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Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain)

The carnivores from Trinchera Dolina level 6 (TD6) in Sierra de Atapuerca include *Ursus* sp., *Crocuta crocuta*, *Mustela palerminea*, *Lynx* sp., *Canis mosbachensis* and *Vulpes praeglacialis*. Approximately 80 human remains belonging to *Homo antecessor* were found in the Aurora Stratum (AS): located in the upper part of the TD6 level (TD6, T36–43). The carnivores from AS are taxonomically similar to the rest of the TD6 level, differing only in the occurrence of *Lynx* sp. The spotted hyaena (*Crocuta crocuta*) inhabited the Atapuerca Sierra during the Early Pleistocene and up to the Middle Pleistocene, after which it is absent. According to palaeomagnetic, U/Th and ESR results, the fossils from TD6 are dated to the Early Pleistocene, which is the earliest certain occurrence in Europe of *Crocuta crocuta*. It is associated with *Mimomys savini*, the arrival of which in Europe can be correlated with the beginning of the Early Biharian. *Crocuta crocuta* may have arrived during the late Early Pleistocene ("Bavelian complex"), and subsequently invaded the rest of the continent during the Middle and Late Pleistocene. Atapuerca TD6-AS represents the most ancient deposits in Europe where *Homo* and spotted hyaenas coexisted and, they probably competed ecologically. The carnivores from TD6 are biochronologically consistent with the end of the Early Pleistocene or early Cromerian (corresponding with the Biharian biochron). The timespan could correspond with oxygen isotope stages 19, 20 or 21.

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Introduction and history of the discoveries

The Sierra de Atapuerca, near Burgos, is a complex system of cavities which were filled with sediments throughout the Quaternary. Several cave fillings have yielded fossils and/or artefacts, including Sima de los Huesos (SH), Trinchera-Galería (TG) and Gran Dolina (TD).

The TD sequence has 17 m of sediments exposed, divided into 11 lithostratigraphic levels (Parés & Pérez-González, 1995). These layers are numbered, from bottom to top, TD1 to TD11. Most of the levels (TD3, TD4, TD5, TD6, TD8, TD10 and TD11) are rich in fossil remains, but TD1, TD2, TD7 and TD9 lack carnivores. Parés & Pérez-Gozález (1995) obtained palaeomagnetic results from 22 samples taken throughout the section. They found that the Matuyama–Bruhnes boundary was located in the lower level of TD7, just above the horizon where the *Homo antecessor* remains were discovered. This study focuses on the TD6 carnivore remains, especially their taxonomic, biostratigraphic and palaeoecological significance. In the upper part of TD6, in the Aurora Stratum (AS), the *H. antecessor* remains were recovered together with pre-Acheulian (or Mode 1) artefacts. The carnivores from Atapuerca TD6-AS include: *Ursus* sp., *Crocuta crocuta*, *Vulpes praeglacialis*, *Mustela palerminea*, *Lynx* sp.

Table 1 Inventory of carnivores from Trinchera-Dolina 6 (TD6) Early Pleistocene site (Sierra de Atapuerca)

Label	Depth (talla)	Skeletal part	Taxon
ATA94-TD6-I16-23	38	Proximal phalanx	*C. crocuta*
ATA94-TD6-J18-47	38	Distal epiphysis of metapodial bone	*Ursus* sp.
ATA94-TD6-I16-43	39	Proximal phalanx	*Ursus* sp
ATA94-TD6-G16-24	39	Anterior premolar	*Ursus* sp.
ATA94-TD6-H16-202	40–41	Distal part of right tibia	*C. mosbachensis*
ATA95-TD6-H16-200	40–41	Distal epiphysis of metapodial bone	Canidae indet.
ATA95-TD6-H16-175	40–41	Left P_3	*V. praeglacialis*
ATA95-TD6-H17-96	40–41	Left M^1	*Lynx* sp.
ATA95-TD6-I16	40–41	Left hemimandible	*M. palerminea*
ATA95-TD6-G17-99	40–41	Right talus	*V. praeglacialis*
ATA95-TD6-G17-103	40–41	Right femur	*V. praeglacialis*
ATA95-TD6-I16-167	42	Right femoral head	*C. mosbachensis*
ATA96-TD6-I18-61	43	Left lower canine	*C. crocuta*
ATA96-TD6-G16-276	48	Medial phalanx	*C. crocuta*
ATA96-TD6-G17-337	49	Medial phalanx	*C. crocuta*
ATA96-TD6-G17-339	49	Distal part of left humerus	*V. praeglacialis*
ATA96-TD6-G17	50	Incisor	*C. crocuta*
ATA96-TD6-H16-509	52	Left unerupted M_3	*Ursus* sp.
ATA96-TD6-I17-133	53	Right unerupted M_3	*Ursus* sp.
ATA96-TD6-G16-305	53	Deciduous canine	*Ursus* sp.
ATA96-TD6-I16-269	52	Mandibular condyle	*C. crocuta*
ATA97-TD6-I16-312	54	Second metacarpal	*C. crocuta*
ATA97-TD6-I16-328	54	Right lower canine	*C. crocuta*
ATA97-TD6-H18	54	Right hemimandible	*M. palerminea*

