides*, *X. rosi*, *Cuon stehlini*), have been referred to the genus *Lycaon* whose the only recent species, *L. pictus* (Temminck, 1820), inhabited in Africa southwards of Sahara (Martínez-Navarro and Rook, 2003). The argument for this view was a lycaon-like morphology: relatively short cranium, hyper carnivorous cheek teeth, presence of the lower molar m3, and absence of a functional articulation surface in Mc II for contact with the Mc I, that suggests a tetradactyl fore limb (Rook, 1994).

In the Early Pleistocene and the beginning of the Middle Pleistocene, *L. lycaonoides* had been widely distributed in Africa as well as throughout Eurasia from Germany to Japan (Martínez-Navarro and Rook, 2003). A fragment of m1 from Petralona Cave corresponds to this species in the structure and dimensions. *L. pictus*, whose the only find outside Africa is from the Middle Pleistocene of Israel (Hayonim Cave; Stiner et al., 2001), possesses a m1 talonid pronouncedly narrower (Martínez-Navarro and Rook, 2003). *Cuon alpinus* (Pallas, 1811), which has been found in the Middle and Late Pleistocene of Europe and Caucasus (Crégut-Bonnoure, 1996), demonstrates smaller size of this tooth as compared to the specimen from Petralona Cave (Baryshnikov, 1996).

We consider juvenile remains from other collection from Petralona Cave, which were determined as *Cuon priscus* by Kurtén and Poulianos (1977, 1981), as belonging to *Lycaon lycaonoides*. This attribution is indirectly confirmed by observation of Kurtén and Poulianos that the examined fragment of the lower molar m2 possesses large protoconid and small metaconid, which is characteristic of *L. lycaonoides*.

Fig. 5. *Vulpes praeglacialis:* right mandible with p4-m3 (PEC 1600), labial view.

Vulpes praeglacialis (Kormos, 1932)
Fig. 5
Material: 4 mandible fr. with p4-m3 PEC 1600 dex, with p2, p3 PEC 1602 sin, with m1, m2 PEC 1602 sin, with all cheek teeth alveoli PEC 1603 dex; 2 canines: c1 PEC 135 dex and PEC 136 sin; humerus dia + distal fr. PEC 130 sin; tibia dia + distal PEC 131 dex; 2 Ph1 PEC 132, 133; Ph2 PEC 134.
Remarks: The fox remains from Petralona Cave have been identified firstly as a new species *Vulpes marinosi* by Sickenberg (1971) and later as *Vulpes praeglacialis* (Kurtén and Poulianos, 1977, 1981) and *V. vulpes* (L., 1758) (Tsoukala, 1989, 1991).

Four mandibles were examined, one of them (PEC 1600) being defined by Sickenberg (1971) as the type specimen of *V. marinosi* (Fig. 5). Two of them possess lower carnassial tooth (Table S5). The length of these m1 (13.9, 14.2 mm) approaches to that (13.7 mm) provided by Kurtén and Poulianos (1981), which makes it possible to attribute foxes from both collections to a single taxon.

The length of m1 in *V. praeglacialis* from Grotte de l'Escale (France) varies from 13.2 to 14.3 mm (Bonifay, 1971). Similar dimensions were established for the teeth of *V. praeglacialis* from Vergranne (France; Bonifay, 1983) and Stránská skála (Czech Republic; Musil, 1972). On the contrary, teeth of *V. vulpes jansoni* from Grotte de l'Escale (Bonifay, 1971) and *V. angustidens* from Stránská skála (Musil, 1972) were found to be markedly larger. The only m1 from Westbury-sub-Mendip in England, which was assigned to *Vulpes* cf. *vulpes* (Bishop, 1982), is longer and narrower than the PEC specimens (Table S5). Few postcranial bones show the rather robust form of this species and are lesser robust than *V. vulpes jansoni* comparing to those of Grotte de l'Escale (Bonifay, 1971; Table S6). Therefore, the fox remains from Petralona Cave may be reliably referred to *V. praeglacialis*.

Family: URSIDAE Fischer von Waldheim, 1817
The osteological material from Petralona Cave has been found earlier to represent several bear species: *Ursus thibetanus mediterraneus* F. Major, 1873, *U. deningeri* (Kurtén and Poulianos, 1977, 1981) and *U. deningeri*, *U. spelaeus* and *U.* cf. *arctos* (Tsoukala, 1989, 1991). The three latter species are present in the examined collection. The decidual teeth are rare

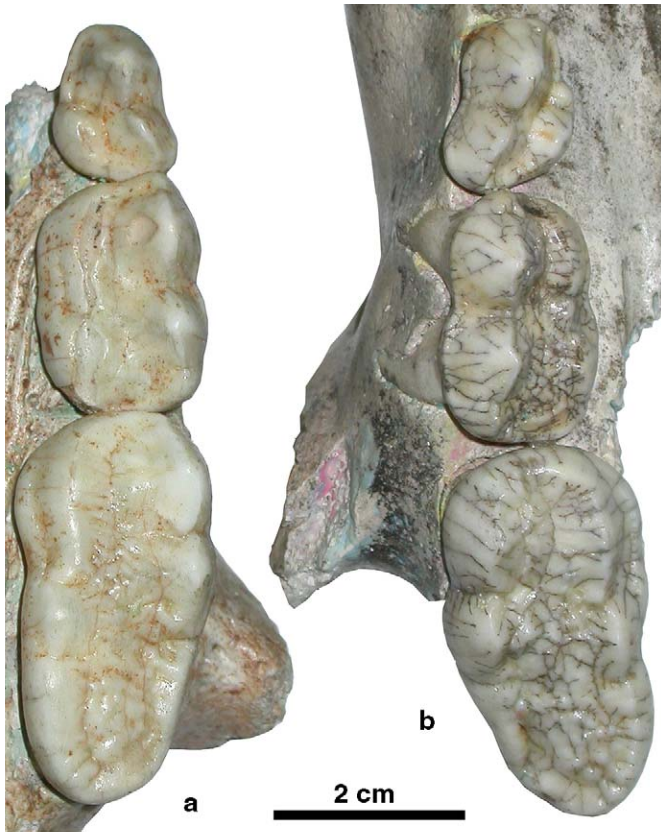

Fig. 6. *U. arctos* (**a**) and *Ursus deningeri* (**b**): upper cheek teeth P4-M2; occlusal view. a, PEC 1191, left; b, PEC 1192, right.

as only mandibles of juveniles are preserved (Pappa et al., 2005).

Ursus deningeri von Reichenau, 1904
Figs. 6–10

Material: Cranium with P4-M2 sin + dex PEC 1002; maxilla fr. with P4-M2 PEC 1192 dex, with M1, M2 PEC 1004 dex, with C1 PEC 1005 dex; 5 I3 PEC 1030, 1033, 1034, 1284 dex, PEC 1218 sin; 2 C1 PEC 1276, 1277 dex; 2 P^4 PEC1217 dex, PEC 1216 sin; 2 M1 PEC 1205, 1206 dex; 6 M2 PEC 1198, 1201, 1203 dex, PEC 1199, 1202, 1204 sin; mandible fr. with c1, p4, m1, m3 PEC 1223 sin, with p4, m2, m3 PEC 1221 sin, 4 with c1 PEC 1226 dex, PEC 1008, 1009, 1220 sin, with p4-m2 PEC 1237 sin; 4 mandible frs. 1229, 1230, 1231, 1234, sin; 6 mandible fr. of juveniles PEC 1238 dex, 1239 sin (with p4), 1232, 1273 dex, 1271, 1272 sin; 4 i3 PEC 1036, 1039, 1042 dex, 1037 sin; 13 c1 PEC 1016, 1017, 1019-1023, 1278-1280, 1282, 1283, 1285, 2 p4 PEC 1241 dex, 1240 sin; 7 m1 PEC 1029, 1046, 1047, 1048 dex, 1030, 1045, 1049 sin; 2 m1 fr. PEC 1245, 1246; 5 m2 PEC 1251, 1253, 1254, 1257 dex, 1260 sin; m2 fr. PEC 1249 dex; 7 m3 PEC 1266-1268 dex, 1269, 1270, 1262, 1263, sin; 2 scapula fr. PEC 1173 dex, 1174 sin; 2 pelvis fr. PEC 1219 dex, 1175 sin; 2 humerus fr. PEC 1169 dex, 1168 sin; femur PEC 1180 dex; femur prox. PEC 1179 dex; femur distal PEC 1184 dex, 1185 sin; radius PEC 1165 sin; radius prox. PEC 1066 sin; ulna PEC 1166 sin; ulna prox. PEC 1062 dex; 2 pisiformes PEC 1071 dex, 1072 sin; 3 Mc1 1077 dex, 1075, 1076 sin; 4 Mc2 1078, 1150 dex, 1152, 1153 sin; 2 Mc3 PEC 1082 dex; 3 Mc4 PEC 1086, 1154 dex, 1084 sin; Mc5 PEC 1157 dex; Mt2 PEC 1151 dex; 2 Mt3 PEC

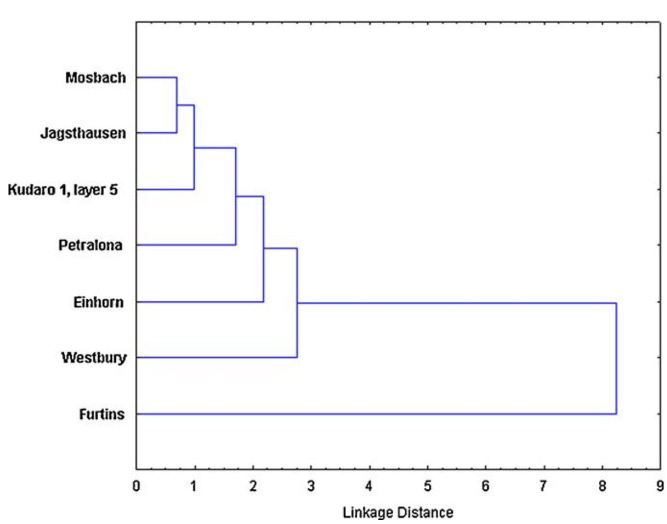

Fig. 7. Hierarchical tree for upper P4 of *Ursus deningeri* according to squared Mahalanobis distances.

