



## PROCAVIIDAE (HYRACOIDEA: MAMMALIA) FROM THE MIDDLE PLEISTOCENE INFILLINGS OF KARAIN CAVE, ANTALYA, TURKEY: BIOGEOGRAPHIC AND PALAEOCLIMATIC IMPLICATIONS

*Procaviidae (Hyracoidea: Mammalia) de los rellenos del Pleistoceno medio de la Cueva de Karain, Antalya, Turquía: implicaciones biogeográficas y paleoclimáticas*

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**Abstract:** Abundant procaviid fossils from archaeological contexts at Karain Cave, Antalya, Turkey, comprise the first record of this extant family of Hyracoidea outside Afro-Arabia. The relatively large body dimensions of the remains, which are attributed to *Procavia capensis* (the rock hyrax) indicate that the climate was relatively cool and humid, more so than the region where the nearest extant neighbours survive, the subspecies *Procavia capensis syriaca*, which is a smaller animal living in Syria, Lebanon, Jordan and Israel.

**Keywords:** Hyracoidea, rock hyrax, Pleistocene, archaeology, palaeoclimate, Karain Cave.

**Resumen:** Abundantes fósiles de procávidos procedentes de los niveles arqueológicos de la cueva Karain, Antalya, Turquía, suministran el primer registro de esta familia actual de Hyracoidea fuera de Afro-Arabia. Las dimensiones corporales relativamente grandes de los restos, que se atribuyen a *Procavia capensis* (damán roquero) indican que el clima era relativamente frío y húmedo, más que en la región donde sobreviven sus vecinos actuales más cercanos, representados por la subespecie *Procavia capensis syriaca*, que es un animal más pequeño que vive en Siria, Líbano, Jordania e Israel.

**Palabras clave:** Hyracoidea, damán roquero, Pleistoceno, arqueología, paleoclima, cueva de Karain.

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## Introduction

Archaeological excavations inside Karain Cave, Antalya, Turkey, have yielded a diverse faunal assemblage associated with a wide range of lithic implements. Among the excavated faunal elements, dentognathic remains of hyracoids are relatively common. The fossils belong to the extant genus *Procavia*, and represent the first record of the family Procaviidae outside Afro-Arabia. The aim of this paper is to put on record the fossil hyraxes from the cave, and to discuss their taxonomic, biogeographic and palaeoclimatic implications.

Procaviidae have been recorded from many sites in Africa (Pickford, 2005) and the Arabian Peninsula where they are generally poorly preserved (Garrod and Bate, 1937) but the family has not been previously reported from Europe or Asia. For this reason, the discovery of abundant, well-preserved fossils of this family in the Pleistocene of Turkey is of exceptional interest as it yields precious evidence concerning dispersal of a tropical African species into the mid-latitudes of Eurasia. The representation of fossils is good enough to remove any doubts about the taxonomy of the species concerned, which is clearly *Procavia capensis*, the extant rock hyrax, but the Karain population shows closer morphometric affinities with extant subspecies of hyraxes from the humid uplands of East Africa, than with the two geographically closer subspecies occurring at present in the Arabian Peninsula, which are smaller and are adapted to generally arid to semi-arid zones.

The associated fauna includes other mammals that originated in Africa, including *Hippopotamus*. The stratigraphic levels from which the Karain hyraxes were excavated also yielded Acheulean stone tools.

## Location, context and faunal association

Karain Cave is located 27 km northwest of Antalya City, Turkey (37°04'40" N, 30°34'15" E) (Fig. 1). Karain Cave is well-known as an important archaeological and tourist destination, having yielded the earliest known Tayacian, Clactonian and Acheulean artefacts (hand axes) from Turkey, as well as remains of Neanderthals associated with skeletal elements of *Hippopotamus*, rhinocerotids and diverse microfaunal and lithic remains (Aydın, 2017). The cave deposits have also yielded abundant fossil reptiles (Zwick and Schleich, 1994) and small mammals (Demirel *et al.*, 2011). Electron Spin Resonance dating was undertaken for Palaeolithic levels within the cave (Rink *et al.*, 1994).



**Fig. 1.-** Location of Karain Cave, Antalya, Mediterranean Region, Turkey.

## Age and context of Karain fossil hyracoids

Karain Lower Palaeolithic levels are divided into 7 different geological units. From youngest to oldest, these levels are referred to as V, V.1, V.1.1, V.1.2, V.2, V.3 and VI. There are 39 different archaeological levels (53 - 91) in these units. The total thickness of the levels that contain the Lower Palaeolithic finds is 3.9 m. The Lower Palaeolithic levels date from about 440-370 Ka BP.

Many of the hyracoid fossils from Karain Cave were collected from geological level V2 (Table 1). Yalçinkaya *et al.* (2009) concluded that « Turkey is an important region which sheltered lower Palaeolithic and upper Palaeolithic populations. It is common to find lower Palaeolithic flakes, worked pebbles and bifaces in Turkey. The latter have been found in stratigraphic context inside Karain E in Antalya. Kilic Kökten had already found Abbevillian, Acheulean and Micoquien bifaces before the 1947 excavations, in 1949 and in 1953. In 2007, a biface on a flake was brought to light in the geological unit V.2 (beneath the Tayacien levels of geological unit V.1) dating to about 400,000 years, if not more ».

In summary, the Karain cave infillings span (with gaps) the period from ca 500,000 years to the present (Otte *et al.*, 1996; Yalçinkaya *et al.*, 2009; Aydın, 2017). The strata have yielded fossils of Neanderthals (Aytekin and Harvati, 2016) as well as archaeological objects of Palaeolithic (Acheulean) cultural affinities (Yalçinkaya *et al.*, 2009). Detailed excavation records indicate that hyrax fossils have been collected from deposits that are associated with these V2 cultural remains of which the age is ca 400 Ka.