The labels include the prefix of Atapuerca and the year of excavation (ATA94), the site and stratigraphic level (TD6) the square (I16), the number of the fossil within this square (23) and additional information, for instance on depth (talla 38=sub-level of excavated sediment). The full label is given as: ATA94-TD6-I16-sublevel (talla) 38-23, although in this list the sub-level (talla) is written separately in order to differentiate the fossils included in the Aurora Stratum (AS).

and *Canis mosbachensis*. In the 8 m^2 test excavation there was no evidence of large-sized felids.

Only three carnivore taxa have previously been recorded from the lower levels of TD: (1) a left tibia of *Panthera gombaszoegensis* (AT76-st-05), (2) an almost complete skull of *Crocuta crocuta* (AT76-z-918) (Morales et al., 1987) and (3) remains of an ursid attributed to *Ursus prearctos* (Torres, 1987). *Crocuta crocuta* was reported at Atapuerca from TD3 (Aguirre & Morales, 1990), although Torres (personal communication), who found the fossils, assigns them to levels TD4–TD5.

The aim of this paper is to describe the recently excavated (1994–1997) carnivore fossils from the test trench in TD6.

Material and methods

An inventory of specimens is given in Table 1. Standard dental and anatomical terms are used. Measurements are mostly taken with digital calipers, as indicated by von der Driestch (1976), and are recorded to the nearest 0·1 mm. Mustelids were measured using a Nikon monocular digital microscope.

Comparative collections: Institute d'Anatomie Compareé (Paris), Museé Regional du Menton (Nice), National Museum of Natural History, Smithsonian Institution (Washington, D.C.), Estación Biológica de Doñana (Sevilla), Istituto di Geología (Florence), Institut Quartärpalä-ontologie (Weimar), Museo Nacional de

Figure 1. *Vulpes praeglacialis*: (a) right femur; (b) right talus bone. *Canis mosbachensis*: (c), (d) distal part of a right tibia; (e) left hemimandible from TD5. *Ursus* sp: (f) right M_3. *Crocuta crocuta*: (g) right lower canine; (h) left lower canine; (i) right second metacarpal; (j) medial phalanx; (k) proximal phalanx; (l) left femur from TD5. Scale bar represents 2 cm except for (1) which represents 0·5 cm.

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Canidae

Vulpes praeglacialis *Kormos, 1932*
The specific assignment is based on a right femur, the distal third of a left humerus, a P_3, and a right talus (Figure 1). In spite of its scarcity, the sample is large enough for positive identification because the red fox,

Vulpes vulpes (both extant and Middle Pleistocene samples), is much larger than the TD6 fossils (Table 2). *V. praeglacialis* dimensions from L'Escale are similar to those of the TD6 remains and to those of the extant arctic fox (*Alopex lagopus*). The greater trochanter of the *V. praeglacialis* femur is comparably developed to that in the L'Escale specimens (Bonifay, 1971). In *V. praeglacialis* P_3 and M_2 have a different morphology from those in *V. vulpes*. The P_3 in *A. lagopus, V. praeglacialis* and the TD6

Table 2 *Vulpes praeglacialis.* **Measurements of the TD6 femur (ATA95-TD6-G17-103), talus (ATA95-TD6-G17-99) and humerus (ATA96-TD6-G17-339) compared with the same species from the site of L'Escale (Bonifay, 1971), and with the *Vulpes vulpes* sample from the Middle Pleistocene site of Sima de los Huesos**

	L'Escale			Dolina (TD6)			*Vulpes vulpes* (SH)		
	Humerus	Talus	Femur	Humerus	Talus	Femur	Humerus	Talus	Femur
GL						110·3			(n=2) 125·3
Bp			(H-7536) 22·4			21·1			(n=4) 26·7 ± 1·3
Bd	(H-7568) 17·8		(H-7504) 17·5	16·1		17·8	(n=5) 21 ± 0·5		(n=4) 20·6 ± 1·7
DCf						9·9			(n=9) 12·3 ± 0·5
TDp						10·2			(n=8) 12·2 ± 0·6
GL		(H-7500) 17·2			15·4			(n=13) 19·6 ± 1·1	
GW		(H-7500) 10·6			9·4			(n=13) 11·7 ± 1·1	

GL: greatest length; Bp: breadth at the proximal end (for femur); Bd breadth at the distal end (for the humerus and the femur); DCf: depth of the caput femoris; TDp: transversal diameter of the proximal epiphysis (of femur); GL: greatest length (for talus); GW: greatest width (for talus).

specimen does not show any posterior denticulate, a feature that is always present in other canids. The smaller size is considered the main diagnostic feature of this fox species, and this criterion has been used to identify the taxon at other Pleistocene sites, such as L'Escale (Bonifay, 1971), Le Vallonnet (Moullé, 1992) and Petralona (Kurtén & Poulianos, 1981).

