

<i>Bollettino della Società Paleontologica Italiana</i>	40 (2), 2001	ISSN 0375-7633	293-302	—	Modena, Giugno 2001
---	--------------	----------------	---------	---	---------------------

Outside Africa: Middle Pleistocene *Lycaon* from Hayonim Cave, Israel

Mary C. STINER
Department of Anthropology
University of Arizona, Tucson

F. Clark HOWELL
Laboratory of Human
Evolutionary Studies
University of California, Berkeley

Bienvenido MARTÍNEZ-NAVARRO
Venta Micena
Granada

Eitan TCHERNOV
Department of Evolutionary Systematics
The Hebrew University, Jerusalem

Ofer BAR-YOSEF
Department of Anthropology
Harvard University, Cambridge

KEY WORDS – *Lycaon*, *Canidae*, Hayonim Cave, Middle Pleistocene, Western Asia.

ABSTRACT – In 1997 a nearly complete adult hemi-mandible of the genus *Lycaon* (*Canidae*) was found in the early Middle Paleolithic layer of Hayonim Cave, Israel. Dating to oxygen isotope (^{18}O) stage 6, or perhaps late stage 7, of the later middle Pleistocene, this is the only unequivocal example of the genus recorded outside of the African continent for any period. The mandible includes three permanent molars, most of the horizontal ramus, and the condyle. It was not in anatomical connection with the cranium at the time of discovery, or with any other skeletal parts. The mandible's morphology is primitive, retaining ancestral features in the dentition and a very robust horizontal ramus. This fossil *Lycaon* occurs in general stratigraphic association with early Middle Paleolithic artifacts and fauna, but it bears no tool marks or burning damage. This unique find raises new questions about the origin, evolution, and dispersal of the genus *Lycaon*.

RIASSUNTO – [Fuori dall'Africa: il *Lycaon* del Pleistocene medio della grotta di Hayonim, Israele] – Nel 1997 gli scavi nei livelli inferiori del Pleolitico medio della grotta di Hayonim (Israele) hanno portato al ritrovamento di una emimandibola quasi completa attribuibile al genere *Lycaon* (*Canidae*). Questo ritrovamento, riferibile al Pleistocene medio finale, stage isotopico (^{18}O) 6 o forse fine del 7, costituisce l'unico chiaro segnale della presenza del genere *Lycaon* al di fuori del continente Africano. La mandibola, ritrovata isolata, conserva i tre molari definitivi, il ramo orizzontale quasi completo ed il condilo. Il reperto, caratterizzato da un ramo orizzontale molto robusto, è morfologicamente primitivo, mantenendo tratti ancestrali nella morfologia dentaria. Questo licaone fossile, trovato in associazione con fauna ed industria litica del Paleolitico medio antico, non presenta tracce di macellazione o di bruciature. Si tratta di un ritrovamento unico, che apre nuovi interrogativi su origine, evoluzione e dispersione del genere *Lycaon*.

RESUMEN – [Fuera de África: Hallazgo de *Lycaon* en el Pleistoceno medio de Hayonim Cave, Israel] – En 1997 fue encontrada una hemimandíbula bastante completa correspondiente al género *Lycaon* (*Canidae*) en los niveles más bajos del Paleolítico medio de Hayonim Cave (Israel). La datación por isótopos de oxígeno (^{18}O) indica el estadio 6, o quizás la parte final del estadio 7, del Pleistoceno medio tardío. Este es el único ejemplo de este género registrado fuera del continente africano en cualquier periodo. Dicha mandíbula incluye los tres molares permanentes, la mayoría de la rama horizontal y el cóndilo. Fue hallada aislada sin conexión anatómica con el cráneo o con otras partes esqueléticas. La morfología de la mandíbula es primitiva, conserva algunas características anatómicas ancestrales en la dentición además de una rama horizontal muy robusta. Este fósil de *Lycaon* se encuentra en asociación con fauna e industria lítica del Paleolítico medio temprano, pero no presenta marcas de descarnación o de haber sido quemada. Este único hallazgo induce nuevas cuestiones sobre el origen, evolución y dispersión del género *Lycaon*.

INTRODUCTION

An isolated, nearly complete right hemi-mandible of *Lycaon* (Text-fig. 1) was recovered in 1997 from near the base of the early Middle Paleolithic layer (E) of Hayonim Cave, in the western Galilee of northern Israel. Hayonim Cave contains bone-rich cultural horizons as young as the Holocene (Bar-Yosef, 1991; Belfer-Cohen & Bar-Yosef, 1981) and as ancient as the earliest Middle Paleolithic (Bar-Yosef, 1998; Meignen, 1998). The sedimentary layer that yielded the *Lycaon* mandible corresponds to oxygen isotope stage 6, or perhaps late stage 7 (following Shackleton & Opdyke, 1973), of the middle Pleistocene epoch. Presented below are a description of the fossil, its taxonomic sta-

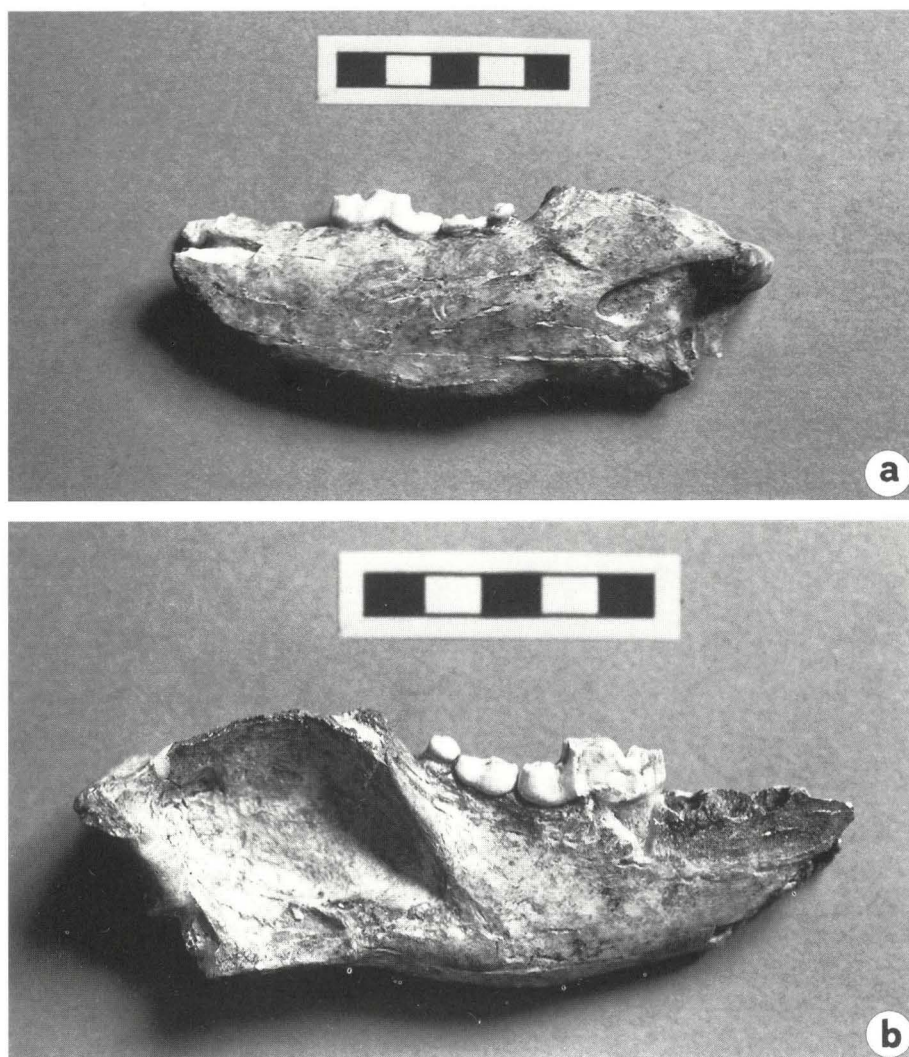
tus and stratigraphic context, and morphometric comparisons to modern *Lycaon pictus* populations and relevant Pleistocene canid fossils. The presence of *Lycaon* in Hayonim Cave is remarkable, as it is the only clear-cut example recorded outside the African continent for any period. Would be exceptions reported from middle Pleistocene sites of central Europe (Kurtén, 1968) have been reclassified to other genera – *L. lycaonoides* at Stranska Skala in the Czech Republic and Gombastzög in Hungary (in Kurtén, 1968, p. 113) are attributed to *Canis* (*Xenocyon*), as first described by Kretzoi (1938) in the latter site. The rich faunal series from Hayonim Cave, and the *Lycaon* fossil's general association with early Middle Paleolithic artifacts, help to set this unique find in community context.