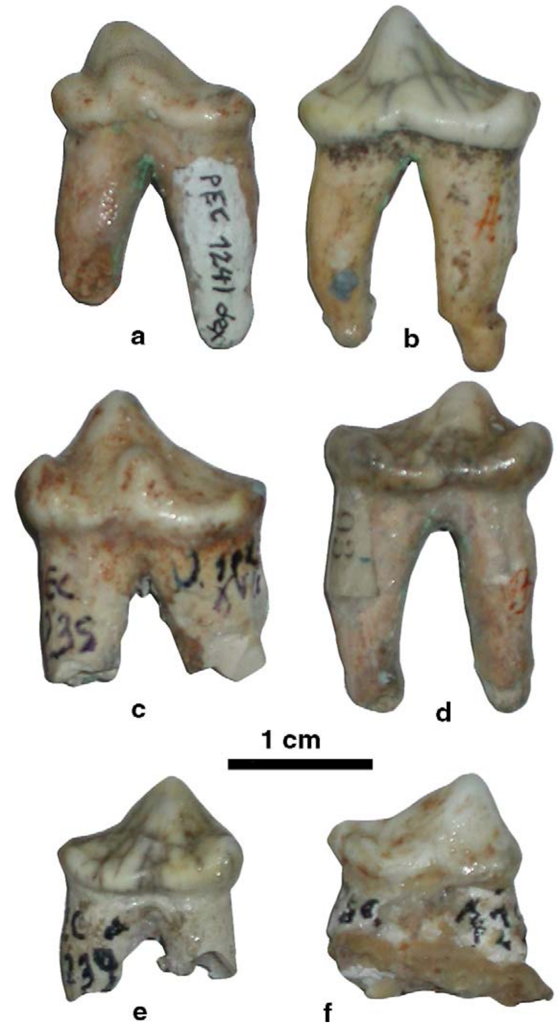

Fig. 8. *Ursus deningeri*: lower premolar p4; lingual view. **a**, PEC 1241, right; **b**, PEC 1248, right; **c**, PEC 1235, right; **d**, PEC 1240, left; **e**, PEC 1239, left; **f**, PEC 1223, left.

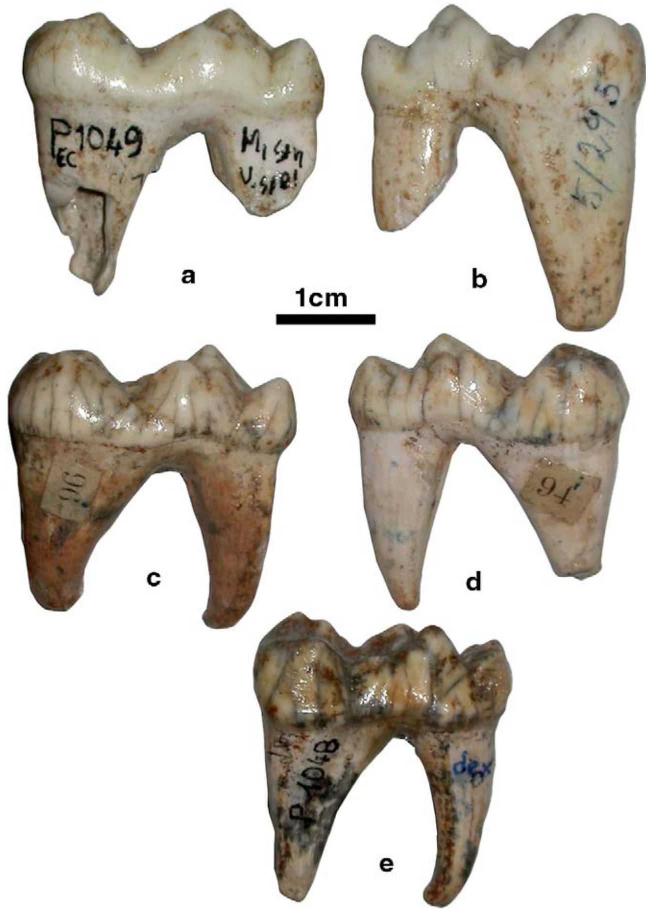

Fig. 9. *Ursus deningeri*: lower molar m1; lingual view. **a**, PEC 1049, left; **b**, PEC 1047, right; **c**, PEC 1045, left; **d**, PEC 1046, right; **e**, PEC 1048, right.

1159, 1160 sin; 4 Mt4 PEC 1095, 1097 dex, 1050, 1094 sin; 2 Mt5 PEC 1099 dex, 1161 sin; 8 Ph1 PEC 1104, 1106, 1108-1111, 1144, 1145; 4 Ph2 PEC 1114, 1116, 1117, 1143; 2 Ph3 PEC 1119, 1121.

Remarks: Previous morphodynamic analysis of some cave-bear cheek teeth belonging to the collection examined in the current study revealed that the cave bear from Petralona Cave occupies an intermediate position between *U. deningeri* and *U. spelaeus*, being closely related to samples from European localities Scharzfeld and Šipka (Rabeder and Tsoukala, 1990). In order to identify the cave-bear cheek teeth in the course of the present study, we added their measurements to the metric data on the tooth samples from various Middle Pleistocene and Late Pleistocene sites of Europe and Caucasus, which have been earlier processed with use of Discriminant Analysis (Baryshnikov, 2006). As a result, most of the cave-bear material from Petralona Cave has been determined as *U. deningeri*. This species comprises a skull of subadult animal (PEC 1002) as well as cranial remains (PEC 1192), which show the length of the cheek tooth row P4-M2 (86.7 mm) markedly shorter than that in *U. spelaeus* (Table S7). Two mandibles (PEC 1220, 1226) are also assigned to *U. deningeri*. In the greatest length and length of the cheek tooth row c1-m3, the latter specimens are smaller when compared to mandibles of *U. spelaeus* (Table S8).

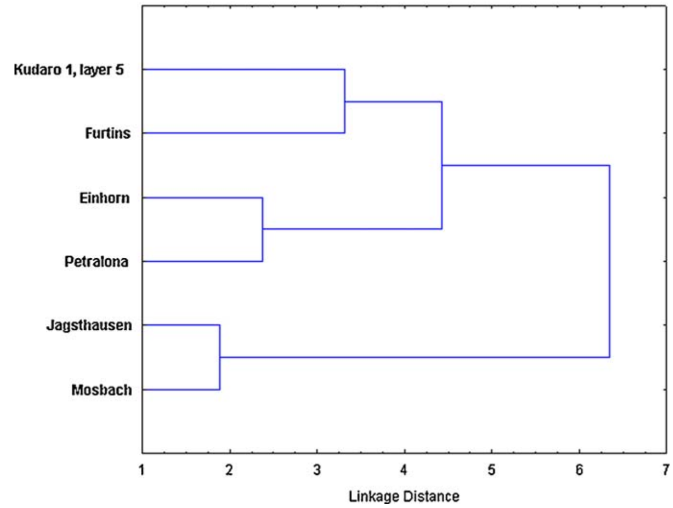

Fig. 10. Hierarchical tree for lower m1 *Ursus deningeri* according to squared Mahalanobis distances.

Twenty-five upper cheek teeth from 37 examined specimens are distributed with the use of Discriminant Analysis within *U. deningeri.* These teeth are found to possess the structure characteristic of this species of cave bears (Fig. 6(b)). Tooth measurements are shown in Tables S9–S11.

We built a dendrogram of similarity for seven samples of the upper carnassial tooth P4 from the European and Caucasian sites (Fig. 7). It was revealed that the teeth from Petralona Cave are grouped together with other collections of *U. deningeri*, but well isolated from the teeth from Les Furtins, which occupy owing to morphometrical characters an intermediate position between *U. deningeri* and *U. spelaeus* (Baryshnikov, 2006); 30 lower cheek teeth from 41 specimens are distributed with the use of Discriminant Analysis within *U. deningeri.* Tooth measurements are shown in Tables S12–S15.