This small fox occurs in Early Pleistocene sites, such as Betfia 2 (Romania; Terzea, 1996), Kamyk and Kozi Grzbiet (early and late Biharian respectively, from Poland; Wolsan, 1993), Le Vallonnet (France, correlated to the Jaramillo subchron; Moullé, 1992), Cúllar-Baza, Spain, (Spain, aminostratigraphically dated to 441 ± 27 ka; Mazo et al., 1985; Torres et al., 1997) Gombasek 1 and Stránská-Skála (Cromer I and Cromer IV respectively, from the Czech Republic) and Venta Micena (VM) (Spain: aminostratigraphically dated to 983 ± 58 ka; Torres et al., 1997). The last occurrence of this species is in the Middle Pleistocene French sites of L'Escale and La Caune de L'Aragò, younger than Cromer IV (o.i.s. 12).

Canis mosbachensis Soergel, 1925
The systematics of wolves in the early Middle Pleistocene of Europe is subject to debate. Different names are used, such as *Canis etruscus mosbachensis*, which refers to an evolved form of the Villafranchian *C. etruscus*. *C. lupus mosbachensis* is included in a subspecific category due to the presence of a paraconid (in M_1) that is higher than the last premolar (P_4), as in *C. lupus* (Torre, 1974). It is generally accepted that *C. etruscus* evolved into a smaller form, *C. mosbachensis*, and that the latter evolved into the larger "true" wolf, *C. lupus*, during the Middle Pleistocene (Kurtén, 1968; Rook & Torre, 1996).

C. etruscus occurs in Asia in deposits dated to 3 Ma (Rook & Torre, 1996), but its arrival in Western Europe occurs in the Middle Villafranchian at the site of Costa S.

Figure 2. *Homotherium latidens:* Specimens from level TD5; (a) left I^3; (b) right lower canine; (c) distal end of the crown of an upper canine; (d) left lower canine. Scale bar represents 0·5 cm.

Giacomo in the Anagni basin, Latium (Italy). It is an abundant taxon in the Upper Valdarno basin and Olivola, both Late Villafranchian sites, as well as at a number of localities prior to the Jaramillo event. *Canis arnensis* from the late Villafranchian has been proposed by Rook & Torre (1996) as a candidate for the ancestor of Middle Pleistocene wolves of the Mediterranean region. These authors postulate two lineages with parallel evolution: one in the Mediterranean area leading from *C. arnensis* to *C.* aff. *arnensis* (advanced form), and another in northern and central Eurasia leading from *C. etruscus* to *C. mosbachensis*. Rook (1993) attributes specimens from L'Escale, Petralona, Huescar-1, Cullar Baza, Le Vallonnet and VM to *C.* aff. *arnensis*, while other authors assign them to *C. mosbachensis*, along with those from Mosbach, Voigstedt, and Hundsheim. Del Campana (1913) described *C. arnensis* as resembling extant jackals and coyotes. Rook & Torre (1996) found another distinctive character, ''a M_1 paraconid relatively low and does not rise over the main cusps of the premolars.'' However, this is a plesiomorphic trait for *Canis*. The length of M_1/length of M_2 ratio should be expected to be greater in *C. arnensis* than in *C. etruscus* (Rook, 1993), but we do not find this to be the case in our analysis (Figure 3).

In our opinion, *C. mosbachensis* and *C.* aff. *arnensis* represent a single ''small wolf'' population at European Early Pleistocene sites, such as at VM, Untermassfeld and Le Vallonnet. It becomes common during the Cromerian, being present at Voigstedt, Süssenborn, Westbury, Mauer, West Runton, Huescar-1, and Boxgrove. Its last occurrence is at L'Aragò and L'Escale (o.i.s. 12).

