

FAUNAL SEQUENCE IN PETRALONA CAVE

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Introduction

In the first description of the fauna of Petralona Cave (Sickenberg 1964) it was tentatively given a late Pleistocene date. However, following the identification of early mid-Pleistocene carnivores (Schütt 1971), the date was revised (Sickenberg 1971). An early date has since been confirmed by study of the large collections excavated during the 1970's (Fortelius and Poulianos 1978, Kretzoi 1977, Kurtén and Poulianos 1977 and in press).

The Carnivora, of which about 1.000 specimens have been available to me, form an important part of the fauna and comprise 15 taxa. Their distribution in the cave sediments makes it possible to distinguish three superposed local faunas. The entire sequence antedates the later mid-Pleistocene and the human skull is associated with the earliest of the 1fs.

Faunal Sequence in Petralona Cave

The 1fs of Petralona Cave, from the oldest to the youngest, are known as the Crenian, Petralonian, and Thermaecian. The distribution of the carnivore taxa within the 1fs is shown in Table 1.

Some of the differences between the lfs concern rare taxa (e.g. *Panthera pardus*, *Felis silvestris* and *Homotherium*) and can be ascribed to changes of sampling. The differences in the composition of the Hyaenidae are, however, diagnostic. On this basis, the lfs may be characterized as follows:

Crenian. Association of *Hyaena perrieri* and *Crocota crocuta praespelaea*. Of these, *H. perrieri* is a Pliocene holdover in Europe, whereas *C. crocuta* is an immigrant with antecedents in India and Africa. Both species are very common in the later Crenian deposits (layers 11-15 or 16) but have not so far been found in the earlier Crenian layers (17-27) from which few fossils are known. A total of 12 carnivore taxa have been identified in the Crenian.

Petralonian (layers 2-9). Association of *Hyaena brevirostris* and *C. c. praespelaea*. Of these, the *Crocota* persists without change from the Crenian and remains common, while *H. brevirostris* is rare. No trace of *H. perrieri* has been found. The total of carnivore taxa in the Petralonian is 12.

Thermaecian. This fauna, restricted to the surface of layer 2 in the cave, is comparatively poor in specimens, yet comprises no less than 6 taxa. The only hyaenid present is *C. crocuta petralonae*, a very large and highly aberrant form.

The most common taxon among Petralonia carnivores is *Ursus deningeri*, which occurs at all levels and exhibits minor changes in the passage from the Crenian to the Petralonian. Another well-represented taxon is *Canis lupus mosbachensis*, in which a gradual size trend can be observed, Petralonian specimens averaging larger than Crenian.

This sequence of three superposed faunas is found in the upper gallery of the cave (e.g. Section A) and in the talus cone formed beneath the original entrance. In the lower gallery, however (including such sites as the Mausoleum, the Outer Mausoleum, and the Mediterranean Hall), only Crenian fauna is found, and this includes surface finds. Thus, the lower gallery was closed off by sedimentation in the Section B area, towards the end of the Crenian, and all the fossil material therein must be referred to the Crenian. This includes "Petralonia Man" from the Mausoleum site.

After the closure of the lower gallery, the upper gallery remained active up to Thermaecian time, when the entrance of the cave was finally closed by the growth of the talus, leaving the Ther-

maecian fossils on the surface of the cave floor. They have subsequently been coated or bedded by dripstone.

Comparison With Other Sites

The carnivore roster from Petralona Cave is characteristic of the early mid-Pleistocene in Europe. Taxa known only from sites of this age are *C. lupus mosbachensis*, *C. priscus*, *V. praeglacialis*, *U. deningeri*, *C. crocuta praespelaea*, and *P. leo fossilis* (and, probably, *F. silvestris hamadryas*). The taxa *H. perrieri*, *H. brevirostris* and *P. gombaszoegensis*, being also present in earlier faunas, give the early mid-Pleistocene as the minimum age. *Meles meles* and *P. pardus*, correspondingly, give the early mid-Pleistocene as the maximum age. Finally, the taxa *U. thibetanus* and *Homotherium* occur in older as well as younger faunas, and *C. crocuta petralonae* is at present unique to Petralona Cave. Thus, all the diagnostic taxa indicate an early mid-Pleistocene age ("Altpleistozän" in the German usage), and no taxon contradicts this dating. This is true for all of the material, from the deepest layers to the surface finds. Thus, the entire active period of the cave falls within the early mid-Pleistocene.