## Material and methods

The Inventory Number of the fossils from Karain Cave start with the abbreviation KE (Karain) followed by the year of excavation, the excavation square number and the archaeological and geological layer (Table 1). At Karain, a grid of 1m squares is laid out to facilitate planning. Thus the inventory number «KE 2007 19K/80 V2» should be read as: Excavation season: 2007, square 19K (this is the 19th square), 80: Archaeological level, V2: Geological level.

Catalogue	Morphology	Measurement
KE 2007 19K/180 V2	P1/-P4/ length	21.4
	M1/-M3/ length	22.6
	Depth mandible at m/1	21.5
KE 2013	p/1-p/4 length	20.9
118/78-86 V3	m/1-m/3 length	21.6
	diastema left length	4.0
	diastema right length	3.8
KE 2005	p/1-p/4 length	18.1
15J/84 V2	m/1-m/3 length	20.6
	diastema length	4.0
KE 2011	m/1-m/3 length	23.7
115/83 V3		

**Table 1.** Measurements (in mm) of dentognathic variables of hyraxes from Karain Cave, Turkey.

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth	Distal breadth	Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
KE 2012 J15/91 V1	I1/ male	5.5	5.6	5.5	<b>KE 2013</b> <b>I18/78-86 V3</b>	p/1 rt	3.7	2.7
KE 2014 I14/91 V1	I1/ male	5.7	5	5.4	<b>KE 2013</b> <b>I18/78-86 V3</b>	p/2 rt	5.5	3.5
KE 2014 I14/91 V1	I1/ male	5.8	6	5.6	KE 2014 I15/91 V1	p/2 rt	5	3.4
KE 2014 I19/91 V1	I1/ female	5.1	5.1	4.3	<b>KE 2013</b> <b>I18/78-86 V3</b>	p/3 rt	6.1	4.4
KE 2007 K19/81 V2	I1/ male	5.5	5.5	4.1	KE 2014 I15/91 V1	p/3 rt	5.6	4.2
KE 2014 I15/91 V1	I1/ male	6.5	6.3	6.6	<b>KE 2007</b> <b>K19/81 V2</b>	p/3 rt	6.1	4.1
KE 2014 I15/91 V1	I1/ male	5.7	5.7	6.5	KE 2011 I15/83 V3	p/3 lt	5.6	4.3
KE 2014 I15/91 V1	I1/ male	5.8	5.9	5.6	<b>KE 2013</b> <b>I18/78-86 V3</b>	p/4 rt	7	5.3
KE 2014 I15/91 V1	I1/ male	6.1	5.2	6.4	KE 2011 I15/83 V3	p/4 rt	7	5
KE 2011 I16/84 V3	I1/ male	6	6.1	5.7	KE 2006 J17/82 V3	p/4 rt	7.3	5.1
KE 2012 J16/81 V1	I1/ male	6.2	6.2	6.4	KE 2006 16J/82 V2	p/4 rt	6.9	4.8
KE 2011 I14/83 V3	P2/ rt	4.9	4.3		KE 2007 K19/81 V2	p/4 rt	6.5	4.3
<b>KE 2007</b> <b>19K/80 V2</b>	P3/ rt	5.5	5.4		KE 2006 16J/82 V2	m/1 rt	7	4.6
<b>KE 2007</b> <b>19K/80 V2</b>	P4/ rt	7.3	6.7		<b>KE 2012</b> <b>J16/90 V1</b>	m/1 lt	7.6	4.7
<b>KE 2011</b> <b>I16/84 V3</b>	P4/ rt	6	5.4		KE 2007 K19/81 V2	m/1 rt	6.8	4.5
<b>KE 2007</b> <b>19K/80 V2</b>	M1/ rt	7.6	7.7		KE 2006 16J/82 V2	m/1 lt	7.3	4.6
<b>KE 2011</b> <b>I16/84 V3</b>	M1/ rt	6.6	6.4		KE 2007 K19/79 V2	m/1 rt	7	4.6
KE 2007 19K/80 V2	M1/ rt	7.1	7.7		KE 2006 J17/82 V3	m/1 rt	6.4	4.8
KE 2011 F17/82 V3	M2/ lt	8	7.8		KE 2011 I15/83 V3	m/1 rt	7	4.5
<b>KE 2007</b> <b>19K/80 V2</b>	M2/ rt	8.2	7.9		<b>KE 2013</b> <b>I18/78-86 V3</b>	m/1 rt	6.8	4.5
KE 2012 J16/81 V1	M2/ rt	8	7.9		<b>KE 2012</b> <b>J16/90 V1</b>	m/2 lt	7.8	5.1
KE 2007 19K/80 V2	M2/ rt	8.1	8.4		KE 2007 K19/79 V2	m/2 rt	7.5	5
<b>KE 2011</b> <b>I16/84 V3</b>	M2/ rt	7	7.2		KE 2011 I15/83 V3	m/2 rt	7.6	4.8
<b>KE 2011</b> <b>I16/84 V3</b>	M3/ rt	7.3	7.6		KE 2007 K19/81 V2	m/2 rt	7.6	5.1
KE 2014 I19/91 V1	M3/ rt	9	8.5		<b>KE 2013</b> <b>I18/78-86 V3</b>	m/2 rt	7.4	5
<b>KE 2007</b> <b>19K/80 V2</b>	M3/ rt	8.9	8.4		KE 2012 J16/81 V1	m/2 lt	8.1	5.3
<b>KE 2013</b> <b>I18/78-86 V3</b>	i/1 rt	3.1	3.7		KE 2014 I15/91 V1	m/3 rt	7.2	5.1
<b>KE 2013</b> <b>I18/78-86 V3</b>	i/1 lt	3.3	3.4		KE 2014 I15/91 V1	m/3 lt	8.7	5.2
KE 2007 19K/80 V2	i/2 lt	5	3.6		<b>KE 2012</b> <b>J16/90 V1</b>	m/3 lt	8	5.3
KE 2014 I16/91 V1	i/2 rt	5	2.8		<b>KE 2007</b> <b>K19/81 V2</b>	m/3 rt	7.1	5.1
<b>KE 2013</b> <b>I18/78-86 V3</b>	i/2 rt	3.8	3.5		<b>KE 2013</b> <b>I18/78-86 V3</b>	m/3 rt	7.7	5
KE 2014 I15/91 V1	di/2 rt	4	2.5		KE 2011 I15/83 V3	m/3 rt root	8	5

**Table 2.** Measurements (in mm) of teeth of *Procapia capensis* from Karain Cave, Turkey (d - deciduous tooth, lt - left, rt - right). In **bold** are teeth in maxillae and mandibles (see text for more explanation of the abbreviations).