The wolf from Atapuerca levels TD5 to TD8 is assigned to *C. mosbachensis*: the hypoconulid basin of M_1 (from TD8) is poorly developed; the second posterior cusplet of P_4 is low and separated from the posterium cingulum. These features distinguish the *C. mosbachensis* line. We have recovered from TD6-AS two specimens of this canid, a distal part of a right tibia and a right femoral head. The tibia is within the L'Escale *C. mosbachensis* range, close in size to the Colle Cruti *C.* cf. *arnensis* specimen (Ficcarelli & Mazza, 1990), and morphologically and metrically similar to the specimens from Il Tasso (Table 3). In Figure 3 we compare a fragment of a left hemimandible from TD5 and a complete left hemimandible from TD8 with other canids: a Z-score profile was developed in which measurements of *Canis etruscus* (*n*=34), *Canis arnensis* (*n*=13) and *Canis apolloniensis* (*n*=3) were standardized to the

Table 3   *Canis mosbachensis* (tibia and femur) from TD6 compared with *Canis l.*
mosbachensis from L'Escale (Bonifay, 1971) and *Canis* cf. *arnensis* from
Colle Curti (Ficarelli & Mazza, 1990)

| | | *C. mosbachensis* Dolina (TD6) | *C. arnensis* Il Tasso | | *C. mosbachensis* L'Escale ($n=10$) | *C.* cf. *arnensis* Colle Curti |
			IGF1238	IGF1242		
BD	(H16-202)	21·8	21·4	21·2	$20\cdot4 \pm 0\cdot95$	~21
Dd	(H16-202)	16·1	14·1	15·5		
DC	(I16-167)	18·8				

BD: breadth of the distal end; Dd: depth of the distal end; DC: depth of the caput
femoris.

Canis mosbachensis mean and standard deviation (sample $n=42$, from L'Escale, Hundsheim and Petralona Middle Pleistocene sites). From Figure 3 we observe that all of the variables of the TD specimens are within the *C. mosbachensis* range. *C. etruscus* is more than one standard deviation above the *C. mosbachensis* mean, except for the indices, which are closer to the rest of the canids. The occurrence of this species in the Sierra Atapuerca is almost continuous throughout the TD sequence, dating from around 800 ka in TD6 to TD8 which is dated to between 563 ± 84 ka and 653 ± 98 ka (Falguères *et al.*, 1999).

Hyaenidae

Crocuta crocuta Erxleben, 1777

In the 1994 field season a proximal phalanx belonging to a hyaenid was recovered in the AS (talla 38). In 1996, at the base of the AS (talla 43) a right lower canine of a hyaenid was found. In TD6, below the human fossil stratum, additional remains of this carnivore were found: two more phalanges, another lower canine (from a different individual), and a second metacarpal. It is also known from levels TD4–5 and TD8 (above and below TD6).

Based on the dimensions of the two canines (Figure 4), the material cannot be assigned to the giant hyaena, *Pachycrocuta brevirostris*, first known in Europe at Olivola, and occurring between 1·6 Ma and possibly 0·5 Ma (Turner, 1992). The hyaenid canines from TD6 fit perfectly in the range of the extant *C. crocuta*.

The genus *Crocuta* represents a polymorphic taxon. The size variation at different Pleistocene sites could be the result of climatic differences (Kurtén, 1957; Klein & Scott, 1989). It is not clear that differentiation of Glacial/Interglacial population can be inferred on the basis of size, but it seems that temperature and mean size in *C. crocuta* are inversely related in keeping with Bergmann's rule (Kurtén, 1957; Kurtén & Poulianos, 1977; Klein & Scott, 1989). The TD6 canines are smaller than the specimens from Middle Pleistocene sites, such as Petralona, (named *C. crocuta spelaea* by Kurtén & Poulianos, 1977) or Ehringsdorf (Lower Travertine), which have larger dimensions than any of the TD canines (TD6 and TD8), and fall at the upper limit of the range of extant populations (Figure 4). The chronology of Ehringsdorf is problematic. For some authors it correlates to substage 5e or Eemian (for discussion, see Kahlke, 1995*b*) and for others it correlates to stage 7 (Blackwell & Schwarcz, 1986). It is certain, however, that this unit contains a fully interglacial mammal fauna. The second metacarpal (length=79·8) recovered from