FOSSIL DESCRIPTION

The right hemi-mandible from Hayonim (H-K21-547) preserves part of the anterior and the complete posterior alveolus of the P_3 , and both P_4 alveoli of the premolar series; no premolar elements are present. All three molar elements (M_1 , M_2 and M_3) are preserved, along with most of the horizontal ramus and the mandibular condyle (Text-fig. 1). The anterior-most section of the mandible and the top of the second lower molar were broken and lost recently, owing to the difficulty of excavating the brecciated sediments in this portion of the site. The dentarium bone is high and robust. Presence of the third lower molar in the Hayonim specimen excludes *Cuon* (Crégut-Bonnoure, 1996; Ewer, 1973; Kurtén, 1968, p. 111). The carnassial hypoconid of the M_1 is large and the entoconid nonexistent. These observations, along with the morphology of other cusps on the lower second molar and the relatively short distance

between the M_3 and posterior margin of the mandibular condyle as compared to wolves (Text-fig. 2), exclude *Canis*. In fact the lower dentition, as well as the thickness and outward cant of the anterior-dorsal horizontal ramus, very closely resemble modern *Lycaon pictus*. The only major exceptions are the substantially greater mandibular depth of the fossil specimen and a relatively large M_3 (see below).

M_1 - The labial face in the area of the trigonid of the lower first molar is partly destroyed. The cusps of the protoconid, the paraconid, and the metaconid are partly destroyed as well, but it still is possible to see that the protoconid is higher and more robust than the paraconid, as is typical of *Lycaon* dental anatomy. The metaconid is a small peak situated in the postero-lingual face of the protoconid. The talonid has one principal cusp, the hypoconid, situated in a lateral-external position, the apex of which is partly destroyed. The lingual area of the talonid has a typical internal cingulum and a small fold that induces a



Text-fig. 1 - Partial right hemi-mandible of the Hayonim canid found at 489 cm below datum in square K21c (H-K21-547, Layer E) in the central excavation area during the 1997 field season, cleaned and stabilized: (a) lingual view; (b) lateral or buccal view. Note that the breaks on the posterior portion of the mandible (ascending ramus) occurred while the bone was relatively fresh. The breaks on the anterior portion, and extending through the M_1 , occurred during excavation from brecciated sediments; scratches on the mandible surface also are from excavation damage.

very small entoconid, a primitive character present in the ancestral species *Canis (Xenocyon) falconeri*. A small crest is present between this internal talonid micro-cusp and the base of the metaconid. Another small crest unites the mesial face of the hypoconid with the distal face of the protoconid.

M₂ - The second lower molar is practically bicuspidate. In the trigonid, only the protoconid, the main cusp of this element, is clearly developed; the metaconid and paraconid are very small (and residual) but present. In the talonid, only the external cusp (the hypoconid) is present, and the internal area is represented by the classic cingulum. The protoconid and hypoconid are united by a small crest.

M₃ - The third molar is round and monocuspidate. Comparative data in Appendix 1a show that its proportions exceed those of extant *Lycaon* populations, whereas the other molars generally do not.

FOSSIL CONDITION AND STRATIGRAPHIC CONTEXT

The *Lycaon* mandible (H-K21-547) comes from a lower stratigraphic unit of Layer E, 489 cm below datum in the central excavation trench of Hayonim Cave (Text-fig. 3). It occurs in general association with early Middle Paleolithic flint artifacts and hearth ash and a diverse vertebrate fauna dominated by mountain gazelle (*Gazella gazella*), fallow deer (*Dama mesopotamica*), and Mediterranean spur-thighed tortoise (*Testudo graeca*) (Stiner & Tchernov, 1998). Although the mandible bears no clear traces of human modification, it occurs within 20 cm of the base of this thick (>1.5 m) bone-rich layer. Radiometric dates by thermo-luminescence and electron-spin-resonance techniques yield an average age of 170,000 years before present for Layer E but with a substantial error range (Valladas, personal comm.; Rink, personal comm. June, 2000). Size variation in the tortoises (Stiner *et al.*, 1999, 2000) and microfaunal associations (Tchernov, 1981, 1992, 1994) indicate that the mandible is probably 200,000 years or older (cf. Valladas *et al.*, 1998; Schwarcz & Rink, 1998).

The mandible was isolated from the rest of the skeleton in antiquity, and its coronoid process was torn away at that time. The dog's other body parts must have been widely scattered prior to burial of the mandible and perhaps never reached the cave, since no other parts of the body were found within the large area excavated. Taphonomic analyses attribute the associated herbivore and reptile faunas principally or wholly to hominids (Stiner & Tchernov, 1998); burning damage is common, some bones have cut marks on them, and cone fractures are far too abundant to have been produced by carnivores (*sensu* Stiner, 1994, pp. 106, 153-156). Few if any traces of gnawing by large carnivores have been encountered (<<1% of total macromammal NISP), although carnivore skeletal remains are present in very low numbers (Tab. 1). What damage can be found on large