The fossils described in this paper are listed in the tables of measurements (Tables 1, 2). Upper teeth are in capital letters (I, C, P, M = Incisor, Canine, Premolar, Molar, respectively) and lower teeth are in lower case letters (i, c, p, m). The meristic position is above a forward slash (/) which represents the occlusal plane. Thus M1/ is an upper first molar and p/4 is a lower fourth premolar.

The differentiation of the genera *Procavia*, *Heterohyrax* and *Dendrohyrax* from each other follows the method of Pickford (2005) which is based on the pioneering work of Hahn (1934). Determination of the sex of upper incisors is based on the method employed by Churcher (1956). Deciduous incisors are distinguished from permanent incisors by their smaller dimensions and by the presence of thinner enamel than the permanent counterparts. Measurements were taken with sliding calipers to the nearest tenth of a mm.

Images were captured with a Sony Cybershot digital camera and were treated using Photoshop Elements15 to remove unwanted background and to increase contrast. Scales were added manually.

#### Systematic Palaeontology

Order Hyracoidea Huxley, 1869

Family Procaviidae Thomas, 1892

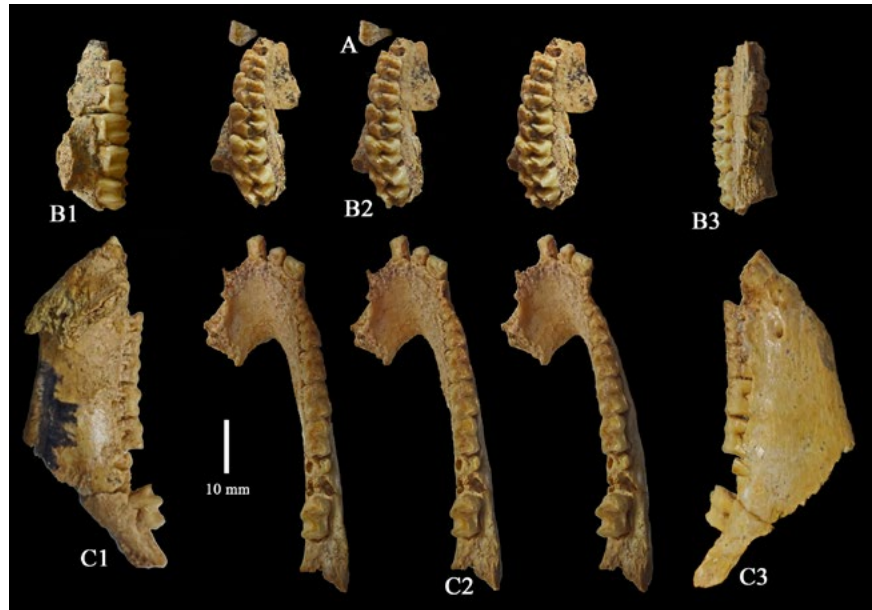
Genus *Procavia* Storr, 1780

Species *Procavia capensis* (Pallas, 1766)

**Material from Karain Cave, Turkey:** mandibles, maxillae and isolated teeth (see Figs. 2-9; Tables 1, 2)

#### Descriptions

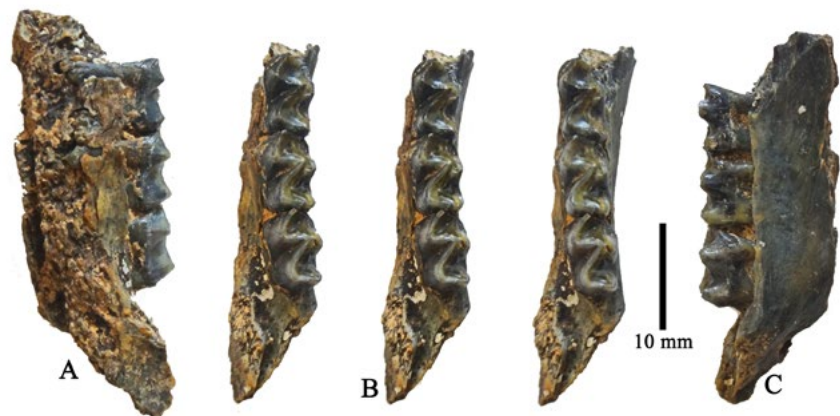
The dentognathic remains from Karain are typical of the genus *Procavia*. The upper central incisor is a tusk-like, ever-growing tooth, triangular in section with shallow sulci on the mesial and distal surfaces (Fig. 8). The lower second incisors are hypsodont, labio-lingually compressed, with three terminal pectinations (Fig. 9). The incisors are separated from the cheek teeth by diastemata (Figs. 2, 3). The



**Fig. 2.-** *Procavia capensis* from Karain Cave, Turkey. A) KE 2011 I 14/83 V3, isolated right P2/ stereo occlusal view; B - KE 2007 19 K /80 V2, right maxilla containing P3/-M3/ (B1 - buccal, B2 - stereo occlusal, B3 - lingual views); C) KE 2013 I 18/78-86 V3, right mandible with symphysis (C1 - lingual, C2 - stereo occlusal, C3 - buccal views).



**Fig. 3.-** *Procavia capensis* from Karain Cave, Turkey. KE 2005 15J 84 V2, right mandible containing p/2-p/3 and m/3 (A - lingual, B - stereo occlusal, C - buccal views).



**Fig. 4.-** KE 2012 J 16/90 V1, left mandible of *Procavia capensis* containing m/1-m/3 from Karain Cave, Turkey (A - buccal, B - stereo occlusal, C - lingual views).