Lower dentition variables and indices
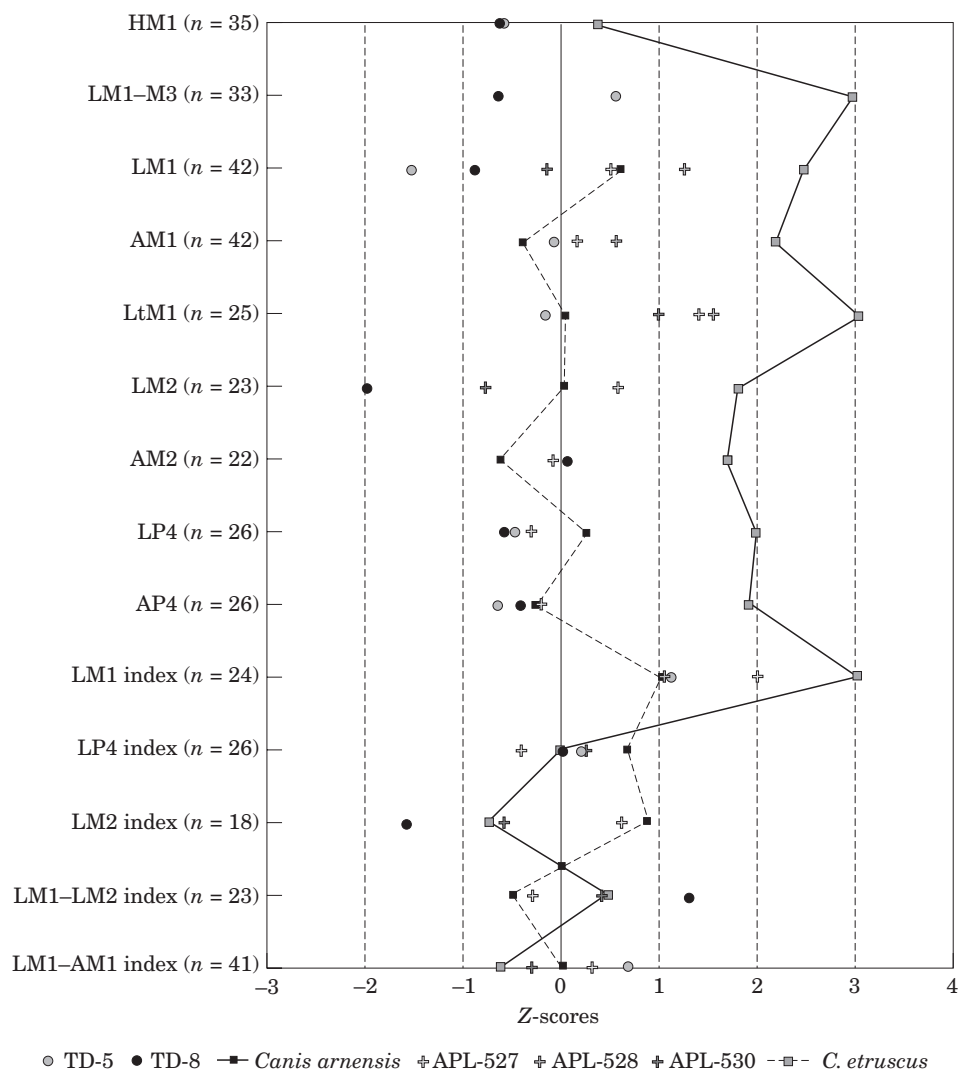(*Canis mosbachensis* sample:L'Escale,
Petralona, Hundsheim and Voigstedt)

○ TD-5 ● TD-8 ─■─ *Canis arnensis* ⊹APL-527 ✦ APL-528 ✚ APL-530 -▪- *C. etruscus*

Figure 3. *Z*-score profiles of dental variables for TD5 (TD5-TD6-G17-14), TD8 (TD8-I16-1), *Canis etruscus* from Valdarno and Olivola ($n=34$), *C. arnensis* from Il Tasso and Upper Valdarno ($n=13$), *C. apolloniensis* from Apollonia 1 ($n=3$; Koufos & Kostopoulos, 1997) and *C. mosbachensis* from L'Escale ($n=24$; Bonifay, 1971), Hundsheim ($n=4$) and Petralona ($n=14$; Kurtén & Poulianos, 1981). Each individual was put in standard form: the *C. mosbachensis* mean is subtracted from it and then divided by the *C. mosbachensis* standard deviation. The central vertical line represents the *C. mosbachensis* average and the discontinuous vertical lines to the right and left represent the *C. mosbachensis* standard deviations. HM_1=mandibular height at M_1; $LM_1–M_3$=$M_1–M_3$ length; LM_1=M_1 length; AM_1=M_1 breadth; LtM_1=M_1 trigonid length; LM_2=M_2 length; AM_2=M_2 breadth; LP_4=P_4 length; AP_4=P_4 breadth; LM_1 index=LM_1/LtM_1 index; LP_4 index=LP_4/AP_4 index; LM_2 index=LM_2/AM_2 index; $LM_1–LM_2$ index=LM_1/LM_2 index; $LM_1–AM_1$ index=LM_1/AM_1 index.
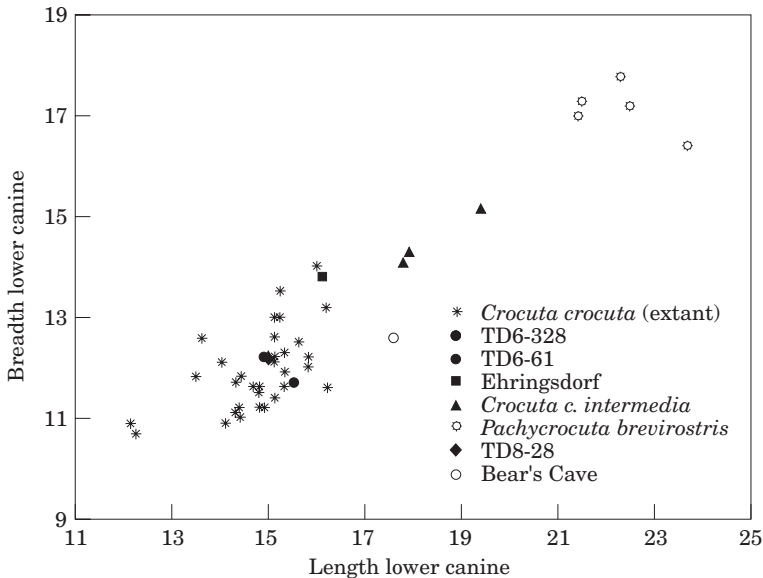
Figure 4. Plot of breadth/length index of lower hyaenid canine. The two specimens from TD6 (TD6-328 and TD6-61) and from TD8 are within the extant *Crocuta crocuta* sample range. *C. intermedia* and the Bear's cave specimens have higher values (Tchernov & Tsoukala, 1997; Turner & Antón, 1996).