The lower premolar p4 is characterized by divided roots (Fig. 8). Its anterior cusp (paraconid), which demonstrates various degrees of development in various specimens, generally expands beyond the anterior margin of the largest cusp (protoconid) that is characteristic of *U. deningeri*. The lingual cusp (metaconid) is developed, being usually well distanced from paraconid; both cusps, however, may be occasionally crowded.

Metaconid of the lower carnassial tooth m1 often consists of two cusps; rarely a small additional cusp is developed in front of it (Fig. 9). Entoconid is present in a shape of a robust cusp slightly divided into two cusps; occasionally, a small supplementary cusp (entoconulid) is developed before it.

The dendrogram of similarity built on the basis of 6 samples of the lower carnassial tooth m1 revealed a somewhat different distribution of the examined sites when compared to that obtained on the basis of upper carnassial tooth (Fig. 10). The teeth from Petralona Cave are grouped together with teeth from Einhorn, Kudaro 1 and Les Furtins caves, being isolated from samples from older sites of Mosbach and Jagsthausen. The results of morphometrical analysis make it possible to compare *U. deningeri* from Petralona Cave with geologically younger populations of this species in Europe.

The postcranial bones are attributed to the two species mainly according to their morphology (arctoid and speleoid characters; Table S16, measurements according to Tsoukala and Grandal, 2002). Several metacarpals and metatarsals have been also examined. These bones are slightly different in size between *U. deningeri* and *U. spelaeus*, being more robust in the latter species (Bonifay, 1971). Most specimens from Petralona Cave belong to *U. deningeri*, except for three metacarpals possessing more pronouncedly widened diaphysis, which provides a possibility to refer these specimens to *U. spelaeus* (Tables S17 and S18). Metacarpal and metatarsal bones considerably vary in the greatest length, which may be explained by sexual dimorphism of the cave bears. In the examined material of *U. deningeri* from Petralona Cave, males and females occur nearly in equal number.

Ursus spelaeus Rosenmüller, 1794
Fig. 11

Material: Cranium with C1 dex, P4-M2 sin + dex PEC 1000 and hemi mandible with c1, m1, m2 PEC 1003 dex (same individual); cranium fr. with P4-M2 sin + dex (worn) PEC 1001; maxilla fr. with M1, M2 PEC 1193 dex; 3 I3 PEC 1031, 1032, 1035 dex; 4 C1 PEC 1010 dex, 1011, 1012, 1013 sin; 4 P4 PEC 1211 dex, 1213, 1214, 1215 sin; 3 M1 PEC 1207, 1209, 1210 sin; 2 M2 PEC 1195, 1196 dex; mandible fr. with m2 PEC 1024 dex, with p4, m2 PEC 1235 dex, with m2 PEC 1236 dex, 1224 dex (molar worn); c1 PEC 1006 dex; 3 mandible frs. PEC 1225, 1227 dex, PEC 1222 sin; 7 c1 1018, 1281, 1284 dex, 1014, 1015, 1274, 1275 sin; p4 PEC 1248 dex; m1 fr. PEC 1242 dex; 6 m2 PEC 1252, 1256, 1258 dex, PEC 1250, 1255, 1259 sin; 3 m3 PEC 1261 dex, PEC 1264, 1265 sin; 3 scapula fr. PEC 1171 dex, 1170, 1172 sin; 5 pelvis fr. PEC 1065, 1177, 1178 dex, 1066, 1176 sin; humerus PEC 1050 dex; 3 humerus distal PEC 1051, 1052, 1053 dex; femur PEC 1055 sin; 2 femur prox. PEC 1182 dex, 1181 sin; femur distal PEC 1183 sin; 3 radius distal PEC 1063 dex, 1064, 1164 sin; 2 ulnae PEC 1056, 1057 sin; 5 ulna prox. PEC 1059, 1167 dex, 1058, 1060, 1061 sin; 2 ulna distal PEC 1067 dex, 1068 sin; tibia PEC 1190 sin; 5 tibia prox. PEC 1186 dex, 1054, 1187, 1188, 1189 sin; patella PEC 1070 dex; pyramidal PEC 1069 dex; scapholunar PEC 1163 sin; astragalus PEC 1162 sin; 2 Mc2 PEC 1079, 1080 dex; 3 Mc3 PEC 1083, 1154 dex, PEC 1081 sin; 4 Mc4 PEC 1087 dex, PEC 1085, 1086, 1155 sin; 2 Mc5 PEC 1090 dex, PEC 1089 sin; Mt2 PEC 1091 dex; 3 Mt4 PEC 1096 dex, 1092, 1093 sin; Mt5 PEC 1098 sin; 6 Ph1 PEC 1100, 1101, 1102, 1103, 1105, 1107; 5 Ph2 PEC 1112, 1113, 1115, 1118, 1142; Ph3 PEC 1120.

Remarks: *U. spelaeus* is represented by the skull PEC 1000 with markedly worn teeth (Fig. 11) as well as by a cranial fragment with similarly heavily worn teeth. Large dimensions allow their attribution to males. This species is also represented by four mandibles. Skull and mandible measurements (according to Von den Driesch, 1976) are given in Tables S7 and S8.

Scatterplot of canonical scores demonstrates that both skulls from Petralona Cave are distributed among specimens of *U. spelaeus* from European localities. These skulls are placed between samples from Zoolithen Cave in Germany and Il'inka in Ukraine, the difference between them being, however, statistically unreliable (Fig. 12).

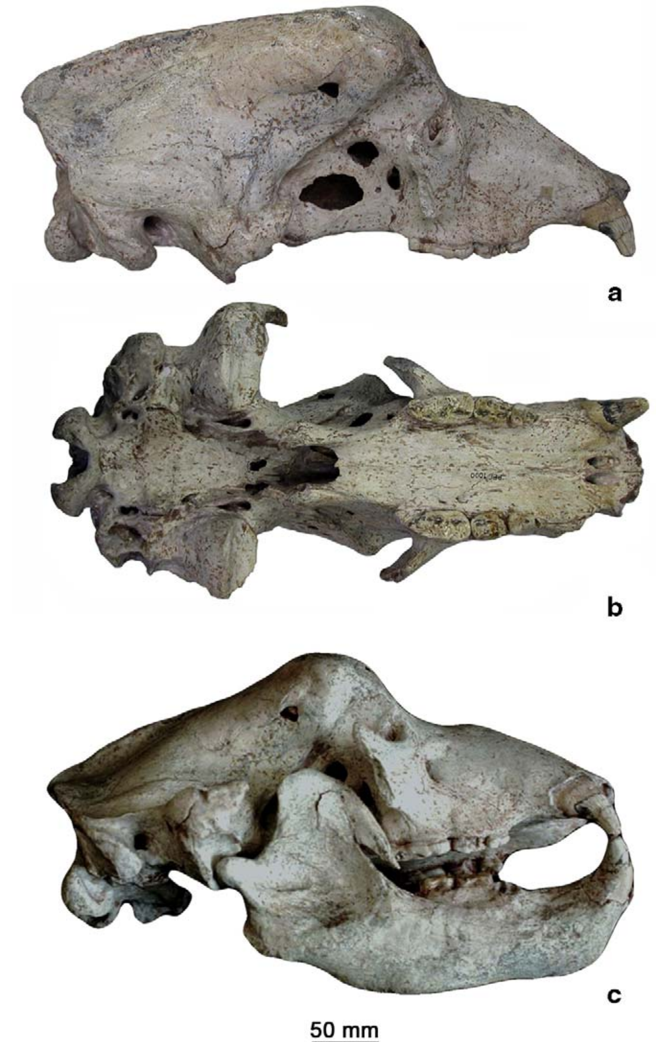

Fig. 11. *Ursus spelaeus*: skull (PEC 1000); lateral (**a**) and ventral (**b**) views and with right mandible (**c**).

In Petralona Cave, only the upper cheek teeth of *U. spelaeus* have been found. Average values of their measurements do not differ from those established for this species in the sites of Western Europe (P4, M2), or slightly smaller (M1) (Baryshnikov, 2006). The available tooth sample is too small for statistical analysis.

The postcranial bones show intense speleoid characters of similar robustness with the cave bear from Macarovec-Jarovec (F.Y.R.O.M.) and Mixnitz, but less robust than the male cave bear from Odessa (Tsoukala, 1989; Table S16).

Ursus arctos Linnaeus, 1758
Fig. 6(a)

Material: 2 maxillary frs. with P4-M2 PEC 1191 sin, and with M1, M2 PEC 1194 dex.