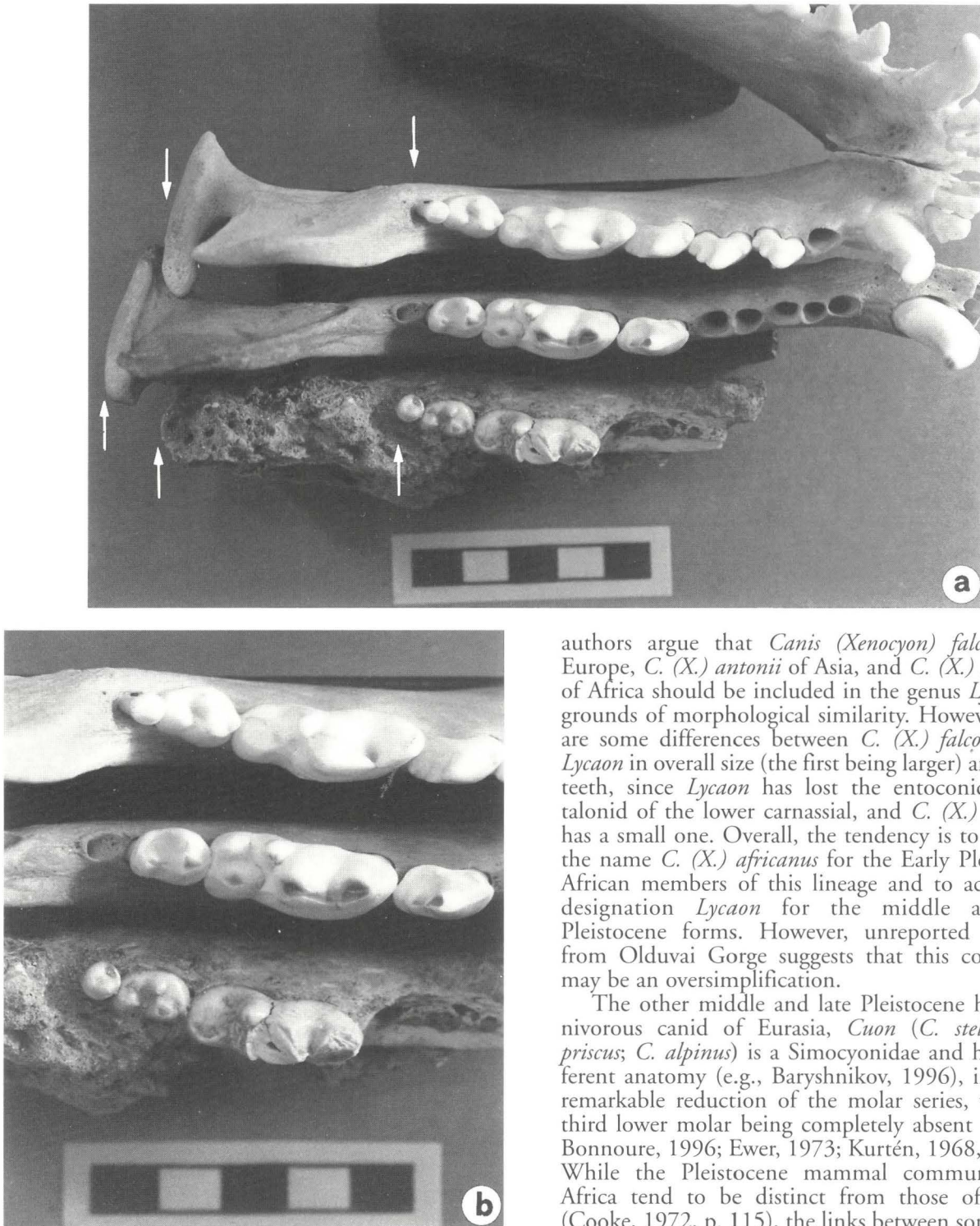
carnivore bones is confined to burning and/or cut marks from human tools. The taphonomic history of the *Lycaon* mandible is unclear, however, as it lacks the kinds of damage needed to diagnose modifying agency. Not without interest, it occurs in a portion of the sediment column where bones are fewer, yet relatively unaffected by dissolution (Stiner *et al.*, 2001). Only two coprolites (probably from hyena) have been found in the central excavation trench, and these occur between the depths of 575-580 cm bd, fully 1 m below where the *Lycaon* mandible or most other bones were found. The possibility that the *Lycaon* mandible is unrelated to anthropogenic debris in the cave can not be excluded, since long accumulation times are indicated for the assemblages overall. However, its location is somewhat marginal to the total bone distribution.

LYCAON EVOLUTION

Lycaon, *Canis*, and *Cuon* are closely related genera, and all may have diverged from a common ancestor in the Pliocene (Kurtén, 1968, p. 111; Wayne, 1993). Unlike *Cuon*, the fossil chronology of *Lycaon* prior to the late Pleistocene is poorly known (Kurtén, 1968; Savage, 1978), and there is virtually no information linking Miocene to Pleistocene canids. Thus, while recent *Lycaon* is exclusively African, the geographic distribution of its predecessors is unclear (see Savage, 1978, p. 255). Re-evaluation of current fossil catalogs and the systematics of the Early and middle Pleistocene large canids of Africa and Eurasia is needed.

Canis africanus Pohle from Olduvai and *Canis atrox* Broom from Kromdraai A must be considered conspecific, based on similarities in anatomy to the European fossil species, *Canis (Xenocyon) falconeri*. The latter is well known from many Early Pleistocene assemblages, although it appears under a variety of synonyms such as *C. (X.) falconeri* at Venta Micena, Cueva Victoria (Martínez-Navarro, 1992a,b; Palmqvist *et al.*, 1999), and Pirro Nord (Rook, 1994); *Canis (X.)* sp. at Apollonia-1 (Koufos & Kostopoulos, 1997); *Xenocyon lycaonoides* at Untermassfeld (Sotnikova, in press); and *Canis* sp. similar in size to *C. falconeri* at 'Ubeidiya (Ballesio, 1986). *Canis atrox* is recorded in North Africa at Ain Hanech (Arambourg, 1979), but mentions of *Lycaon* or "cf. *Lycaon* sp." from the Kalochoro Member in the Nachukui Fm. (West Turkana) in Africa (>1.88 MYA) are based on a trigonid fragment of the lower carnassial that could be *Lycaon*, but probably is not (Harris *et al.*, 1988, pp. 35-36).

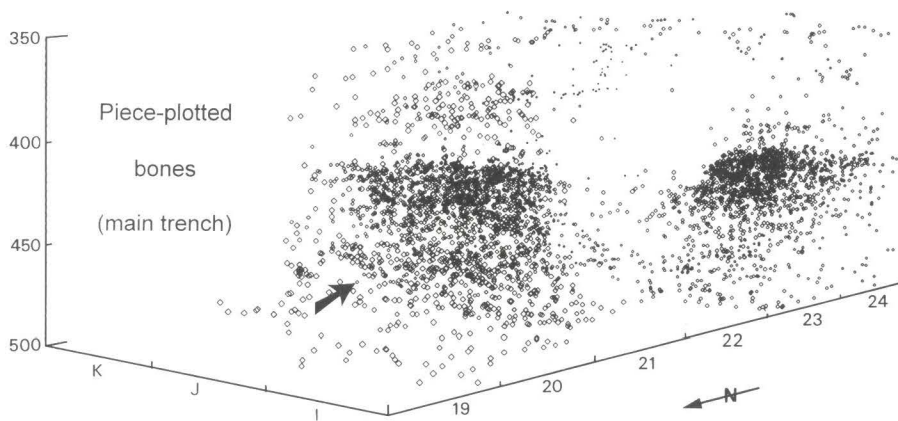
The relation of the Early Pleistocene *C. (X.) falconeri* and *Canis africanus* to *Lycaon* is reasonably clear. *Lycaon* is the only recent canid with a tetradactyl forelimb – a very reduced facet on the McII where this element articulates with the McI. In his general revision of *Canis (Xenocyon)* ex gr. *falconeri*, Rook (1994) notes this character in one Early Pleistocene specimen from Pirro Nord in Italy. Some



Text-fig. 2 - The Hayonim *Lycaon* mandible (darkest specimen at bottom of trio) compared to modern *Lycaon pictus* (top of trio) and *Canis lupus* (middle specimen). (a) General mandible configurations, noting the shorter distance between the maximum posterior extension of the mandibular condyle and the posterior edge of the M₁ alveolus in modern and middle Pleistocene *Lycaon* relative to that of modern *C. lupus*. (b) Detail of the molars.

authors argue that *Canis* (*Xenocyon*) *falconeri* of Europe, *C. (X.) antonii* of Asia, and *C. (X.) africanus* of Africa should be included in the genus *Lycaon* on grounds of morphological similarity. However, there are some differences between *C. (X.) falconeri* and *Lycaon* in overall size (the first being larger) and in the teeth, since *Lycaon* has lost the entoconid in the talonid of the lower carnassial, and *C. (X.) falconeri* has a small one. Overall, the tendency is to preserve the name *C. (X.) africanus* for the Early Pleistocene African members of this lineage and to accept the designation *Lycaon* for the middle and late Pleistocene forms. However, unreported material from Olduvai Gorge suggests that this conclusion may be an oversimplification.