Table 1 lists the distribution of Petralona carnivore taxa at 9 early mid-Pleistocene sites, all of which have *C. lupus mosbachensis* and *U. deningeri*. At three of the sites, *Hyaena perrieri* is present; the remaining six have *H. brevirostris*. I know of no mid-Pleistocene site at which the two species of *Hyaena* occur in association. The evidence from Petralona Cave indicates that the faunas with *Hyaena perrieri* are older, and may be regarded as Crenian equivalents, while those with *H. brevirostris* are younger, and correlatives of the Petralonian. *Crocota crocuta* occurs in both faunas (its absence at some sites, e.g. Mauer and l'Escale, may be accidental, because hyaenids are very rare at both), as in Petralona Cave.

Detailed statistical study of evolving lineages in forms like the wolf and the cave bear, both of which are often represented by large samples, may be used to test these assumptions. I have compared wolf (*C. l. mosbachensis*) data for l'Escale and Westbury with those for Petralona Cave, and found that the l'Escale wolf is closer to the Crenian wolf, whereas the Westbury wolf is closer to the Petralonian wolf. Again, the bear (*U. deningeri*) from Westbury dif-

TABLE
1

Taxon	Petralona lfs			Crenian equivalents			Süssen- born	Kone- prusy	Petralonian equivalents		Vértes- szöllös	Westbury
	C	P	T	Mosbach	l'Escale	Mauer			Stránská skála	Gombaszög		
<i>Canis lupus mosbachensis</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cuon priscus</i>	+	+	+	+	-	-	-	-	+?	-	-	+
<i>Vulpes praeglacialis</i>	+	+	-	-	-	-	-	-	+	-	?	+
<i>Meles meles</i>	+	+	-	+	+	-	-	-	-	+	-	-
<i>Ursus thibetanus</i>	+	+	-	+	-	+	-	+	-	-	-	-
<i>U. deningeri</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hyaena perrieri</i>	+	-	-	+	+	+	-	-	-	-	-	-
<i>H. brevirostris</i>	-	+	-	-	-	-	+	+	+	+	+	+
<i>Crocota crocuta praespelaea</i>	+	+	-	+	-	-	+	-	+	+	-	+
<i>C. c. petralonae</i>	-	-	+	-	-	-	-	-	-	-	-	-
<i>Panthera leo fossilis</i>	+	+	+	+	-	+	-	-	+	-	+?	+
<i>P. gombaszuoensis</i>	+	+	+	-	+	-	+	+	+	+	+	+
<i>P. pardus</i>	+	-	-	+	-	+	-	+	+	+	-	-
<i>Felis silvestris hamadryas</i>	+	+	-	-	-	+?	-	?	+?	?	-	-
<i>Homotherium sp.</i>	-	+	-	+	-	+	+	+	+	+	-	+

fers in some details from the Crenian bear of Petralona Cave, but is close to the Petralonian form. These results support the interpretation suggested here.

No exact equivalent of the apparently short-lived Thermaecian fauna can be identified at present. The taxa are diagnostically early mid-Pleistocene, but the highly derived *C. crocuta petralonae* suggests a somewhat later date than any of the Petralonian equivalents of Table 1, with the possible exceptions of Koneprusy and Vértesszöllös, sites where *Crocuta* has not yet been identified.

Notes on Hyaenid Taxa

Hyaena perrieri Croizet and Jobert. This species, which is closely related to the living *H. brunnea* Thunberg, appeared in Europe at the beginning of the Villafranchian (ca. 3.5 Myr) and persisted to the end of the Crenian, when it became extinct. Its geographic distribution extended through northern Asia to China in the east.

Hyaena brevirostris Aymard. The species is related to *H. perrieri* and may have descended from an early population of the latter. It is known from the Villafranchian of India, Java and China, and spread into Europe in late Villafranchian times; its main distribution, however, is Asiatic. During the Crenian it apparently was locally extinct in Europe, but reappeared in Petralonian times. Its final extinction in Europe may antedate its last known occurrence in Asia, which is at Choukoutien.

Crocuta crocuta (Erzleben). The antecedents of the spotted hyena probably lie with *C. sivalensis* (Falconer and Cautley) of the Indian region, and with related African forms in the Villafranchian. It entered Europe in the Crenian, in the form of an archaic subspecies, *C. c. praespelaea* Schütt, which survived to the late Petralonian. At this time, however, a rapid change seems to have occurred, giving rise to *C. c. petralonae* Kurtén. The highly derived characters of this taxon (which may be a distinct species) make it improbable that it gave rise to later Pleistocene *Crocuta* in Europe, and it may have become extinct during or after Thermaecian times. The species *C. crocuta*, however, was present in Africa, and may have repopulated Europe in the later mid-Pleistocene. It also spread to Asia, appearing in China in Choukoutien times, and ranging also into

Korea and into the Indian region. In Europe, it appeared in faunas usually ascribed to the Holsteinian interglacial. This rather small subspecies, *C. c. intermedia* (De Serres), probably gave rise to the typical cave hyena *C. c. spelaea* (Goldfuss) of the late Pleistocene.