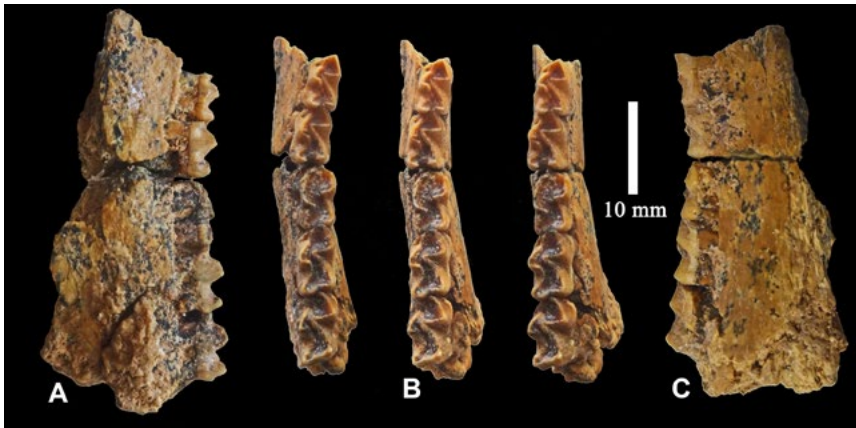


Fig. 5.- KE 2007 K 19/81 V2, right mandible of *Procavia capensis* containing p/3-m/3 from Karain Cave, Turkey (A - lingual, B - stereo occlusal, C - buccal views).

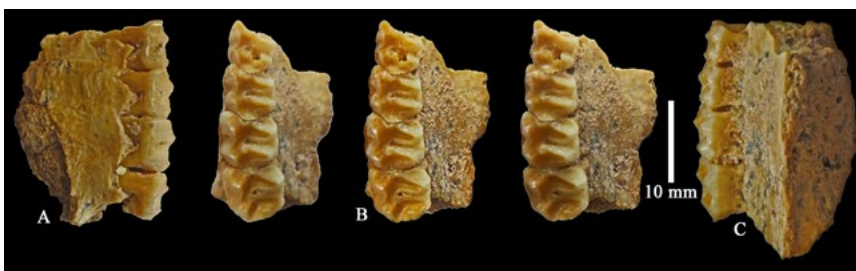


Fig. 6.- KE 2011 I 16/84 V3, right maxilla of *Procavia capensis* from Karain Cave, Turkey (A - buccal, B - stereo occlusal, C - lingual views).

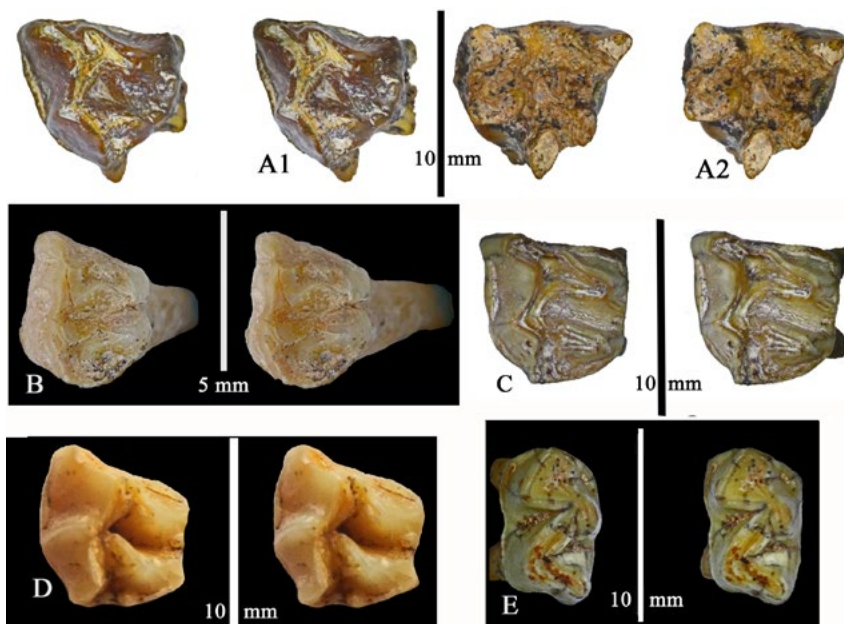


Fig. 7.- Stereo views of isolated upper (A-D) and lower (E) cheek teeth of *Procavia capensis* from Karain Cave, Turkey. A) KE 2014, I 19/91 VI, right M3/ (A1 - occlusal, A2 - radicular view to show roots); B-E) stereo occlusal views of B) KE 2011 I 14/83 V3, right P2/; C) KE 2012 J16/81 VI, right M2/; D) KE 2007 19K/80 V2, right upper molar; E) KE 2012 J16/81 VI, left m/2.

upper premolars are molariform and are in contact with each other. The upper molars have tall, but not very prominent parastyles and mesostyles and weak metastyles, the ensemble comprising an undulating ectoloph (Figs. 2, 6, 7). The protocone and hypocone have prominent precristae that are directed mesio-buccally towards the paracone

and metacone respectively. There is a well-developed mesial cingulum and a variable buccal cingulum. The molars are semi-hypsodont and develop roots.

The lower cheek teeth are formed of two crescents (Figs. 2-5) and the lower third molar does not have a hypoconulid. The lower cheek teeth have a mesio-buccal cingulum. The lower premolars and molars have four roots each.

## Discussion

The fossil hyrax remains from Karain Cave appear to represent but a single species. The proportions of the molar row to the length of the diastema, to the depth of the mandible and to the length of the premolar row, all indicate affinities with the extant rock hyrax (*Procavia capensis*) and exclude appurtenance to the genera *Heterohyrax* or *Dendrohyrax* (Pickford, 2005) (Figs. 10-13). Detailed examination of the teeth and radicular system accord with this identification.