The other middle and late Pleistocene hypercarnivorous canid of Eurasia, *Cuon* (*C. stehlini*; *C. priscus*; *C. alpinus*) is a Simocyonidae and has a different anatomy (e.g., Baryshnikov, 1996), including remarkable reduction of the molar series, with the third lower molar being completely absent (Crégut-Bonnoure, 1996; Ewer, 1973; Kurtén, 1968, p. 111). While the Pleistocene mammal communities of Africa tend to be distinct from those of Europe (Cooke, 1972, p. 115), the links between some Asian and African lineages, such as *Cuon*, may have been more fluid than previously supposed. *Lycaon* is preceded in early Pleistocene Africa by a large wolf-like canid that went extinct, and it is assumed that *Lycaon* took over part or all of its vacated niche (Bigalke, 1972, p. 161). *Lycaon* was especially widely distributed in Africa during the middle Pleistocene, from Algeria to the southern Cape (Kurtén, 1968, p. 114;



Text-fig. 3 - The stratigraphic position of the *Lycaon* specimen (large arrow) among the total distribution of piece-plotted bones in the central excavation area of Hayonim Cave. Note that the nearly empty vertical trough in the center of the sediment column is due to dissolution (see Stiner *et al.*, 2001) and does not extend to the area containing the mandible.

Savage, 1978, p. 254) in Africa, and now we have clear evidence that it existed in western Asia as well. The *Lycaon* specimen from Hayonim Cave appears to be the only securely identified example in western Eurasia. However, a distal left tibia of a late middle Pleistocene canid from Yarimburgaz Cave in western Turkey (Howell, unpublished data; Farrand & McMahon, 1997) *may* represent a second non-African example; it is distinct from *Cuon*, *C. lupus* or *C. (X.) falconeri*. This specimen (A.40, #2) comes from the lower level (14) in the upper chamber of Yarimburgaz Cave, but its correlation with cave bear and hominid occupations of the lower chamber have not been determined.

COMPARISONS TO MODERN *LYCAON PICTUS*

The dental dimensions (mm) of the M_2 of the Hayonim specimen fall within the size ranges of modern African populations of *Lycaon pictus* (Text-fig. 4),

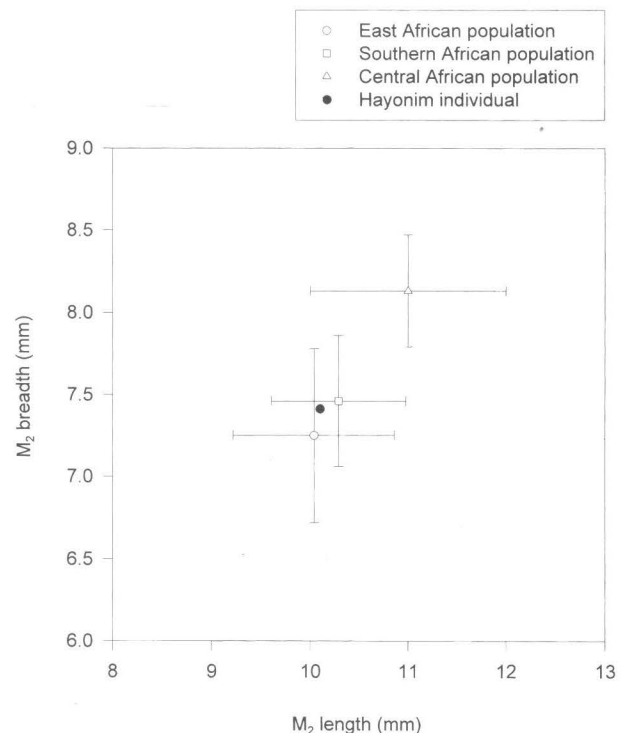
measurement type	East Africa		Southern Africa		Central Africa	
	mean	sd	mean	sd	mean	sd
M_2 , L (mm)	10.04	.82	10.29	.69	11.00	1.0
M_2 , B (mm)	7.25	.53	7.46	.40	8.13	.34
body weight (kg)	22.22	3.19	27.82	5.18	—	—

(L) length; (B) breadth.

Source: Girman *et al.* (1993, p. 455), based on a total of 47 individuals (males and females combined) from skeletal collections at the British Museum of Natural History in London and Smithsonian Institution in Washington, D. C.

Tab. 1 - Dental measurement and body weight statistics for the lower second molar of modern *Lycaon pictus* skeletal populations from East, Southern, and Central Africa (males and females combined).

but best resemble those of the smaller-bodied Southern and East African skeletal samples (Tab. 1) documented by Girman *et al.* (1993). Text-figures 5 and 6 compare first and second lower molar measurements for males and females in a different Southern African sample (Tab. 2) collected by Kieser and Groeneveld (1992). Here some differences in tooth



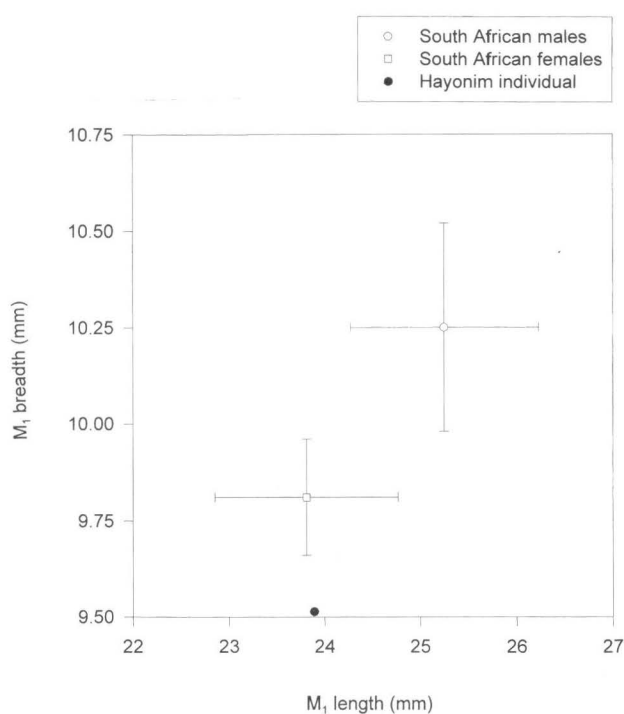
Text-fig. 4 - Length (L, or anterior-posterior) and breadth (B, or bucco-lingual) comparisons of the lower second molar (means and sd in mm) of three modern populations of *Lycaon pictus* to those of the Hayonim mandible. Measurements of modern skeletal populations from East, Central, and Southern Africa are from Girman *et al.* (1993, p. 455).