the lowest TD6 level (talla 54) is within the range of the extant sample ($n=7$; $\bar{X}=85{\cdot}4$, max$=90{\cdot}5$, min$=75{\cdot}7$; Cardoso, 1993). A complete femur from TD5 (length$=247{\cdot}5$) also coincides with the extant sample range ($n=10$; $\bar{X}=244{\cdot}7$, max$=274$, min$=226$; Cardoso, 1993; $n=9$, $\bar{X}=245$; Turner & Antón, 1997). In conclusion, the canines and postcranial elements from TD5, TD6 and TD8 indicate that *Crocuta* from these levels was small compared with those from Late Pleistocene sites (*C. c. spelaea*), but was similar in size to the living spotted hyaena.

Ursidae

Ursus *sp. Linné, 1758*
In 1994 a distal epiphysis of a metapodial of an ursid was recovered from TD6-AS (talla 38). In the 1996 field season, two M_3s from a single individual were found in talla 52–53. One of them is broken, and both are

germs with no wear and with the roots just beginning to form. This stage of development corresponds to a juvenile individual younger than two years of age (Couturier, 1954; Torres, 1987).

In the *deningeri-spelaeus* group M_3 is characterized by extreme size and by a labial indentation. This latter feature is not present in the TD6 specimen which does not have distinct cusps. The talonid is short, and exhibits a rounded outline. Its dimensions (length $M_3=20{\cdot}4$; breadth $M_3=16{\cdot}6$) are comparable to extant Iberian *Ursus arctos* ($n=33$; $\bar{X}$ length $M_3=19{\cdot}4\pm1{\cdot}8$; $\bar{X}$ breadth $M_3=14{\cdot}7\pm1{\cdot}3$), although there is a certain degree of overlap with the smallest specimens of *U. deningeri* from SH in the Atapuerca Sierra ($n=76$; $\bar{X}$ length $M_3=24{\cdot}04\pm2{\cdot}1$; $\bar{X}$ breadth $M_3=17{\cdot}5\pm1{\cdot}2$) and from Le Vallonnet (Moullé, 1992). Torres (1987) assigned remains of an ursid from the lowermost levels to *U. prearctos* due to its similarity to the type material figured

Table 4   **Measurements for specimens of *Homotherium latidens* from TD5**

	C_1 (TDE5-T61-H16-10)	C_1 (TDE5-T63-F18-1)	I^3 (TDE5-T64-G16-61)
APD	13·1	13	10·1
TD	9·2	9·4	10·3

C_1: lower canine; I^3: third upper incisor; APD: anteroposterior diameter; TD: transversal diameter.

by Boule (1906) from Grotte du Prince. However, the paucity of the sample does not allow a specific determination.

Felidae

Lynx *sp. Kerr, 1792*
This medium-sized felid is represented in TD6 only by an M^1 (length=5·5, width=3·2). It is smaller than *L. spelaea* from L'Escale ($7·3 \times 3·5$; Bonifay, 1971), but larger than an extant sample ($n=12$) of *L. pardina* from Montes de Toledo (Spain) with values of $4·5 \pm 0·38$ and $2·8 \pm 0·24$. We are unable to make a specific identification, given the scarcity of the material. However, we can at least confirm the presence of the genus in TD6. Also, in Sierra de Atapuerca *L. pardina spelaea* is a common taxon at TG and SH, both placed between o.i.s 9 and 11 (García & Arsuaga, 1998; García *et al.*, 1997).