Remarks: In previous studies (Tsoukala, 1989, 1991), two maxillary fragments and few isolated teeth have been referred to *U. arctos*. Despite the morphometrical analysis of the cheek teeth does not separate confidently *U. arctos* from *U. deningeri*,

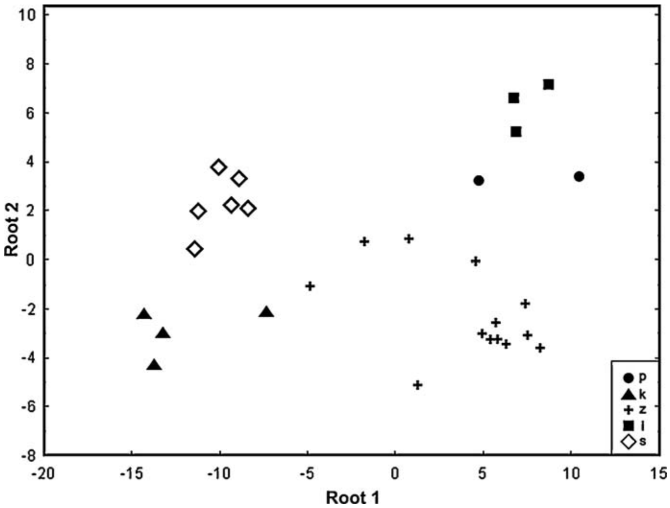

Fig. 12. Scatterplot of canonical scores for male cave bear skulls. *Ursus deningeri*: k, Kudaro 3 Cave (layer 3-4), Caucasus; *U. spelaeus*: i, Il'inka, Ukraina; p, Petralona Cave, Greece; s, Secrets Cave, Urals; z, Zoolithen Cave, Germany.

we assign to *U. arctos* two specimens with P4-M2 (PEC 1191) and with M1-M2 (PEC 1194), most probably of the same individual (Fig. 6(a)). Both specimens are characterized by a short upper tooth row and measurements of P4, M1 and M2 less than minimum parameters of these teeth in *U. deningeri* from Petralona Cave (Tables S7, S9–11).

Measurements (mm): PEC 1191, length C1-M2 ca. 146, length P4-M2 ca. 82.5; PEC 1194, length P4-M2 80.4. In addition, PEC 1194 possesses the alveolus of P3 and P1. Presence of the first premolar P1 is frequent in *U. arctos*, but extremely rare in *U. deningeri*.

Family: HYAENIDAE Gray, 1821

Previous findings of hyena bones and teeth in Petralona Cave belong to the species *Hyaena perrieri* and *Crocuta crocuta* (with 2 subspecies*: C. c. praespelaea* and *C. c. petralonae*; Kurtén and Poulianos, 1981) and to *Pliohyaena perrieri, Crocuta spelaea intermedia* and *Crocuta* sp. (Tsoukala, 1989, 1991). In addition, a tooth fragment assigned to *Hyaena brevirostris* has been recorded (Kurtén and Poulianos, 1977).

The examined collection contains fossil remains of adult animals and cubs. Numerous carnivore coprolites resembling droppings of the recent African *Crocuta crocuta* (see Brain, 1981: fig. 58) are also found (Fig. 13). The presence of hyenas of different individual age as well as their coprolites indicates the use of Petralona Cave as a den by both hyena species.

Pliocrocuta perrieri (Croizet and Jobert, 1828)
Figs. 14–18

Material: Cranium with dC1 sin, D2-D4 sin + dex, P4 dex, M1 sin PEC 28; 2 maxilla frs. with P2-P4 PEC 18 dex, with P1, P2 PEC 20 dex; 3 C1 PEC 40, 41 dex, 36 sin; 2 P3 PEC 27 dex, PEC 29 sin; 3 hemi mandibles with c1-m1 PEC 4, 8 dex, 6 sin; mandible fr. with p3, p4 PEC 45 sin, 2 with m1 PEC 10 dex, 11 sin; c1 PEC 38 sin; 5 p3 PEC 23, 26 dex, 22, 34, 39 sin; 2 mandible frs. with d2-d4, m1 PEC 14 dex and 13 sin; d3 PEC 35 sin; d4 PEC 44 sin; atlas PEC 99; 2 scapula frs. PEC 47 dex, 46

Fig. 13. Hyena coprolites from Petralona Cave.

sin; 2 humerus frs. PEC 88 dex, 89 sin; 2 femori PEC 83, 84 dex; 2 radii PEC 68, 69 sin; ulna prox. PEC 73 dex; 4 tibiae PEC 78, 81 dex, 79, 80 sin; Mt 4 PEC 98 sin.

Remarks: *Pliocrocuta perrieri* and *Crocuta crocuta* are close in size, but carnassial teeth of the first species are markedly shorter (Tables S19 and S20). The upper P4 possesses shorter metastylar blade, whereas the lower m1 has enlarged talonid. The upper P2 in *P. perrieri* is approximately half as long as P4, but in *C. crocuta* it is markedly shorter. In addition, *P. perrieri* possesses a lower carnassial tooth m1 with a well-differentiated metaconid,

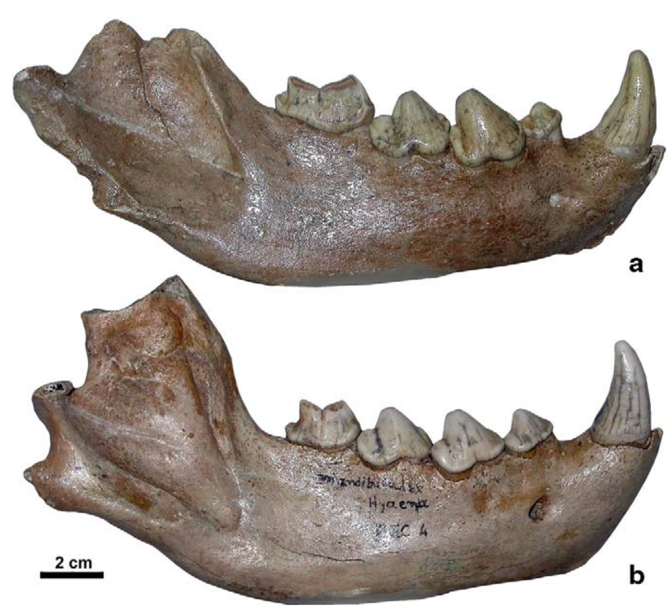

Fig. 14. *Crocuta crocuta* ssp. (**a**) and *Pliocrocuta perrieri* (**b**): right mandibles with c1, p2-m1; labial views. a, PEC 5, b, PEC 4.

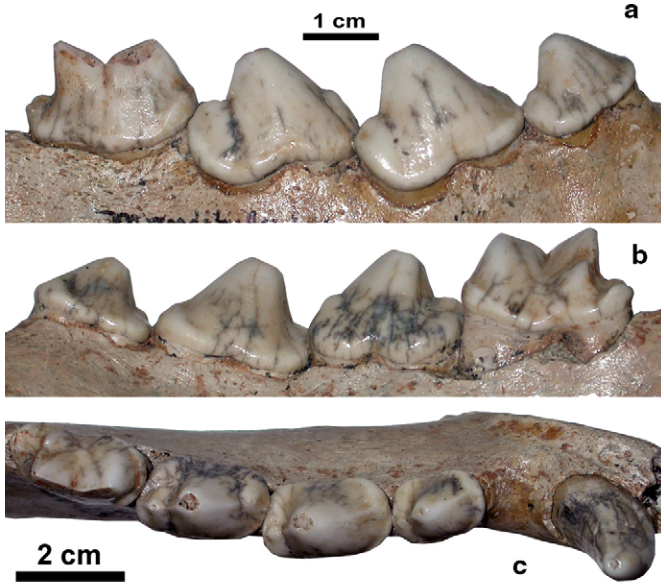

Fig. 15. *Pliocrocuta perrieri*: right lower cheek teeth with p2-m1 (PEC 4); labial (**a**) and lingual (**b**) with the same scale and occlusal (**c**) views.

which is reduced or lost in *C. crocuta* (Figs. 14(a, b) and 15). The dental system of *P. perrieri* is adapted to bone crushing, while in *C. crocuta* it demonstrates reinforcement of trenchant function. Presumably, *P. perrieri* predominantly consumed carrion, whereas *C. crocuta* from the Pleistocene of Europe was not only a scavenger but as well a predator.

In the material examined, *P. perrieri* is represented by two maxillary fragments (PEC 18, 20; Fig. 16(b)), three mandibular fragments (PEC 4, 6, 8), and several isolated teeth (PEC 10, 11, 22, 26). Dimensions of jaws and teeth are similar to specimens found in other Middle Pleistocene European localities (Mosbach, l'Escale, Lunel-Viel; Tables S19 and S20. Lower carnassial tooth m1 with a distinctive metaconid and two talonid cusps (Fig. 15); this tooth structure is regarded to be primitive for this species (Sotnikova, 1989).