## Taxonomy

At the genus rank, classification of the extant hyracoids is reasonably stable, with most authors accepting the presence of three genera, *Procavia* (Rock Hyrax), *Dendrohyrax* (Tree Hyrax) and *Heterohyrax* (Bush Hyrax) (Hahn, 1934). The literature reveals, however, that at the species and subspecies rank, there is little agreement between authors. Kingdon (2003) for example, listed five species of *Procavia* (*P. capensis*, *P. habessinica*, *P. johnstoni*, *P. welwitschii* and *P. ruficeps*), whereas Dorst and Dandelot (1970) and Olds and Shoshani (1982) combined all five into a single species *Procavia capensis*. At the subspecies level, there is a great deal of fluidity in the quantity of taxa accepted. Over 40 subspecies have been named of which 17 were considered to be valid by Olds and Shoshani (1982) (Fig. 14). Kingdon (2003) considered that five of these subspecies deserve recognition as full species. Bloomer (2009) and Maswanganye *et al.* (2017) go further, and on the basis of molecular data, suggest that, currently, hyrax diversity is woefully underestimated.

From the point of view of crano-dental dimensions and proportions, the fossil hyrax remains from Karain are clearly attributable to *Procavia*, rather than to *Heterohyrax* or *Dendrohyrax* (Figs 10-13). We accept that there is currently a single extant species of the genus, *Procavia capensis*, and that the Karain fossils belong to this taxon. However, determining the subspecies of the Karain remains is delicate, in that their dimensions agree most closely to high-altitude (higher than 1,200 metres), equatorial African populations included in *P. c. capillosa*, *P. c. mackinderi*, *P. c. jacksoni*, *P. c. matschiei* and *P. c. johnstoni*, which live in relatively humid, coolish, upland habitats, rather than the geographically closer subspecies *P. c. syriaca*, *P. c. jayakari* and *P. c. ruficeps* which are adapted to more arid, generally warmer conditions (Fig. 14). For this reason, we leave the subspecies identification open, but this does not detract from the zoogeographic interest of the Karain population, which lies well outside the present-day range of the species.

#### Palaeoecological and palaeoclimatic considerations

The extant hyrax populations living closest to Karain comprise *Procavia capensis syriaca* with populations some 600 km to the southeast in Syria/Lebanon/Jordan/Israel. Overall, this subspecies is smaller in body size than the Karain population, as is the other, even smaller-bodied subspecies from the Arabian Peninsula, *Procavia capensis jayakari* in Yemen and Oman (Dhofar) (Figs. 10-13).

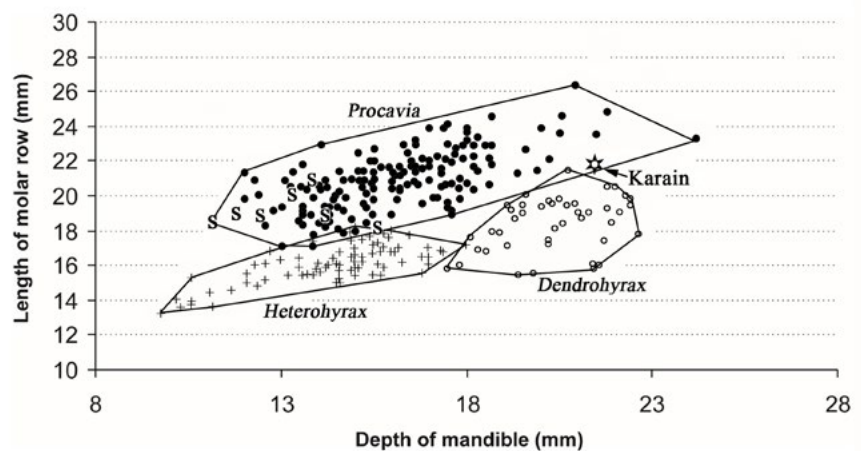
The relationship between body size and ambient temperature in *Procavia capensis* was studied by Yom-Tov (1993) who found that in Southern African populations (Namibia, South Africa) body size correlated with temperatures (as predicted by Bergmann's Rule, populations from cooler zones are larger than those from warmer climates) but that the species was adapted



**Fig. 8.-** Upper central incisors of *Procavia capensis* from Karain Cave, Turkey. A) KE 2011 I 16/84 V3, male right I1/ (A1 - mesial, A2 - anterior, A3 - distal views); B) KE 2007 K 19/81 V2, female left I1/ (B1 - mesial, B2 - stereo anterior views, B3 - distal view); C) KE 2012 J15/91 VI, male right I1/ (C1 - distal, C2 - anterior, C3 - mesial view); D) KE 2007 19K/80 V2, female right I1/ (D1 - mesial, D2 - stereo anterior views, D3- distal view).



**Fig. 9.-** Lower incisors of *Procavia capensis* from Karain Cave, Turkey. A) KE 2007 19K/80 V2, left i/2 (A1 - labial, A2 - mesial, A3 - lingual views); KE 2014 I 15/91 VI, right di/2 (B1 - lingual, B2 - mesial, B3 - labial, B4 - distal views).



**Fig. 10.-** Bivariate plots of length of lower molar row and depth of mandible at m/1 in Procaviidae. Karain (hollow star symbol) falls within the range of variation of *Procavia capensis*, but far from the subspecies *Procavia capensis syriaca* (S) (data for extant hyraxes are from Pickford, 2005).