Homotherium latidens *Owen, 1846*
This lion-sized sabre-toothed cat is present in level TD5 (Figure 2; Table 4). The crenulations of the teeth leave no doubt about the identity of these remains. This large cat is known throughout Europe and Asia from around 3 Ma, having its last occurrence in Western Europe 458 ka ago in Fontana Ranuccio (Gliozzi *et al.*, 1997). TD6 has not yet yielded any large-sized felids (such as *Homotherium*). In palaeo-ecological terms, the absence of such a large predator in the meat-eater category of Van Valkenburgh (1988) is difficult to explain.

Mustelidae

Mustela palerminea *Petenyi, 1864*
This is one of the smallest mustelids. *M. praenivalis* (as well as the extant weasel) is smaller still when populations of both species are compared, but some individuals of weasels and stoats may overlap (Table 5). One left hemimandible with M_1–M_2 was found in the AS (talla 40–41). Another right hemimandible was recovered in TD6. Both specimens share features related to robustness of the mandibular ramus. The torus is well marked at the level of the roots of the teeth (this was never observed in any of the more than 30 extant *M. erminea* mandibles studied by N.G.). All dimensions of the fossil specimens fall within the *M. erminea* range and more than twice standard deviations from the mean of the *M. nivalis* sample from La Fage (Hugueney, 1975). The height of the horizontal ramus in the TD6 mustelids is similar to the *Mustela palerminea* values from La Fage and to a *Mustela erminea* sample from the north of Spain, and it is always greater than in *M. nivalis* or *M. praenivalis*. We consider both specimens from TD6 to belong to *Mustela palerminea*. This species is found at Early Pleistocene (e.g., Betfia V) and early Middle Pleistocene localities (e.g., Gombasek).

Chronology discussion and conclusions

The carnivores from Atapuerca TD6-Aurora Stratum include *Ursus* sp., *C. crocuta*, *M. palerminea*, *Lynx* sp., *C.*

Table 5 Comparison of *Mustela palerminea* from TD6 with other mustelids

	TD6 H18 (t54)	TD6 I16 (t40–41)	*M. erminea* (extant)	La Fage (*M. nivalis*)	*M. palerminea*	*M. praenivalis*
LM$_1$	4·8	5·0	5·7 ± 0·54	4·2 ± 0·16	5·5 (n=2)	3·8 (n=1)
WM$_1$	1·6	1·8	2·1 ± 0·18	1·3 ± 0·02	2·1 (n=2)	1·1 (n=1)
LP$_4$	2·4		2·9 ± 0·25	2·1 ± 0·05	2·9 (n=1)	2·1 (n=1)
LP$_2$–M$_2$				9·1 ± 0·77	12·3 (n=1)	8·9 (n=1)
LC–M$_2$	13·4		14·9 ± 1·12	10·8 ± 1·2	14·9 (n=1)	
LM$_{1–2}$		5·9		4·9 ± 0·26	6·5 (n=2)	4·7 (n=2)
HM$_1$	4·2	4·4	4·0 ± 0·34	2·9 ± 0·26	4·6 (n=2)	2·8 (n=1)
MdT	2·3	2·7	2·5 ± 0·25	1·8 ± 0·10	2·5 (n=2)	1·6 (n=1)
APDC$_i$	2·2		2·8 ± 0·34	2·4 ± 0·02		

Data from La Fage Middle Pleistocene site (France) are from Pleistocene Hugueney (1975); (the sample from La Fague is larger than thirty individuals). The extant *Mustela erminea* sample (n=29), includes data from several localities of northern Spain (i.e., Burgos, León, Galicia, Santander and Asturias). Variables as in Figure 3 and Table 4. MdT=mandibular thickness.

mosbachensis and *V. praeglacialis* (Figures 5 & 6). All these species are compatible with a late Early Pleistocene age. Since the Matuyama–Bruhnes boundary was detected in TD7 (Parés & Pérez-González, 1995), the TD6 remains are older than 780 ka. Direct dates on the fossils using ESR and U/Th methods are consistent, ranging from 780 to 886 ka (Falguères *et al.*, 1999).

The faunal and palynological evidence from TD6 does not indicate a cold climate (García Antón, 1995; van der Made, 1998), so the most likely correlation is with a warm period, such as o.i.s. 19 or 21. However, we cannot totally disregard a possible correlation with o.i.s. 20, given the lack of extreme glacial conditions in the Iberian Peninsula.

The carnivore sample from TD6-AS is fragmentary and scarce. This rarity may be explained by taphonomic factors, including human or hyaena activity.