Age of Petralonian Man

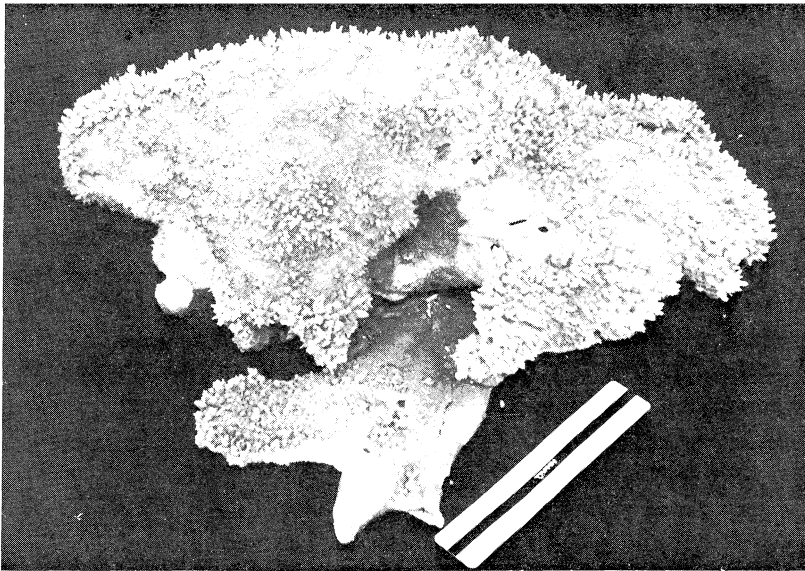
As noted above, the hominid of Petralona Cave is associated with latest Crenian fauna. Unfortunately, no absolute dates of this If or of its equivalents are at present available. However, of the Petralonian equivalents, the Stránska skála If has been dated palaeomagnetically as uppermost Matuyama chron (Kukla 1970), or 0.7 Myr. The age of the Crenian might be of the order of 0.8. Myr.

On the other hand, absolute ages of 0.25 Myr and less have been proposed for Petralona Man (e.g. Hennig et al. 1981). The methods used (amino acid racemization and electron spin resonance studies) are, however, still beset with difficulties, and the resulting ages are certainly much too recent to apply to the associated fauna. The alternative hypothesis that Petralona Man is a more recent intruder, appears highly improbable in view of what is known of the cave and its biostratigraphy. The complete absence of later fauna suggests that there has been no entrance into the cave since Thermaecian times, and none to the lower gallery since late Crenian time. In this connexion it is also worthy of note that the morphology of Petralona Man, while consistent with a Crenian date, would appear anachronistic in the late Pleistocene.

BIBLIOGRAPHY

- Fortelius, M. and N.A. Poulianos, 1978. *Dicerorhinus* cf. *hemitoechus* (Mammalia Perissodactyla) from the middle Pleistocene cave at Petralona - Chalkidiki - North Greece. *Anthropos* 5: 15-43.
- Hennig, G.J., W. Herr, E. Weber, and N.I. Xirotiris, 1981. ESR-dating of the fossil hominid cranium from Petralona Cave, Greece. *Nature* 292: 533-536.
- Kretzoi, M. 1977. The fauna of small vertebrates of the middle Pleistocene at Petralona. *Anthropos* 4: 131-143.
- Kurtén, B. and A.N. Poulianos, 1977. New stratigraphic and faunal mate-

- rial from Petralona Cave, with special reference to the Carnivora. *Anthropos* 4: 47-130.
- Kurtén, B. and A. N. Poulianos. Fossil Carnivora of Petralona Cave: Status of 1980. *Anthropos*, 8, 1981:9-57.
- Poulianos, A. N. 1982. The Cave of the Petralonian Archanthropinae. Athens (in English).
- Schütt, G. 1971. Die Hyänen der Mosbacher Sande (Altpleistozän, Wiesbaden/Hessen) mit einem Beitrag zur Stammesgeschichte der Gattung *Crocuta*. Mainz. *Naturw. Arch.* 10: 29-76.
- Sickenberg, O. 1964. Die Säugetier-Fauna der Höhle Petralona bei Thessaloniki. *Geol. Geophys. Res. Inst. Geol. Athens* 9: 1-16.
- Sickenberg, O. 1971. Revision der Wirbeltierfauna der Höhle Petralona (Griech. Mazedonien). *Ann. Geol. Pays Hellen.* 23: 230-264.



Crocuta crocuta petralonae.