measurement (mm)	Hayonim specimen H-K21-547	modern Southern African population			
		males		females	
		mean	sd	mean	sd
M ₁ , L	23.8	25.25	.98	23.81	.96
B	9.5	10.25	.27	9.81	.15
M ₂ , L	10.1	10.73	.31	11.26	.39
B	7.4	7.37	.40	7.41	.36
horizontal ramus height below carnassial notch of M ₁	31.8	24.76	1.69	23.33	1.60
horizontal ramus breadth below carnassial notch of M ₁	14.2	12.71	.81	12.84	.95

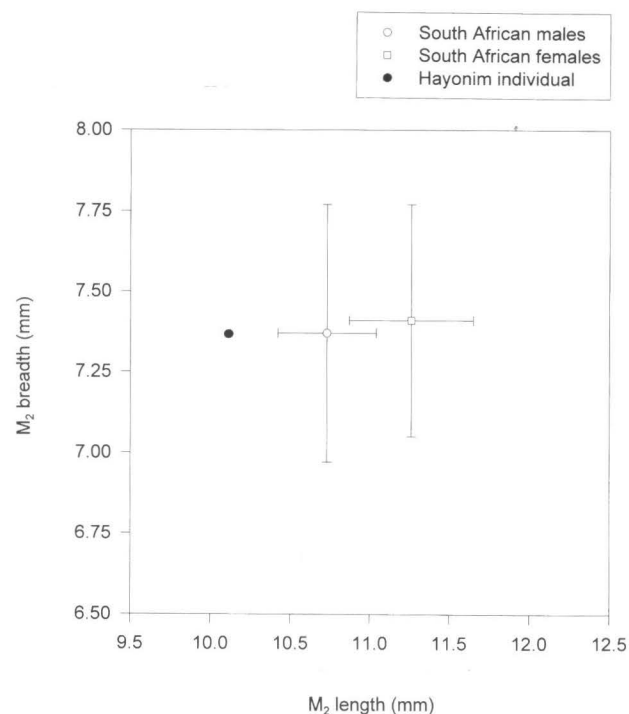
(L) length; (B) breadth.

Source: Kieser & Groeneveld (1992, p. 134), based on 18 males and 16 females in the collections of the Transvaal Museum in Pretoria and the General Anatomy Museum at Witwatersrand University.

Tab. 2 - Comparison of osteometric measurements of the Hayonim mandible to those for a modern *Lycaon pictus* skeletal population from Southern Africa.



Text-fig. 5 - Length (L) and breadth (B) comparisons of the lower first molar (means and standard deviations in mm) of males and females in one modern *Lycaon pictus* skeletal population from Southern Africa to those of the Hayonim mandible. Measurements of modern skeletal samples are from Kieser & Groeneveld (1992, p. 134).



Text-fig. 6 - Length (L) and breadth (B) comparisons of the lower second molar (means and standard deviations in mm) of males and females in one modern *Lycaon pictus* skeletal population from Southern Africa to the Hayonim mandible. Measurements of modern skeletal samples are from Kieser & Groeneveld (1992, p. 134).

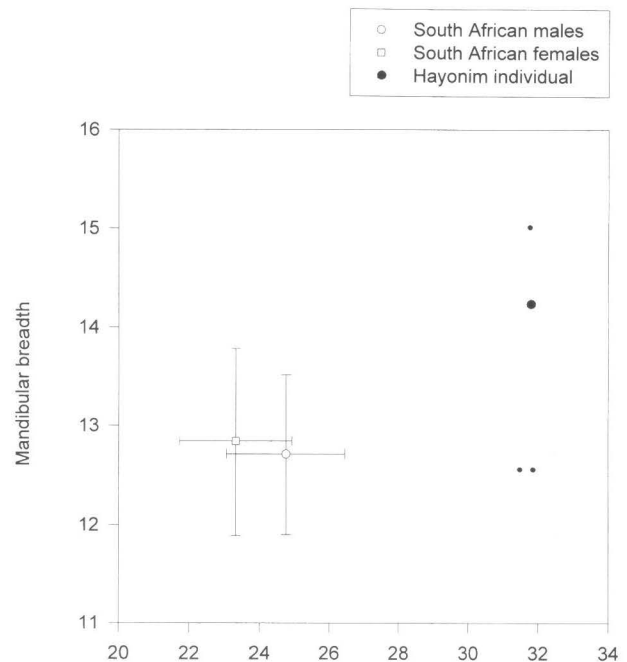
shape are apparent, as the M_1 of Hayonim specimen falls within the modern morphometric range in length but not in breadth, and the M_2 differs from the modern sample in its length but not its breadth. More striking is the height of the Hayonim mandible (Text-fig. 7), which is far greater than for the modern *Lycaon* population – 1.5 x, or about 3 standard deviations from the norm – yet whose medio-lateral thickness only slightly exceeds the modern morphometric range. [Both measurements were positioned below the carnassial notch of the M_1 , following Kieser and Groeneveld (1992)]. *Canis (X.) falconeri* of Venta Micena, for which we have analogous measurements, also possessed a very robust mandible. As noted above the M_3 of the Hayonim specimen is larger than those of recent *L. pictus* populations, and is comparable to the dimensions of *C. (X.) falconeri* (Appendix 1).

Thus, while the Hayonim specimen merits the generic assignment of *Lycaon*, it was a somewhat different animal than its modern counterpart, retaining an archaic pattern of robusticity consistent with that of *Canis (Xenocyon) falconeri*. Greater relative mandibular robusticity is also known in certain other mammalian lineages of the early and middle Pleistocene (Tchernov, 1968). Whether subsequent gracilization is attributable to changes at the species level or a distinct biomechanical architecture is debateable; the pattern seems to follow orthogenetic (chronocline) changes and could derive from some complex of intra-community coevolution (Tchernov, 1968).

LYCAON BIOGEOGRAPHY AND ECOLOGY

Lycaon pictus, the sole surviving representative of its genus, was widespread in subsaharan Africa until very recently, avoiding only thick rain forest and the driest deserts (Girman *et al.*, 1993). Built for speed and endurance, these wild dogs are obligate meat-eaters with unique hunting and social adaptations (Ewer, 1973, p. 41; Moehlman, 1986), and they are the most successful hunters on average of all of the modern canids (Estes & Goddard, 1967; Krüger *et al.*, 1999). The dispersal capabilities of *L. pictus* populations within Africa are great, owing to the large litters supported by each pack (Ewer, 1973; Fanshawe, 1989; Maddock & Mills, 1994), vast territories (Fuller & Kat, 1990), and the ability to traverse long distances in short periods (McNutt, 1996).