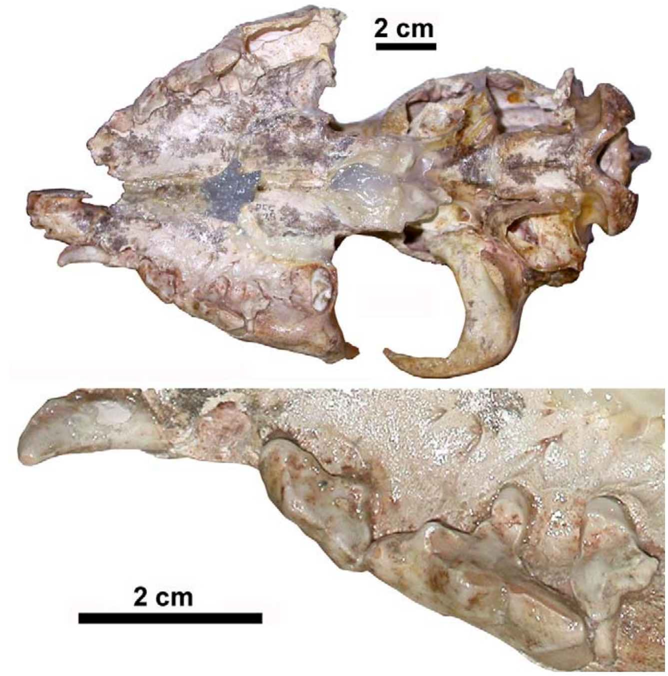

Fig. 17. *Pliocrocuta perrieri*: skull with deciduous teeth and M1 (PEC 28); occlusal view.

There are, as well, bone remains of juveniles with deciduous teeth, including a skull (PEC 28, condylobasal length 191 mm) with erupting P4 (Fig. 17) and three mandibles (PEC 13, 14, 44; Fig. 18). Tooth measurements in cubs from Petralona Cave correspond to those of *P. perrieri* from French sites (Saint-Vallier, Perrier; Tables S21 and S22).

The comparison of deciduous dentition between *P. perrieri* and *C. crocuta* revealed shorter metastylar blade in upper D3, lower d3 not diminished with regard of d4, and d4 with the developed metaconid in the former species (Baryshnikov and Averianov, 1995). Therefore, milk teeth of *P. perrieri* are less modified towards reinforcement of the cutting specialization than in *C. crocuta*, i.e. both species revealed similar evolution of the deciduous and permanent dentition. The presence (*Pliocrocuta*) or absence (*Crocuta*) of the metaconid in the lower carnassials of the Petralona material follows the milk carnassials d4, respectively (Pappa et al., 2005).

The majority of the postcranial remains are well-preserved complete bones, which are more slender than those of *C. crocuta* (Table S23).

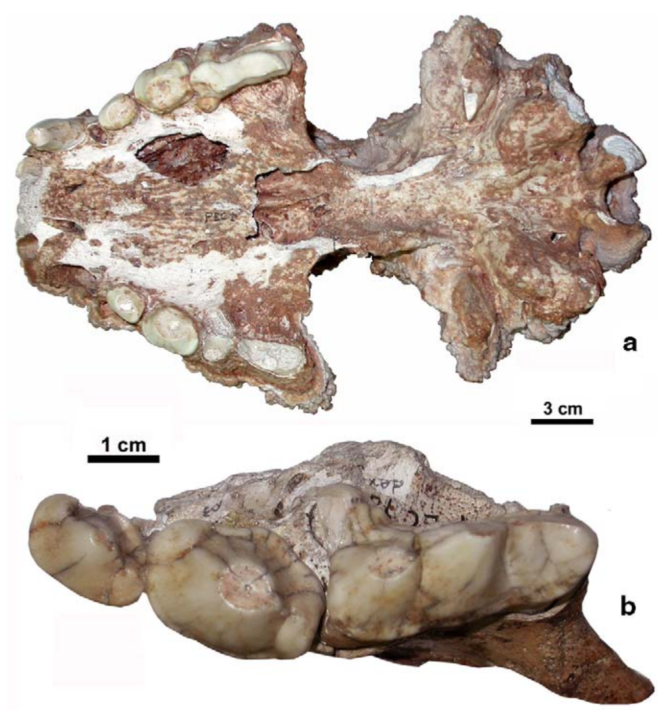

Fig. 16. *Crocuta crocuta* ssp.: skull (**a**) and *Pliocrocuta perrieri*, right upper cheek teeth P2-P4 (**b**); occlusal views. a, PEC 1, b, PEC 18.

Pachycrocuta brevirostris (Aymard, 1846)

Material: Maxilla fr. with: P2-P4 PEC 17 sin.

Remarks: Maxillary fragment with P2-P4 is referred by us to *Pachycrocuta brevirostris*, based on its very robust tooth (Table S19). In the length of the upper carnassial tooth P4, the

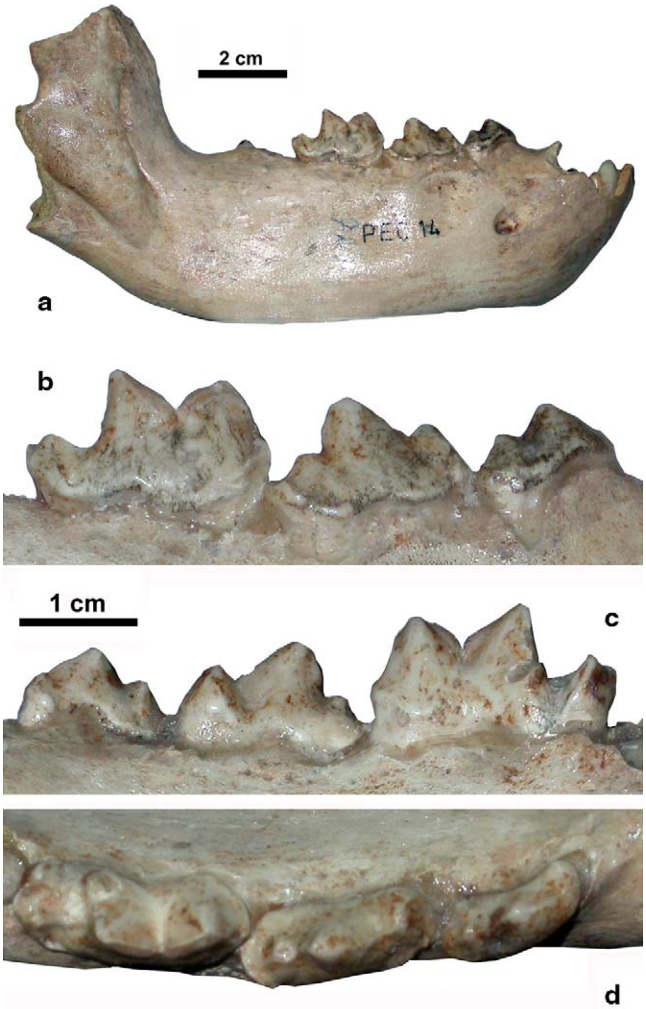

Fig. 18. *Pliocrocuta perrieri*: mandible with deciduous teeth (PEC 14); labial (**a, b**), lingual (**c**) and occlusal (**d**) views.

sample from Petralona Cave markedly exceeds the largest specimens of *Crocuta crocuta praespelaea* from Mosbach and *C. c. spelaea* from different localities of Western Europe, which possess this tooth not longer than 44.2 mm (Schütt, 1971). At the same time, tooth dimensions in PEC 17, compared to those in *P. brevirostris* (Howell and Petter, 1980; Turner and Antón, 1996), are lesser strong in P2, but stronger in P3 and especially in P4.

In Western Europe, the giant hyena is known from many localities of Early and Middle Pleistocene (Venta Micena, Untermassfeld, Stranska Skala, Gombaszoeg, Süssenborn, Westbury-sub-Mendip and others), disappearing approximately 500 kyr B.P. (Turner and Antón, 1996). In N. Greece, the species has been revealed in the Earliest Pleistocene faunas of Libakos, at the end of the Early Pleistocene in the locality of Kalamoto (Mygdonia basin) (Tsoukala and Chatzopoulou, 2005), coexistence of *Pachycrocuta brevirostris* and *Pliocrocuta perrieri* being recorded in the locality of Gerakarou (Kostopoulos et al., 2002).

Crocuta crocuta (Erxleben, 1777)
Figs. 14(a), 16(a) and 20

Material: 1 cranium with C1 sin, P2-P4 sin + dex PEC 1; cranium fr. (occ.) PEC 30; 2 maxilla frs. with P3, P4 PEC 16 dex, 19 sin; 2 C1 PEC 1024, 42 dex; P2 PEC 32 sin; P3 PEC 24 dex; P4 PEC 21 sin; 5 mandible frs. with c1, p2-m1 PEC 2, 5 dex, PEC 7, c1, p2-p4 PEC 3, 9; 2 c1 PEC 97 dex, 95 sin; p4 PEC 32 dex; m1 PEC 12 dex; mandible fr. (juvenile) with d3, d4 PEC 15 dex; 2 scapula frs. PEC 85 dex, 61 sin; 2 humeri PEC 86, 87 dex; femur PEC 82 dex; 5 radii PEC 62, 64, 66, 67 dex, 63 sin; 2 ulnae PEC 70, 71 dex; ulna prox. PEC 72 sin; 4 tibiae PEC 74, 75, 77 dex; 76 sin; scapholunare PEC 60 dex; calcaneus PEC 61 dex; 3 Mc2 PEC 49 dex, 55, 57 sin; 3 Mc3 PEC 52 dex, 48, 50 sin; 2 Mc4 PEC 56 dex, 51 sin; Mc5 PEC 53 sin; Mt3 PEC 58 sin; Mt4 PEC54 sin; 7 Mpp frs. PEC 59 a–g.