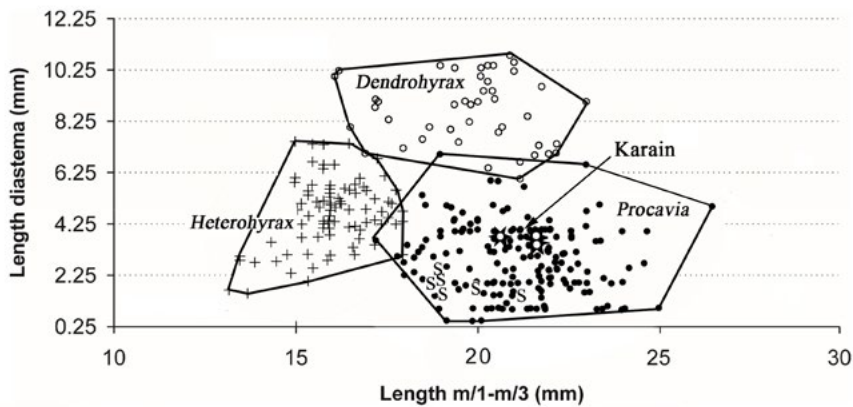


Fig. 11.- Bivariate plot of length of lower diastema relative to length of lower molar row of extant hyracoids. Karain is shown by a hollow star symbol, and specimens from the Arabian Peninsula are shown as 'S' (data for extant hyraxes are from Pickford, 2005).

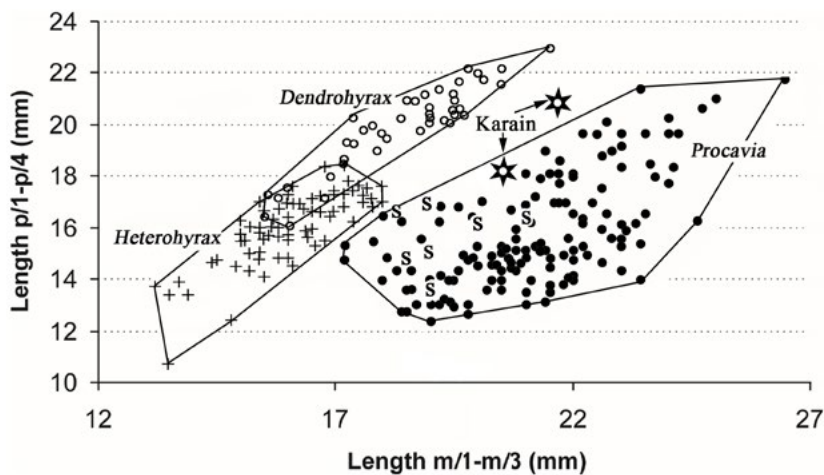


Fig. 12.- Bivariate plot of length of lower premolar row relative to length of lower molar row of extant hyracoids. Karain is shown by a hollow star symbol, and specimens from the Arabian Peninsula are shown as 'S' (data for extant hyraxes are from Pickford, 2005).

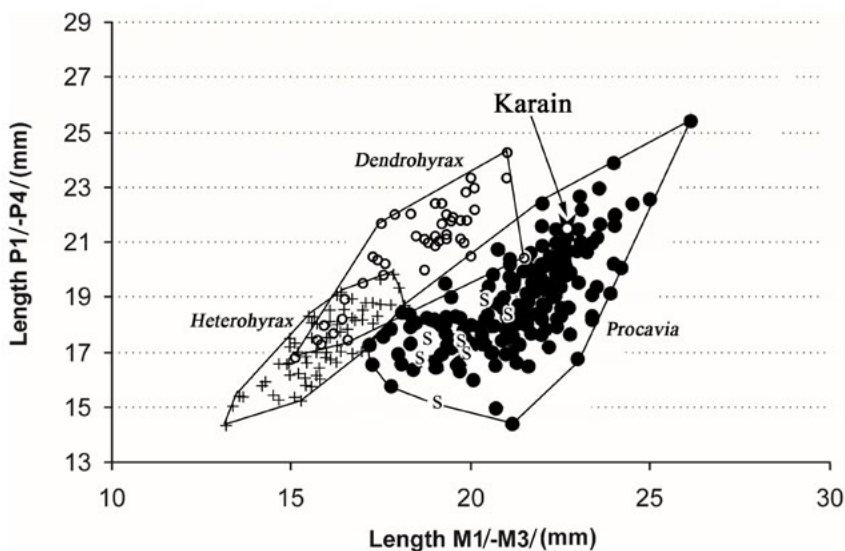


Fig. 13.- Bivariate plot of length of upper premolar row relative to length of upper molar row of extant hyracoids. Karain is shown by a hollow star symbol, and specimens from the Arabian Peninsula are shown as 'S' (data for extant hyraxes are from Pickford, 2005).

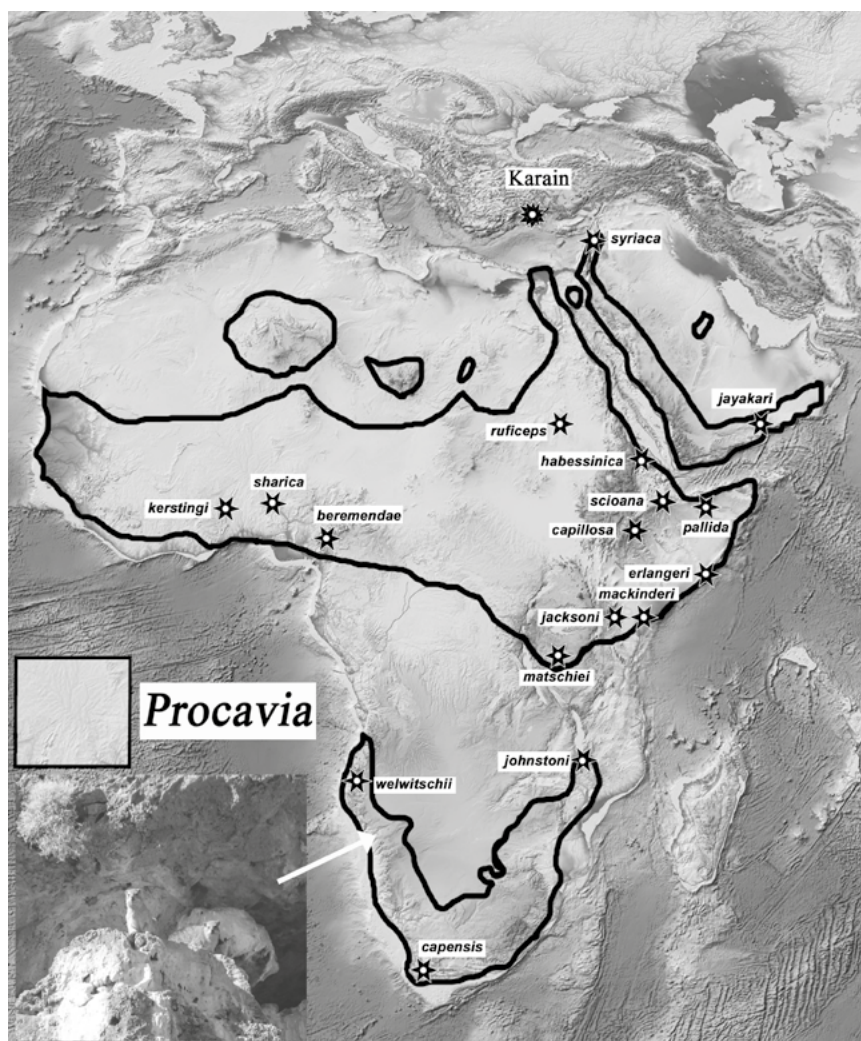
to maximum temperatures where they lived rather than to minimal temperatures of the coldest periods of the year. He considered that during cold periods (seasonal or daily temperature variations) individuals tended to avoid low temperatures by hiding in holes and caves where the temperature is slightly higher (not less than 16 °C) than outside, only emerging into the open when ambient temperature was greater than 11 °C (as in Israel populations). Thus the species shows an interesting behavioural component to survival in environments which are subject to relatively great temperature fluctuations on a seasonal or daily basis.