These facts about *Lycaon* raise the question of why the genus did not spread easily into Eurasia. Such behavior has been described for the Early Pleistocene form of *C. (X.) falconeri* at the site of Venta Micena (Palmqvist *et al.*, 1999). And other large predators, such as felids and hyenids, dispersed from Africa more than once during the Pleistocene, hominids among them (Martínez-Navarro & Palmqvist, 1995, 1996; Turner, 1984, 1986a). There is now a long list of African taxa which extended their ranges to western Asia, particularly among the artiodactyls (pigs [2], hip-



Text-fig. 7 - Comparison of mandibular height and breadth (means and standard deviations in mm) of males and females in one modern *Lycaon pictus* skeletal population from Southern Africa to the Hayonim mandible. Both measurements are aligned with the carnassial notch of the M_1 . Measurements of modern skeletal samples are from Kieser & Groeneveld (1992, p. 134). Additional small filled circles represent three individuals of *Canis (X.) falconeri* from Venta Micena, which also possessed a very robust mandible of similar proportions.

pos [2/3], giraffes [1], antelopes [at least 4 tribes, 5 genera], but also murid rodents [2] and viverrid carnivores.

Two factors may contribute to the up-to-now perception of *Lycaon* as an exclusively African group. First, *Lycaon* is a numerically rare species that lives at low population densities in the eastern and southern African ecosystems it currently inhabits (e.g., Woodroffe & Ginsberg, 1999), greatly limiting its paleontological visibility. Second, *Canis lupus* and *Cuon alpinus*, two other social hunting canids, have occupied vast areas of the northern hemisphere for some time. Their predecessors may have limited expansions of *Lycaon* populations during much of the Pleistocene and Holocene. *Cuon* and *Lycaon* are especially similar in their ecology (Kurtén, 1968, p. 114), and *Cuon* is well documented in some areas of western Asia and Europe from the middle Pleistocene onward (Baryshnikov, 1996; Crégut-Bonnouire, 1996; Kurtén, 1968). Today, *Lycaon pictus* is the more tropically adapted of the pair (Girman *et al.*, 1993, p. 458), perhaps explaining its apparently brief stratigraphic span in western Asia, and its complete absence from Europe. Africa is the most uniformly tropical and sub-tropical of all modern continents, with 78%

specimen	horizontal ramus height behind the:												
	L M ₁	B M ₁	Ltrig M ₁	L M ₂	B M ₂	L M ₃	B M ₃	L M ₁ -M ₃	MCB	P ₄	M ₁	M ₂	M ₃
<i>Lycaon:</i>													
Hayonim H-K21-547	23.8	9.5	17.2	10.1	7.4	5.4	5.3	40.4	28.3	31.1	34.6	37.0	35.6-36.7
OM-7516 l.m.	21.8	9.1	15.5	9.0	7.2	—	—	34.2	29.3	24.7	26.3	26.9	29.0
OM-7516 r.m.	21.4	9.1	15.6	9.3	7.1	4.4	4.4	34.5	29.2	24.3	26.7	26.5	29.1
OM-7424 l.m.	24.6	9.4	16.5	11.0	7.6	5.0	4.7	39.2	30.6	23.2	25.2	26.5	29.8
OM-7424 r.m.	25.1	9.4	16.6	10.9	7.6	—	—	40.0	30.4	22.9	24.6	27.1	29.9
OM-7425 l.m.	23.8	9.0	17.1	11.1	7.5	5.1	4.3	39.2	31.0	23.2	25.6	26.5	30.4
OM-7425 r.m.	23.6	9.0	16.9	10.6	7.1	5.0	4.5	39.3	31.7	23.5	25.9	27.1	30.3
OM-7436 l.	22.2	8.5	15.6	9.8	6.9	4.5	4.5	36.5	27.8	22.0	23.9	24.3	27.9
OM-7436 r.	22.9	8.4	15.5	9.9	6.9	4.6	4.6	36.6	27.4	21.7	23.7	24.2	27.0
OM-7373 l.	23.7	8.7	16.0	10.1	7.2	—	—	36.8	27.6	23.0	24.7	24.5	27.2
OM-7373 r.	23.3	8.5	16.5	9.4	6.9	4.4	4.0	35.9	28.8	22.2	23.5	23.6	26.0
OM-7889 l.	22.3	8.5	15.8	8.5	6.3	—	—	34.6	24.9	21.5	22.9	24.0	27.0
OM-7426 l.m.	23.7	8.7	16.3	10.1	7.3	4.6	4.5	37.7	27.7	20.9	23.5	24.4	28.8
OM-7426 r.m.	23.1	8.8	16.2	9.7	7.1	4.6	4.4	36.9	27.8	20.5	23.2	25.0	28.4
M-4044 l.	27.7	10.6	19.4	10.7	7.8	5.0	4.7	43.0	29.2	20.3	26.4	27.9	29.6
M-4044 r.	27.5	10.8	19.6	11.0	7.9	4.9	5.4*	43.2	27.0	20.4	26.6	27.8	30.1
M-4002 l.	26.9	10.1	17.7	11.1	8.4	5.1	4.7	40.5	31.0	24.9	27.6	29.0	32.6
M-4002 r.	26.1	10.0	18.3	11.3	8.4	5.1	4.3	41.0	31.6	23.0	25.8	29.2	31.5
M-6198 r.	23.3	9.2	15.9	8.5	6.8	3.9	3.2	34.7	—	—	—	—	—
<i>Canis (Xenocyon) falconeri:</i>													
Venta Micena VM-7000 r.	—	11.3	20.5	—	—	—	—	—	—	32.0	32.5	—	—
Venta Micena VM-7000 l.	27.6	11.0	20.1	12.1	8.7	5.2	4.8	44.0	34.6	31.4	32.1	37.4	38.4
Venta Micena VM-2255 l.	24.5	10.0	18.3	12.7	8.6	5.9	5.1	43.2	27.6	31.5	32.1	34.9	37.2
Venta Micena VM-2256 r.	25.3	9.9	18.4	11.9	8.3	6.2	5.3	42.6	—	31.3	32.7	35.9	37.5
Venta Micena VM-2257 l.	28.6	11.1	—	13.9	9.4	6.6	5.7	—	—	—	—	—	—
Cueva Victoria CV-sn-a r.	29.5	12.0	—	11.7	9.1	—	—	—	—	—	—	—	—
Cueva Victoria CV-sn-b r.	27.5	10.0	—	11.0	8.0	—	—	—	—	—	—	—	—
Upper Valdarno IGF-865 l.	28.8	11.4	19.3	13.0	9.8	6.6	5.7	—	—	32.9	—	—	—
Upper Valdarno IGF-865 r.	28.0	11.7	18.9	13.1	9.2	6.7	5.9	—	—	32.0	—	—	—
Colle Curti MUC-204	—	—	—	13.0	9.2	—	—	—	—	—	—	—	—
Pirro Nord PN-47	—	—	—	10.0	7.5	—	—	—	—	—	—	—	—
'Ubediya UB II-23	—	—	—	10.6	7.5	—	—	—	—	—	—	—	—
OLD-II (BMNH) M-15017	25.1	10.0	18.8	10.8	7.8	—	—	—	—	—	—	—	—
OLD74 Bed-I-87 l.	28.0	11.0	19.2	11.2	8.6	5.3	5.3	43.5	—	31.3	32.4	37.8	—
OLD-II (BMNH) M-15018 l.	—	—	—	10.0	7.8	—	—	—	—	—	—	—	—
OLD-II (BMNH) M-15019 l.	—	—	—	10.0	7.8	—	—	—	—	—	—	—	—
Kromdraai A KA-1288 r.	28.0	11.2	19.3	—	—	—	—	—	—	—	—	—	—
Campbellpore	—	—	—	—	—	—	—	—	—	—	—	—	—
AMNH-96580 l.	28.4	12.0	20.2	12.6	9.2	—	—	—	—	—	—	—	—
AMNH-96579 l.	28.3	11.2	18.8	12.7	8.8	—	—	—	—	—	—	—	—
Fan Tsun AMNH-97052 l.	30.5	12.0	22.0	12.0	9.6	6.2	6.1	—	—	—	—	—	—
Fan Tsun AMNH-97052 r.	—	12.2	—	12.6	9.0	6.7	6.4	—	—	—	—	—	—