Remarks: The Pleistocene cave hyena, which was widely distributed in the Northern Eurasia at that time (Baryshnikov, 1999), is occasionally regarded to be the distinct species *C. spelaea* (Goldfuss, 1823). However mitochondrial DNA data revealed that cave hyena from Eurasia and recent spotted hyena *C. crocuta* from Africa are intermingled in phylogenetic analyses (Rohland et al., 2005). This result questions a taxonomic delineation of the Pleistocene spotted hyenas.

Within the material examined, we referred to this species an almost entire skull (PEC 1; Fig. 16(a)), a cranial fragment (PEC 30) and three mandibles (PEC 5, 7, 9; Fig. 14(a)).

The remains of spotted hyena from Petralona Cave were attributed to two subspecies: *C. c. praespelaea* Schütt, 1971 and *C. c. petralonae* Kurtén, 1977 (Kurtén and Poulianos, 1977, 1981), or has been referred to *C. spelaea intermedia* (de Serres, 1828) (Tsoukala, 1989). Measurements of the examined material (Tables S24 and S25) show that hyena from Petralona Cave is well distinguished from *C. c. petralonae* by narrower upper and lower premolars, differing from *C.* c. *intermedia* by larger size, especially expressed in the palatal breadth and narrow upper premolar P2.

In the morphometric data, the spotted hyena from the examined collection resembles the subspecies *C. c. praespelaea* from the early Middle Pleistocene of Europe; however, the

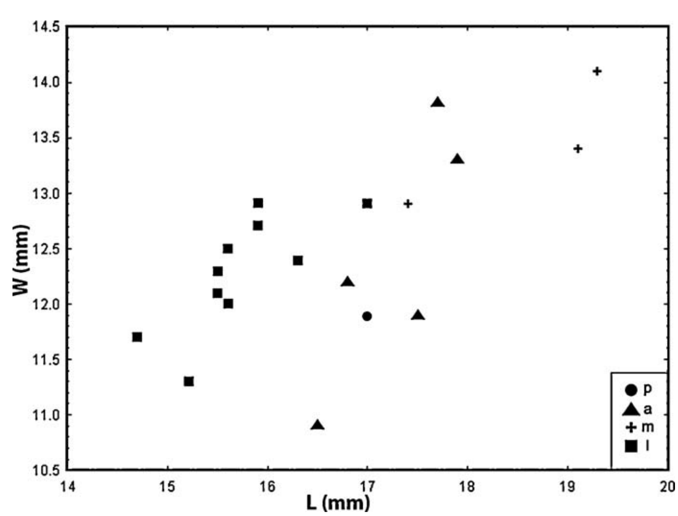

Fig. 19. Scatterplot diagram between length (L) and width (W) of upper premolar P2 in hyenas. *Crocuta crocuta* ssp.: Petralona (p); *C. c. spelaea*: Arcy-sur-Cure (a); *C. c. praespelaea*: Mosbach (m); *C. c. intermedia*: Lunel-Viel (l).

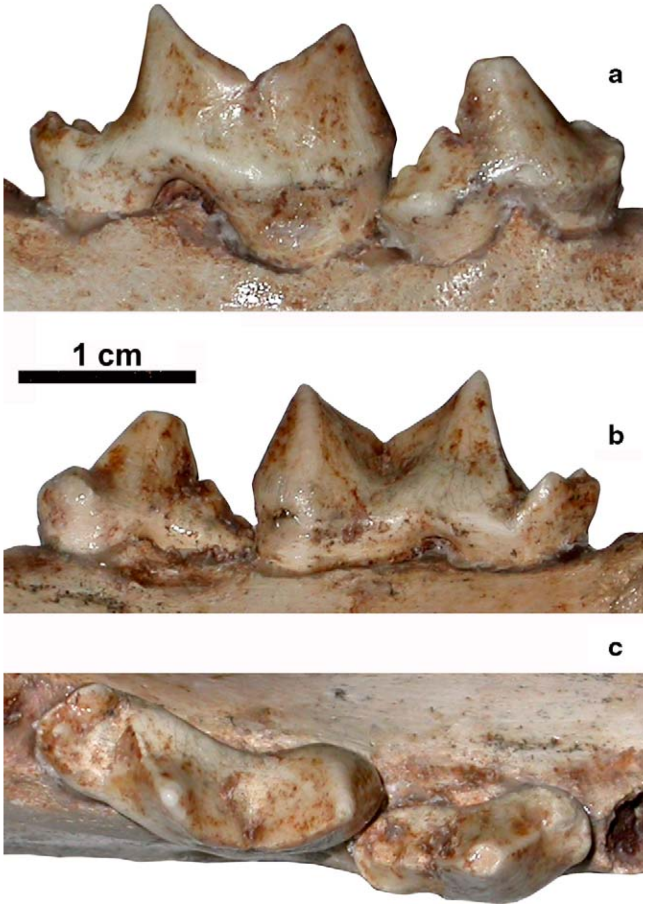

Fig. 20. *Crocuta crocuta* ssp.: right lower deciduous cheek teeth with d3-d4 (PEC 15); labial (**a**), lingual (**b**) and occlusal (**c**) views.

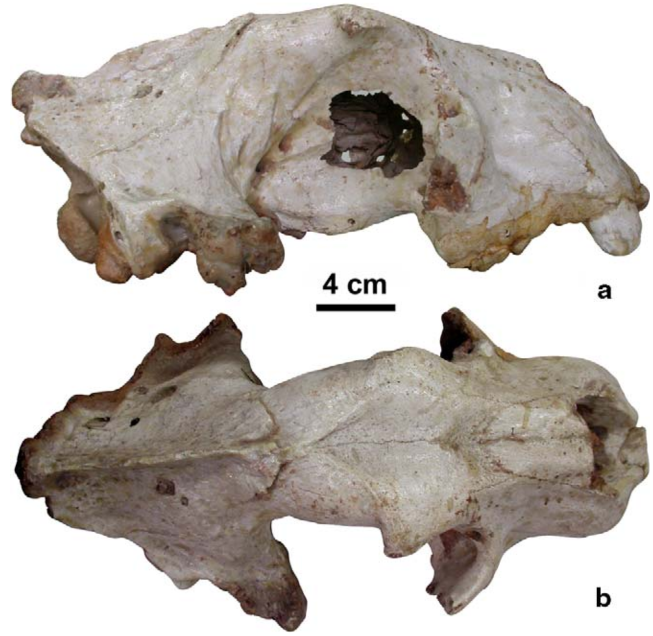

Fig. 21. *Panthera leo spelaea*: skull (PEC 90); lateral (**a**) and dorsal (**b**) views.

only P2 is markedly smaller (Fig. 19), which that relates it with the younger subspecies *C. c. spelaea* occurring in Europe in the late Middle and Late Pleistocene (Baryshnikov, 1999). Therefore, the issue on the subspecies assignment of the hyena under study remains open; we design it as *C. crocuta* ssp.

There is the mandible fragment with deciduous teeth d3 and d4 (PEC 15) in the material examined (Fig. 20). The d4 has no metaconid, but two cusps are developed in talonid, as in *C. c. intermedia* from locality of Lunel-Viel in France (Bonifay, 1971). In the subspecies *C. c. spelaea*, metaconid and talonid cusps of d4 are absent (Baryshnikov and Averianov, 1995). Teeth measurements of PEC 15 are noticeably smaller than those in *C. c. spelaea* found near Bukhtarma River in the eastern Kazakhstan (Table S26), despite these measurements are similar to those of the lower deciduous teeth from Petralona Cave, published earlier (Kurtén and Poulianos, 1981). The majority of the postcranial remains are well preserved complete bones, more robust than those of *P. perrieri* (Tables S27 and S28).

Family: FELIDAE Fischer von Waldheim, 1817

Bone remains of felids from Petralona Cave belong to *Panthera leo spelaea*, *P. gombaszoegensis* Kretzoi, 1938, *P. pardus* (Linnaeus, 1758), *Felis silvestris* and *Homotherium*

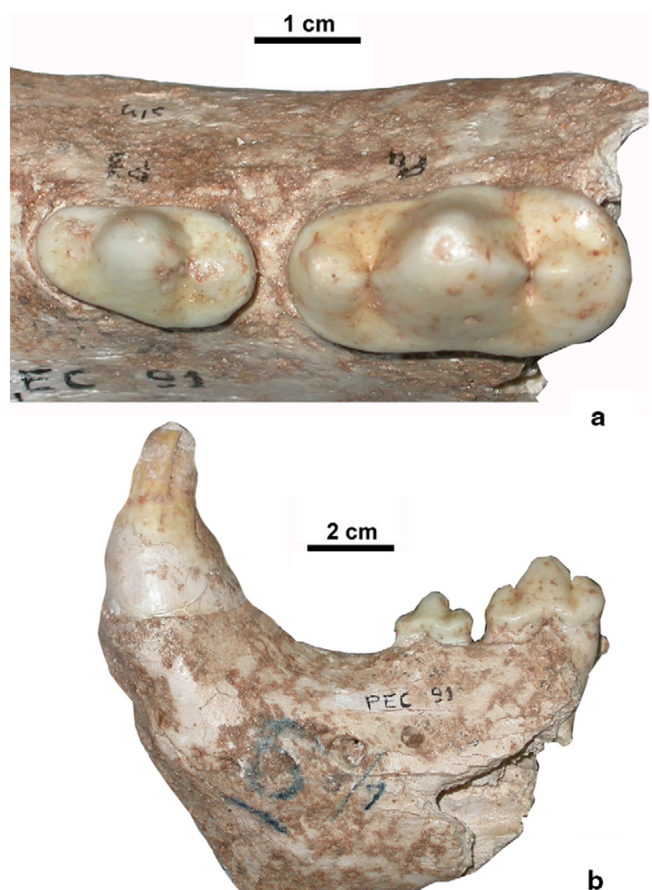

Fig. 22. *Panthera leo spelaea*: left mandible fragment with c1, p3, p4 (PEC 91); occlusal (**a**) and labial (**b**) views.