It is plausible that during the Middle Pleistocene, the Karain area was relatively humid and cool, which could account for the large body size of the hyraxes that lived there compared with their nearest surviving neighbours, the populations of smaller individuals that today live in the Arabian Peninsula or those further afield, such as *Procavia capensis ruficeps*, that populate the torrid lowlands of Africa. The presence of *Hippopotamus* remains in Karain Cave provides support for such an inference of tropical to subtropical conditions at the time of deposition. Detailed study would be warranted should more abundant and more complete fossil hyrax remains be found at Karain.

#### *Palaeobiogeography and archaeology*

The Karain hyracoid assemblage is by far the most comprehensive Quaternary hyrax collection known outside Africa. Fossil remains of *Procavia* are well known from southern and eastern Africa (Pickford, 2005) where they span the Pliocene to Recent periods, but even though they are poorly represented in the Arabian Peninsula they are widespread. However, few of the Arabian remains have been described in detail or illustrated. Garrod and Bate (1937) listed *Procavia* cf. *syriaca* at Mugharet el-Wad and Mugharet el-Tabun, 19 km south of Haifa,

Israel, associated with ancient human remains. Hooijer (1961) briefly mentioned the absence of *Procavia* at Ksâr'Akil, Lebanon in contrast to its presence in the Mount Carmel sites. Haas (1972) listed *Procavia* at Djebel Qafze Cave. Gilead (1991) recorded *Procavia* at three Upper Palaeolithic localities in the Levant. Goren-Inbar *et al.* (2000) listed a single lower incisor from sediments in the east bank of the Jordan River at Gesher Benot Ya'akov, Israel, which they attributed to *Procavia syriaca*. The age of the deposits span the Late Biharian (ca 800-740 Ka) and are thus potentially the oldest known from the region. Monchot (2005) mentioned a minimum of three individuals of *Procavia capensis* at Guela Cave, Mount Carmel, Israel, in association with Mousterian cultural remains. Jensen *et al.* (2005), reported remains of a minimum of three individuals of *Procavia capensis* in excavations at Shakarat Al-Musay'id (Neolithic) not far from Petra. Yeshurun *et al.* (2007) reported the presence of *Procavia* sp. at Misliya Cave, Mount Carmel, in association with early Middle Palaeolithic cultural remains. On the basis of these records it is inferred that *Procavia* survived in the Arabian Peninsula on a continuous basis at least since the middle Palaeolithic. It is presumed that hyraxes dispersed to Karain from Africa via the Arabian Peninsula, but there is little direct evidence of this.



**Fig. 14.-** Present day distribution of *Procavia capensis* and the fossil occurrence at Karain, Turkey. The inset shows two individuals of *Procavia capensis* sunning themselves at Blässkopf Cascade Tufa Cliffs, Naukluft Mountains, Namibia. In the map, currently accepted subspecies of *Procavia capensis* are represented by stars. The dimensions of the Karain fossil sample most closely resemble those of the upland equatorial African cluster of *Procavia capensis* (*P. c. capillosa*, *P. c. mackinderi*, *P. c. jacksoni*, *P. c. matschiei* and *P. c. johnstoni*) which live in relatively humid but cool upland habitats, rather than the geographically closer but smaller subspecies *P. c. syriaca*, *P. c. jayakari* and *P. c. ruficeps* which are adapted to more arid, warmer conditions (data about extant subspecies are from Olds and Shoshani, 1982).

## Conclusions

Middle Palaeolithic levels within Karain Cave, Antalya Turkey, aged ca 400,000 years, have yielded abundant remains of hyrax (*Procavia capensis*) associated with Acheulean lithic implements. This is the first record of procaviid Hyracoidea in the Pleistocene outside Afro-Arabia, extending the known geographic range some 600 km northwest from the nearest extant hyraxes in Syria. The state of preservation of the majority of the fossils is excellent, permitting detailed comparisons with extant taxa. The body size of the Karain hyraxes is larger than that of extant specimens of *Procavia capensis syriaca* and *Procavia capensis jayakari* from the Arabian Peninsula, according in this respect to high-altitude taxa from East Africa. This suggests that the palaeoclimate at Karain was relatively cool and humid, more so that the conditions in which hyraxes survive in the Arabian Peninsula.

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## Author contributions

Manuscript preparation, M.P. and S.M.; experimental design, M.P.; methodology, M.P.; data curation, S.M., H.T.,



K.Ö., G.K., Y.A., E.E., M.K. and B.F.; analysis and results, M.P. and S.M.; planning and research development, S.M., H.T., K.Ö., G.K., Y.A., E.E., M.K. and B.F.; funding acquisition, S.M.