Appendix 1 - Metric comparisons (mm) of the Hayonim mandible to those of recent *Lycaon pictus* samples and late Pliocene-early Pleistocene *Canis (Xenocyon) falconeri*. (L) length; (B) breadth; (MCB) mandibular condyle breadth; (l) left; (r) right; (m) mandible; (*) asymmetrical individual whose right tooth is significantly larger than the left. (OM) National Museum of Kenya; (M) Hebrew University of Jerusalem. Metric data collected by Martínez-Navarro with the exception of specimens from Cueva Victoria (from Pons-Moyà & Moyà-Solà, 1978), Colle Curti, Old-II M-150181, Old-II M-15019, Campbellpore 965791, and Fan Tsun 97052 (from Rook, 1994), and Kromdraai (from Turner, 1986b).

of its area falling within the equatorial bands, and 96% of its lands lie below 1500 m ASL (Girman *et al.*, 1993). Moisture availability is highly variable, but savanna/steppe (19%) and open woodland (31%) constitute much of the recent environments of this continent (Keast, 1972, p. 451); much of its desert lands (30%) could also have been well-vegetated habitats suitable for wild dogs prior to the Holocene. These conditions ultimately may have selected for characters in recent *Lycaon* that are specific to Africa.

SUMMARY AND IMPLICATIONS

The *Lycaon* mandible from Hayonim Cave retains ancestral dental features. The tiny entoconid of the M_1 is pleisiomorphic. A larger version of this feature occurs in *Canis (X.) falconeri*, but it is entirely absent in modern *Lycaon*. Pleisiomorphy is also evidenced for the M_2 . While the sizes of the M_1 and M_2 of the Hayonim specimen are generally consistent with those of modern *Lycaon pictus*, these teeth have somewhat different proportions. The horizontal ramus of the Hayonim mandible is much higher dorso-ventrally relative to thickness than is observed for any modern *Lycaon* population, and the M_3 is relatively large. These last two features bear a strong resemblance to the ancestral species, *Canis (X.) falconeri*.

The presence of *Lycaon* in western Asia during the late middle Pleistocene re-opens the question of where and over how large an area this distinctive genus evolved. The mandible from Hayonim Cave associates with a relatively dry phase of the late middle Pleistocene and a mix of Eurasian and Afro-Arabian community elements. Biogeographic interpretations of the Hayonim specimen must remain tentative with respect to the "directionality" of population incursions. This unique case provides a new point of departure for exploring Pleistocene canid evolution, and raises hope for understanding the early history of an enigmatic lineage.

ACKNOWLEDGMENTS

This research was supported by grants from the National Science Foundation (to M.C.S., SBR-9511894; to O.B.-Y., SBR-9409281), the Israel-United States Binational Science Foundation (to E.T. & M.C.S.), and the Leakey and Levi Sala CARE Foundations (to B.M.-N.).

REFERENCES

- ARAMBOURG, C., 1979, Vertébrés Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux): 141 pp., 61 pls., Editions de la Fondation Singer-Polignac.
- BALLESIO, R., 1986, Les carnivores du Pléistocène d'Oubeidiyeh (Israel). In Tchernov, E. (ed.), Les Mammifères du Pléistocène inférieur de la Vallée du Jourdain à Oubeidiyeh: Mem. et Trav. du Centre de Recherche Français de Jérusalem, 5: 63-91.
- BAR-YOSEF, O., 1991, The archaeology of the Natufian layer at Hayonim Cave. In Bar-Yosef, O. & Valla, F. (eds.), The Natufian Culture in the Levant: International Monographs in Prehistory: 81-93.
- , 1998, The chronology of the Middle Paleolithic of the Levant. In Akazawa, T., Aoki, K. & Bar-Yosef, O. (eds.), Neanderthals and Modern Humans in West Asia: Plenum Press: 39-56.
- BARYSHNIKOV, G., 1996, The dhole, *Cuon alpinus* (Carnivora, Canidae), from the Upper Pleistocene of the Caucasus: Acta Zool. Cracov., 39 (1): 67-73.
- BELFER-COHEN, A. & BAR-YOSEF, O., 1981, The Aurignacian at Hayonim Cave: Paleorient, 7: 19-42.
- BIGALKE, R. C., 1972, The contemporary mammal fauna of Africa. In Keast, A., Erk, F. C. & Glass, B. (eds.), Evolution, Mammals, and Southern Continents: State University of New York Press: 141-194.
- COOKE, H. B. S., 1972, The fossil mammal fauna of Africa. In Keast, A., Erk, F. C. & Glass, B. (eds.), Evolution, Mammals, and Southern Continents: State University of New York Press: 89-139.
- CRÉGUT-BONNOURE, E., 1996, Ordre des Carnivores. In Guérin, C. & Patou-Mathis, M. (eds.), Les Grands Mammifères Plio-Pleistocènes d'Europe: Collection Préhistoire, Masson, Paris: 156-167.
- ESTES, R. D. & GODDARD, J., 1967, Prey selection and hunting behavior of the African wild dog: Journal of Wildlife Management, 31 (1): 52-70.
- EWER, R. F., 1973, The Carnivores: 494 pp., Cornell University Press.
- FANSHAWE, J. H., 1989, Serengeti's painted wolves: Natural History, 3/89: 56-67.
- FARRAND, W. R. & MCMAHON, J. P., 1997, History of the sedimentary infilling of Yarımburgaz Cave, Turkey: Geoarchaeology, 12 (6): 537-565.
- FULLER, T. K. & KAT, P. W., 1990, Movements, activity, and prey relationships of African wild dogs (*Lycaon pictus*) near Aitong, southwestern Kenya: African Journal of Ecology, 28: 330-350.
- GIRMAN, D. J., KAT, P. W., MILLS, M. G. L., GINSBERG, J. R., BORNER, M., WILSON, V., FANSHAWE, J. H., FITZGIBBON, C., LAU, L. M. & WAYNE, R. K., 1993, Molecular genetic and morphological analyses of the African wild dog (*Lycaon pictus*): Journal of Heredity, 84: 450-459.
- HARRIS, J. M., BROWN, F. H. & LEAKEY, M. G., 1988, Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya: Contributions in Science, Natural History Museum of Los Angeles County, 399: 1-128.
- KEAST, A., 1972, Comparisons of contemporary mammal faunas of southern continents. In Keast, A., Erk, F. C. & Glass, B. (eds.), Evolution, Mammals, and Southern Continents: State University of New York Press: 433-501.
- KIESER, J. A. & GROENEVELD, H. T., 1992, Mandibulodental allometry in the African wild dog, *Lycaon pictus*: Journal of Anatomy, 181: 133-137.
- KOUFOS, G. & KOSTOPOULOS, D., 1997, New carnivore material from the Plio-Pleistocene of Macedonia (Greece) with description of a new canid: Münchner Geowissen. Abht. (A), 34: 33-63.
- KRETZOI, M., 1938, Die Ruobtiere von Gombaszög nebst einer Übersicht der Gesamtfaua: Ann. Hist. Nat. Mus. Nation. Hungarici, Pars Miner. Geol. Paleont., Budapest, 31: 88-157.
- KRÜGER, S. C., LAWES, M. J. & MADDOCK, A. H., 1999, Diet choice and capture success of wild dog (*Lycaon pictus*) in Hluhluwe-Umfolozi Park, South Africa: Journal of Zoology, London, 248: 543-551.
- KURTÉN, B., 1968, Pleistocene Mammals of Europe: 317 pp., Aldine Publishing Co.