Fig. 23. *Felis silvestris*: mandible with p3-m1 right (PEC 1604); labial (**a**) and lingual (**b**) views.

sp. (Kurtén and Poulianos, 1977, 1981), and to *Panthera leo spelaea* and *Felis silvestris* (Tsoukala, 1989, 1991). The two latter species are represented in the examined collection.

Panthera leo spelaea (Goldfuss, 1810)
Figs. 21 and 22

Material: Cranium with C1, P3 fr., P4, M1 dex PEC 90; mandible fr. with c1, p3, p4, PEC 91 sin; p4 PEC 92 dex; humerus distal fr. PEC 93 sin; radius PEC 96 sin; calcaneus PEC 94 dex.

Remarks: The cave lion is represented in the examined material by an entire skull (PEC 90; Fig. 21), which may be attributed to a male, owing to its canine size (see Turner, 1984), as well as by a mandible fragment with a canine, p3 and p4 (PEC 91; Fig. 22) and an isolated p4 (PEC 92). Fossil lions from Petralona Cave were assigned to *P. l. fossilis* (von Reichenau, 1906) (Kurtén and Poulianos, 1977, 1981; Schütt and Hemmer, 1978) and *P. l. spelaea* (Goldfuss, 1810) (Tsoukala, 1989, 1991).

By its large size, the skull PEC 90 (Table S29) resembles the lion skull from Azé I.3 in France with the basal length 347.7 mm (OIS 6; Argant, 1991). The latter specimen was referred to *P. l. fossilis* from the Middle Pleistocene of Europe (Sotnikova and Nikolskiy, 2006), which is not accepted by A. Argant (pers. comm.) as *P. l. fossilis* did not lived beyond OIS 9. In *P. l. spelaea* from the Late Pleistocene, the basal length is noticeably smaller, not exceeding 340 mm (Dietrich, 1968; Vereshchagin, 1971). The very robust fossil lion has been found in Mokhnevskaya Cave in Middle Urals (Russia) in the assemblage of thermophilic mammal species, which is dated, most probably, by the latest Interglacial (Baryshnikov, 2002). Its cranial dimensions somewhat exceed those of specimens from Petralona Cave and Azé I.3. Therefore, large size of PEC 90 does not contradict its attribution to *P. l. spelaea*.

The measurements of the lower teeth from Petralona Cave correspond to those in *P. l. fossilis* from the localities of Mosbach and Mauer in Germany (Schütt, 1969). Premolar p3 is more reduced with respect to p4 than in *P. l. spelaea* from Gailenreuth in Germany and Secrets Cave in Ural, Russia (Table S30). Summarizing, our morphometric analysis provides the possibility to refer the fossil lion from Petralona Cave to *P. l. spelaea*. This subspecies occurred in Europe in the late Middle and Late Pleistocene. Analysis of ancient mtDNA revealed a considerable difference between recent lion and cave lion (Barnet et al., 2009), which supports attribution of cave lion to a distinct species.

Few postcranial bones mostly well preserved represent the Petralona lion (Table S31).

Felis silvestris Schreber, 1777
Fig. 23

Material: 2 mandible fr. with p3-m1, PEC 1604 dex, and m1, PEC 1605 dex; 2 canines: C1 PEC 124 dex, c1 PEC 125 dex.

Remarks: The fossil European wild cat is represented by two mandible fragments (PEC 1604, 1605) (Fig. 23). Tooth measurements reveal no difference with those of form *F. silvestris* from the Late Pleistocene Jaurens cave in France (Table S32).

Kurtén and Poulianos (1977, 1981) regarded the wild cat from Petralona Cave to be a separate subspecies *F. s. hamadryas*. The examined specimens possess p4 and m1 shorter than in the holotype of this subspecies. In addition, in the proportions of the p4 crown (ratio between the protoconid length and greatest length), PEC 1604 is distinct from the teeth of *F. s. hamadryas*, being placed among specimens from the Holsteinian localities (see Kurtén and Poulianos, 1977: Fig. 12). Thus morphometric characters relate *F. silvestris* from the collection examined to wild cats from the late Middle and Late Pleistocene of Europe.

3. Conclusions

As a result of our analysis, 11 carnivore species are represented in the collection examined: *Canis arnensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Ursus deningeri*, *U. spelaeus*, *U. arctos*, *Pliocrocuta perrieri*, *Pachycrocuta brevirostris*, *Crocuta crocuta*, *Panthera leo spelaea*, and *Felis silvestris*. This assemblage of Pleistocene species is typical of the eastern part of the European Mediterranean.

The Petralona cave was used as place of inhabitation by carnivores, and not by Man. Except the famous skull, none of the specimens found up to now belongs to hominids. The carnivore inhabitation is proved by:

- the numerous herbivore bone remains (11 species) that were brought into the cave by carnivores, excluding accidental presence;
- the presence of many hyaenid coprolites;
- the presence of many specimens which belong to juvenile and/or very juvenile carnivores.

On some specimens, special breakage, puncture or depressed fractures made mainly by canines of scavengers, as well as incisal gnawing have been observed.

The Petralona ''old collection'' studied here consists of fossils collected from the floor of the cave. The Pleistocene mammal fauna of Petralona Cave contains two biostratigraphic assemblages: one belonging to the early Middle Pleistocene (including species with Villafranchian affinities) and other belonging to the late Middle-Late Pleistocene (Crégut-Bonnoure and Tsoukala, 2005). The assemblages were found mixed together due to the action of flowing water in the cave. The movement of flowing water in the cave in the past can be demonstrated by the scattered skeletons, the numerous isolated teeth or by the rounding and abrasion of bones.

Despite the re-described collection of Carnivora has no stratigraphic context, our data allow the clarification of its geological age. The collection is regarded to contain three biostratigraphic species-groups. The earliest group includes *Canis arnensis*, *Lycaon lycaonoides*, *Vulpes praeglacialis*, *Pliocrocuta perrieri*, and *Pachycrocuta brevirostris*. It belongs to the early Middle Pleistocene. The second group consists of the late Middle Pleistocene species: *Ursus deningeri*, *Crocuta crocuta,* and, possibly, *Panthera leo spelaea* and *Felis silvestris*. The third, Late Pleistocene group is formed by *U. spelaeus* and, probably, *U. arctos*.

Further research in the Petralona cave by international group of specialists and new systematic excavations, since there are still thousands of fossils *in situ*, many of them destroyed, will help us to learn more about the stratigraphy and palaeontology of this important cave.

Acknowledgements

We thank Dr. V. Eisenmann (MNHN), Dr. C. Guérin (UCBL), Dr. J.-P. Brugal (LGQM), Dr. A. Currant (NHM), Dr. W.-D. Heinrich (MNHU), Dr. H. Lutz (NMM), and Dr. M. Apel (NMW) for providing us with the possibility to examine collections. We also thank C. Guérin, A. Argant, A. Averianov and an anonymous reviewer for their very useful comments on the manuscript. Svetlana Baryshnikova and E. Vlachos assisted us in the work with manuscript.

The study of G. Baryshnikov was financially supported by the Russian Foundation for Basic Researches (project no. 09-04-01770-a).

Appendix A. Supplementary data

Supplementary data associated with this article (Tables S1–S32) can be found, in the online version, at doi:10.1016/j.geobios.2010.01.003.

References

Argant, A., 1991. Carnivores quaternaires de Bourgogne. Documents des Laboratoires de Géologie de Lyon 115, 1–301.

Barnett, R., Shapiro, B., Barnes, I., Ho, S.Y.W., Burger, J., Yamaguchi, N., Higham, T., Wheeler, H.T., Rosendahl, W., Sher, A.V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G.F., Martin, L.D., Harington, C.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., 1986. Pleistocene wolves (genus *Canis*) of the Greater Caucasus. Trudy Zoologicheskogo Instituta AN SSSR, Leningrad 149, pp. 33–52 (in Russian, with English summary).

Baryshnikov, G., 1996. The dhole, *Cuon alpinus* (Carnivora, Canidae), from the Upper Pleistocene of the Caucasus. Acta Zoologica Cracoviensia 39, 67–73.