## References

- Aydın, Y., 2017. A Lower Paleolithic Section from the Pleistocene Period: Karain. *Geological Bulletin of Turkey*, 60: 529-556.
- Aytek, A.I., Harvati, K., 2016. The human fossil record from Turkey. In: *Paleoanthropology of the Balkans and Anatolia*. Vertebrate Paleobiology and Paleoanthropology book series (K. Harvati, M. Roksandic, Eds), 79-91.
- Bloomer, P., 2009. Extant hyrax diversity is vastly underestimated. *Afrotherian Conservation*, 7: 11-16.
- Churcher, C.S., 1956. The fossil Hyracoidea of the Transvaal and Taungs deposits. *Annals of the Transvaal Museum*, 22: 477-501.
- Demirel, A., Andrews, P., Yalçinkaya, I., Ersoy, A., 2011. The taphonomy and palaeoenvironmental implications of the small mammals from Karain Cave, Turkey. *Journal of Archaeological Science*, 38 (11): 3048-3059.
- Dorst, J., Dandelot, J., 1970. *A Field Guide to the Larger Mammals of Africa*. London, Collins, 288 p.
- Garrod, D.A.E., Bate, D.M.A., 1937. *The Stone Age of Mount Carmel: Excavations at the Wady Elmughara*. Volume 1, Oxford, Clarendon Press, 240 p.
- Gilead, I., 1991. The Upper Palaeolithic Period in the Levant. *Journal of World Prehistory*, 5 (2): 105-154.
- Goren-Inbar, N., Feibel, C.S., Verosob, K.L., Melamed, Y., Kislé, M.E., Tchernov, E., Saragusti, I., 2000. Pleistocene Miletstones on the Out-of-Africa Corridor at Gesher Benot Ya'akov, Israel. *Science*, 289 (5481): 944-947.
- Haas, G., 1972. The Microfauna of the Djebel Qafze Cave. *Palaevvertebrata*, 5: 261-270.
- Hahn, H., 1934. Die Familie der Procaviidae. *Zeitschrift für Säugetierkunde*, 9: 207-358.
- Hooijer, D.A., 1961. The Fossil Vertebrates of Ksâr' Akil, a Palaeolithic Rock-Shelter in the Lebanon, *Zoologische Verhandlungen*, 49 (1): 1-68.
- Huxley, T.H., 1869. *An Introduction to the Classification of Animals*. John Churchill and Sons, London. 147 p.
- Jensen, C.H., Hermansen, B.D., Bille Petersen, M., Kinzel, M., Hald, M., Bangsgaard, P., Lynnerup, N., Thuesen, I., 2005. Preliminary Report on the Excavations at Shakarat Al-Musay'id, 1999-2004. *Annual of The Department of Antiquities of Jordan*, 49: 115-134.
- Kingdon, J., 2003. *The Kingdon Field Guide to African Mammals*. Christopher Helm, London, 476 p.
- Maswanganye, K.A., Cunningham, M.J., Bennett, Chimimba, C.T., Bloomer, P., 2017. Life on the rocks: Multilocus phylogeography of rock hyrax (*Procavia capensis*) from southern Africa. *Molecular Phylogenetics and Evolution*, 114: 49-62.
- Monchot, H., 2005. Un assemblage original au Paléolithique moyen: Le repaire à Hyènes, porc-épics et Hominidés de la Grotte Geula (Mont Carmel, Israël). *Paléorient*, 31 (2): 27-42.
- Olds, N., Shoshani, J., 1982. *Procavia capensis*. *Mammalian Species*, 171: 1-7.
- Otte, M., Yalçinkaya, I., Kozłowski, J., Taşkıran, H., Bar-Yosef, O., 1996. Paléolithique ancien de Karain (Turquie). *Anthropologie et Préhistoire*, 107: 149-156.
- Pallas, P., 1766. *Miscellanea Zoologica: quibus novae imprimis atque obscurae animalum species describuntur et observationibus iconibusque illustrantur*. P. van Cleef, Hagae, 224 p.
- Pickford, M., 2005. Fossil hyraxes (Hyracoidea, Mammalia) from the Late Miocene and Plio-Pleistocene of Africa, and the phylogeny of the Procaviidae. *Palaentologia Africana*, 41: 141-161.
- Rink, W.J., Schwarcz, H.P., Grün, R., Yalçinkaya, I., Taşkıran, H., Otte, M., Valladas, H., Mercier, N., Bar-Yosef, O., Kozłowski, J., 1994. ESR Dating of the Last Interglacial Mousterian at Karain Cave, Southern Turkey. *Journal of Archaeological Science*, 21 (6): 839-849.
- Storr, G., 1780. *Prodromus methodi mammalium*. Litteris Reissianis, Tubingen, 43 p.
- Thomas, O., 1892. On the species of the Hyracoidea. *Proceedings of the Zoological Society of London*, 1892: 50-76.
- Yalçinkaya, I., Özçelik, K., Kartal, M., Taşkıran, H., 2009. Diffusion des cultures à bifaces en Turquie. *Anadolu/Anatolia*, 35: 1-38.
- Yeshurun, R., Bar-Oz, G., Weinstein-Evron, M., 2007. Modern hunting behaviour in the early Middle Paleolithic. Faunal remains from Misliya Cave, Mount Carmel. *Journal of Human Evolution*, 53 (6): 656-677.
- Yom-Tov, Y., 1993. Does the Rock Hyrax, *Procavia capensis*, conform with Bergmann's Rule?. *Zoological Journal of the Linnean Society*, 108 (2): 171-177.
- Zwick, A., Schleich, H.H., 1994. Quartäre Reptilienfunde von der Grabungstelle Karain (S-Türkei). (Reptilia : Testudines, Squamata). *Courier Forschungs-Institut Senckenberg*, 173: 267-281.

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