- MADDOCK, A. H. & MILLS, M. G. L., 1994, Population characteristics of African wild dogs *Lycaon pictus* in the Eastern Transvaal lowveld, South Africa, as revealed through photograph records: *Biological Conservation*, 67: 57-62.
- MARTÍNEZ-NAVARRO, B., 1992a, Revisión sistemática de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada, España). In Gibert, J. (ed.), *Proyecto Orce-Cueva Victoria (1988-1992): Presencia humana en el Pleistoceno inferior de Granada y Murcia*, Ayuntamiento de Orce: 21-85.
- , 1992b, *Megantereon* sp. (Carnivore, Mammalia) de Venta Micena (Orce, Granada, España): *Rev. Esp. Paleont.*, Extra: 113-117.
- & PALMQVIST, P., 1995, Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus: *Journal of Archaeological Science*, 22 (4): 569-582.
- & —, 1996, Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece): *Journal of Archaeological Science*, 23: 869-872.
- M McNUTT, J. W., 1996, Sex-biased dispersal in African wild dogs, *Lycaon pictus*: *Animal Behaviour*, 52: 1067-1077.
- MEIGNEN, L., 1998, Hayonim Cave lithic assemblages in the context of the Near Eastern Middle Paleolithic: a preliminary report. In Akazawa, T., Aoki, K. & Bar-Yosef, O. (eds.), *Neanderthals and Modern Humans in West Asia*: Plenum Press: 165-180.
- MOEHLMAN, P. D., 1986, Ecology of cooperation in canids. In Rubenstein, D. I. & Wrangham, R. W. (eds.), *Ecological Aspects of Social Evolution, Birds and Mammals*: Princeton University Press: 64-86.
- PALMQVIST, P., ARRIBAS, A. & MARTÍNEZ-NAVARRO, B., 1999, Ecological study of large canids from Lower Pleistocene of southeastern Spain: *Lethaia*, 32: 75-88.
- PONS-MOYÀ, J. & MOYÀ-SOLÀ, S., 1978, La fauna de carnívoros del Pleistoceno medio (Mindel) de la cueva Victoria (Cartagena, España): *Acta Geológica Hispánica*, XIII (2): 54-58.
- ROOK, L., 1994, The Plio-Pleistocene Old World *Canis* (*Xenocyon*) ex gr. *falconeri*: *Bollettino della Società Paleontologica Italiana*, 33: 71-82.
- SAVAGE, R. J. G., 1978, Carnivora. In Maglio, V. J. & Cooke, H. B. S. (eds.), *Evolution of African Mammals*: Harvard University Press: 249-267.
- SCHWARZ, H. P. & RINK, W. J., 1998, Progress in ESR and U-Series chronology of the Levantine Paleolithic. In Akazawa, T., Aoki, K. & Bar-Yosef, O. (eds.), *Neanderthals and Modern Humans in West Asia*: Plenum Press: 57-67.
- SHACKLETON, N. J. & OPDYKE, N. D., 1973, Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core, V28-238: *Quaternary Research*, 3: 39-55.
- SOTNIKOVA, M., 2001, The fossil Canidae from the Pleistocene deposits of Untermassfeld near Meiningen. In Kahlke, R. D. (ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen) (teil 2): Römisch Germanisches Zentralmuseum* (in press).
- STINER, M. C., 1994, *Honor among Thieves: A Zooarchaeological Study of Neandertal Ecology*: 447 pp., Princeton University Press.
- , KUHN, S. L., SUROVELL, T. A., GOLDBERG, P., MEIGNEN, L., WEINER, S. & BAR-YOSEF, O., 2001, Bone preservation in Hayonim Cave (Israel): a macroscopic and mineralogical study: *Journal of Archaeological Science*: 28 (in press).
- , MUNRO, N. D. & SUROVELL, T. A., 2000, The tortoise and the hare: small game use, the Broad Spectrum Revolution and Paleolithic demography: *Current Anthropology*, 41 (1): 39-73.
- & TCHERNOV, E., 1998, Pleistocene species trends at Hayonim Cave: Changes in climate versus human behavior. In Akazawa, T., Aoki, K. & Bar-Yosef, O. (eds.), *Neanderthals and Modern Humans in West Asia*: Plenum Press: 241-262.
- TCHERNOV, E., 1968, Succession of Rodent Faunas during the Upper Pleistocene of Israel: 152 pp., *Mammalia Depicta*, Paul Parey.
- TURNER, A., 1984, Hominids and fellow-travellers: Human migration into high latitudes as part of a large mammal community. In Foley, R. (ed.), *Hominid Evolution and Community Ecology*: Academic Press: 193-218.
- , 1986a, Correlation and causation in some carnivore and hominid evolutionary events: *South African Journal of Science*, 82: 75-76.
- , 1986b, Miscellaneous carnivore remains from Plio-Pleistocene deposits in the Sterkfontein valley (Mammalia, Carnivora): *Annals of the Transvaal Museum*, 34: 203-226.
- VALLADAS, H., MERCIER, N., JORON, J.-L. & REYSS, J.-L., 1998, GIF Laboratory dates for Middle Paleolithic Levant. In Akazawa, T., Aoki, K. & Bar-Yosef, O. (eds.), *Neanderthals and Modern Humans in West Asia*: Plenum Press: 69-75.
- WAYNE, R. K., 1993, Molecular evolution of the dog family: *Trends in Genetics*, 9 (6): 218-224.
- WOODROFFE, R. & GINSBERG, J. R., 1999, Conserving the African wild dog *Lycaon pictus*: I. Diagnosing and treating causes of decline: *Oryx*, 33 (2): 132-142.

(manuscript received September 19, 2000
accepted January 12, 2001)

Mary C. STINER

Dept. of Anthropology, Building 30
University of Arizona
Tucson, AZ 85721, U.S.A.
Email: mstinер@u.arizona.edu

F. Clark HOWELL

Laboratory of Human Evolutionary Studies
Museum of Vertebrate Zoology
University of California-Berkeley
Berkeley, CA 94720, U.S.A.

Bienvenido MARTÍNEZ-NAVARRO

Venta Micena 74
18858 Orce
Granada, Spain

Eitan TCHERNOV

Department of Evolutionary Systematics & Ecology
The Hebrew University of Jerusalem
91940 Jerusalem, Israel

Ofer BAR-YOSEF

Department of Anthropology
Peabody Museum, Harvard University
Cambridge, MA 02138, U.S.A.