Baryshnikov, G., 1999. Chronological and geographical variability of *Crocuta spelaea* (Carnivora, Hyaenidae) from the Pleistocene of Russia. In: Haynes, G., Klimowicz, J., Reumer, J.W.F. (Eds.), Mammoths and the mammoth fauna: studies of an extinct ecosystem. Deinsea 6, pp. 155–174.

Baryshnikov, G., 2002. The Pleistocene black bear (*Ursus thibetanus*) from the Urals (Russia). Lynx, Praha n.s., 2001, 32, 33–43.

Baryshnikov, G., 2006. Morphometrical variability of check teeth in cave bears. In: Proceedings of the 12th International Cave Bear Symposium, Thessaloniki/Aridea, 2–5 November 2006, Scientific Annals, Geology of School, Aristotle University of Thessaloniki 98, pp. 81–102.

Baryshnikov, G.F., Averianov, A.O., 1995. Deciduous teeth of carnivorous mammals (order Carnivora). Part V. Families Protelidae and Hyaenidae. Trudy Zoologicheskogo Instituta RAN 263, pp. 46–84 (in Russian, with English summary).

Bishop, M.J., 1982. The mammal fauna of the early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset. The Palaeontological Association, London, Special Papers in Palaeontology 28, pp. 1–108.

Bonifay, M.F., 1971. Carnivores quaternaires du Sud-Est de la France. Mémoires du Muséum national d'histoire naturelle, NS, C, 21 (2), 43–377.

Bonifay, M.F., 1983. Les canidés de Vergranne. Annales scientifiques de l'Université de Franche-Comté, Besançon, Géologie, 4e série, 5, 111–123.

Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. The University of Chicago Press, Chicago, 365.

Crégut-Bonnoure, E., 1996. Ordre des carnivores. In: Guérin, C., Patou-Mathis, M. (Eds.), Les Grands Mammifères Plio-pléistocènes d'Europe. Collection Préhistoire. Éditions Masson, Paris, pp. 156–167.

Crégut-Bonnoure, E., Tsoukala, E., 2005. The Pleistocene bovids from the Petralona Cave (Macedonia, Greece): new interpretations and biostratigraphical implications. Quaternaire, h.s. 2, 161–178.

Dietrich, W.O., 1968. Fossile Löwen im europäischen und afrikanischen Pleistozän. Paläontologische Abhandlungen, Abteilung A. Paläozoologie 3, 323–366.

Garrido, G., Arribas, A., 2008. *Canis accitanus* nov. sp. A new small dog (Canidae, Carnivora, Mammalia) from the Fonelas P-1 Plio-Pleistocene site (Guadix basin, Granada, Spain). Geobios 41, 751–761.

Howell, F.C., Petter, G., 1980. The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae). Their relationships with Miocene ictitheres: Palhyaena and Hyaenictitherium. Geobios 13, 579–623.

Kanellis, A., 1962. To Vouno: ''Das Gebirge''. Zeitschrift für Deutschen-Griechische Bergsteiger-Verbandes 91–102.

Kostopoulos, D.S., Vassiliadou, K., Koufos, G.D., 2002. The beginning of Pleistocene in the Balkan area according to the mammal record; palaeozoogeographical approach. Annales Géologiques des Pays Helléniques 39 (A), 253–278.

Koufos, G.D., 1987. *Canis arnensis* Del Campana, 1913 from the Villafranchian (Villanyian) of Macedonia (Greece). Paleontologia i Evolució 21, 3–10.

Koufos, G., Tsoukala, E., 2007. Petralona Cave. Editions Aristotle University, Thessaloniki, pp. 1–134.

Kurtén, B., 1974. A history of coyote-like dogs (Canidae, Mammalia). Acta Zoologica Fennica 140, 1–38.

Kurtén, B., Poulianos, A.N., 1977. New stratigraphic and faunal material from Petralona Cave with special reference to the Carnivora. Anthropos 4, 47–130.

Kurtén, B., Poulianos, A.N., 1981. Fossil Carnivora of Petralona Cave: Status of 1980. Anthropos 8, 9–56.

Martínez-Navarro, B., Rook, L., 2003. Gradual evolution in the African hunting dog lineage: Systematic implications. Comptes Rendus Palevol 2, 695–702.

Musil, R., 1972. Die Caniden der Stránská skála. Anthropos 20, 77–106.

Papamarinopoulos, S., Readman, P.W., Maniatis, Y., Simopoulos, A., 1987. Palaeomagnetic and mineral magnetic studies of sediments from Petralona Cave, Greece. Archaeometry 29, 50–59.

Pappa, S., Tsoukala, E., Lazaridis, G., Rabeder, G., 2005. Milk Teeth of Quaternary Carnivores from Northern Greek Caves, Preliminary Report. In: Ambros, D., Gropp, C., Hilpert, B., Kaulich, B. (Eds.), Neue Forschungen zum Höhlenbären in Europa. Abhandlung Band 45, Naturhistorische Gesellschaft Nürnberg, pp. 169–182.

Rabeder, G., Tsoukala, E., 1990. Morphodynamic analysis of some cave-bear teeth from Petralona Cave (Chalkidiki, N. Greece). Beiträge zur Paläontologie von Österreich 16, 103–109.

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 and Evolution 22, 2435–2443.

Rook, L., 1994. The Plio-Pleistocene Old World *Canis* (*Xenocyon*) ex gr. *falconeri*. Bollettino della Societá Paleontologica Italiana 33, 71–82.

Rook, L., Torre, D., 1996. The latest Villafranchian - early Galerian small dogs of the Mediterranean area. Acta Zoologica Cracoviensia 39, 427–434.

Schütt, G., 1969. Untersuchungen an Gebiss von *Panthera leo fossilis* (v. Reichenau, 1906) und *Panthera leo spelaea* (Goldfuss, 1810). Neues Jahrbuch für Geologie und Paläontologie 134, 192–220.

Schütt, G., 1971. Die Hyänen der Mosbacher Sande (Altpleistozän, Wiesbaden/ Hessen) mit einem Beitrag zur Stammesgeschichte der Gattung Crocuta. Mainzer naturwissenschaftliches Archiv 10, 29–76.

Schütt, G., Hemmer, H., 1978. Zur Evolution des Löwen (*Panthera leo* L.) im europäischen Pleistozän. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 4, 228–255.

Sickenberg, O., 1964. Die Säugetierfauna der Höhle Petralona bei Thessaloniki (Vor. Mit.). Geological and Geophysical Research 9, 1–16.

Sickenberg, O., 1971. Revision der Wirbeltier fauna der Höhle Petralona (Griech. Mazedonien). Annales géologiques des Pays Helléniques 23, 230–264.

Sotnikova, M.V., 1989. Late Pliocene - Early Pleistocene Carnivora: Stratigraphic significance. Trudy Geologicheskogo Instituta AN SSSR, Moscow 440, 1–123 (in Russian).

Sotnikova, M., Nikolskiy, P., 2006. Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters. Quaternary International 142/143, 218–228.

Stiner, M.C., Howell, F.C., Martínez-Navarro, B., Tchernov, E., Bar-Yosef, O., 2001. Outside Africa: Middle Pleistocene *Lycaon* from Hayonim Cave, Israel. Bollettino della Societá Paleontologica Italiana 40, 293–302.

Stringer, C., Howell, F.C., Melentis, J., 1979. The significance of the fossil hominid skull from Petralona, Greece. Journal of Archeological Sciences 6, 235–253.

Tsoukala, E., 1989. Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave, Chalkidiki (N. Greece). Aristotle University of Thessaloniki, School of Geology, Scientific Annals 1, 1–360 (in Greek with English summary).

Tsoukala, E., 1991. Contribution to the study of the Pleistocene fauna of large mammals (Carnivora, Perissodactyla, Artiodactyla) from Petralona Cave, Chalkidiki (N. Greece). Preliminary report. Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences de Paris (2) 312, 331–336.

Tsoukala, E., Chatzopoulou, K., 2005. A New Early Pleistocene (latest Villafranchian) site of large mammals in Kalamoto of the Mygdonia basin (Macedonia, Greece). Preliminary report. Mitteilungen der Kommission für Quartärforschung Österreich Akademie der Wissenschaften 14, 213–233.

Tsoukala, E., Grandal d'Anglade, A., 2002. System of measurements on Ursidae skeleton. In: Proceedings of the International Meeting, Man and Bear, Auberives-en-Royans, 4–6 November 1997, France. ERAUL, Université de Liège 100, pp. 265–287.

Turner, A., 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. Annales Zoologici Fennici 21, 1–8.

Turner, A., Antón, M., 1996. The giant hyena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). Geobios 29, 455–468.

Vereshchagin, N.K., 1971. The cave lions of Holarctics. Trudy Zoologicheskogo Instituta AN SSSR 49, 123–199 (in Russian).

Von den Driesch, A., 1976. A Guide to the Measurement of Animal Bones from Archaeological Sites, 1. Harvard University, Peabody Museum of Archaeology and Ethnology, Peabody Museum Bulletin, pp. 1–136.