This study has helped refine the temporal range of certain taxa in Europe. This is the case for *C. crocuta*, which is now placed chronologically between o.i.s. 20 and 21. *Crocuta* was thought to have made its first appearance in Europe during the early Middle Pleistocene. *C. crocuta* remains of undoubted taxonomic assignment are recorded from Selva Vecchia (Italy), but the chronology of this site is unclear because the associated species cover a wide time span, up to around 500 ka. Betfia V (Romania) is placed by Terzea (1996) immediately below the Jaramillo event. Kretzoi (1941) included ?*Crocuta* sp. among the carnivores from this site based on a fragmentary first phalanx that clearly belongs to a hyaenid. The size and ambiguity of the sample, however, suggests that a possible attribution to a hyaenid other than *Crocuta* is possible. Given the dubious chronology of Selva Vecchia and the unclear taxonomic attribution of the Betfia material, the *C. crocuta* remains from the lowermost levels of TD (TD4–5) represent the oldest occurrence of undoubted stratigraphical and chronological position in Europe.

The route by which the first spotted hyaenas migrated from Africa (or Asia) to Europe is uncertain. One possible route is through the Arabian Peninsula, where *Crocuta* was already present at Oubeidiya (1·5 Ma), then through Anatolia and finally crossing the Bosphorous and Dardanelles at the Black Sea (which in the cold periods was passable due to low sea level). Another
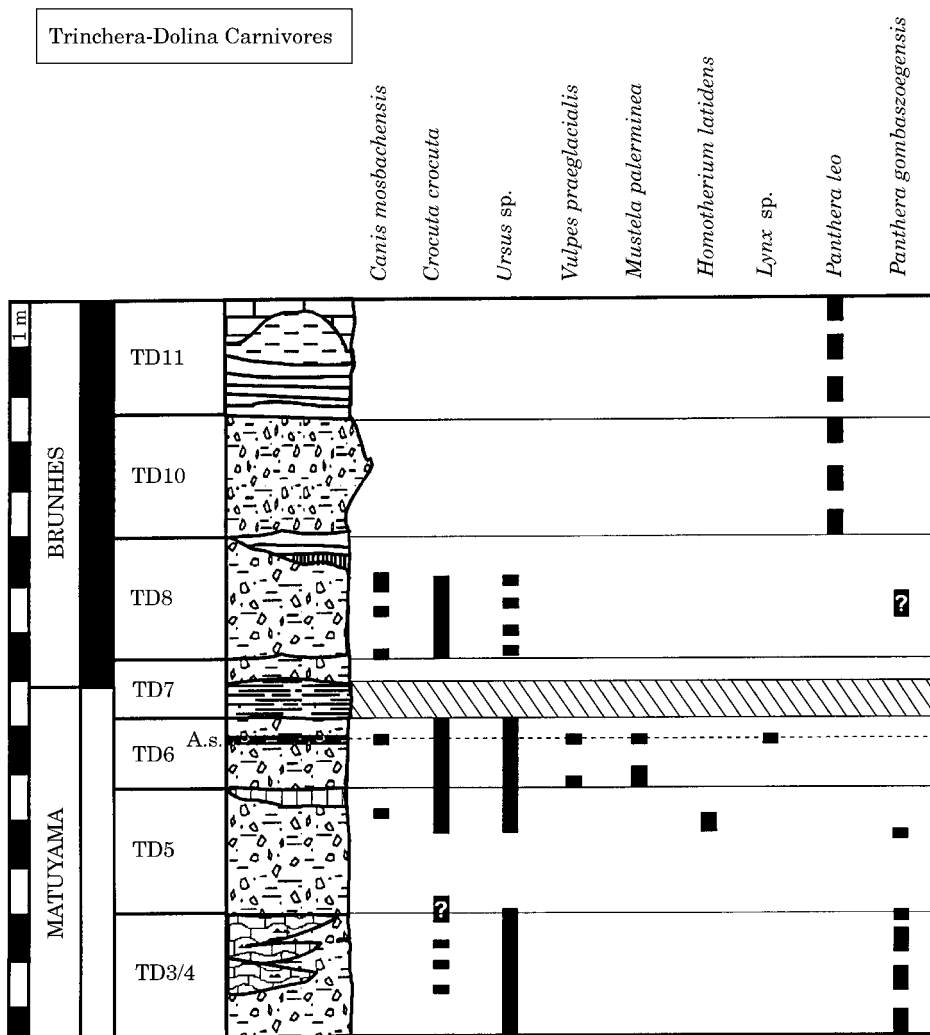
Figure 5. Distribution of TD6 carnivores. Taxa from the uppermost and lowermost levels (TD10-TD11-TD3/4) are only partially figured. *Panthera leo* is only present in Trinchera Dolina in TD10 and TD11, while *Homotherium latidens* is present in TD5 and *Panthera gombaszoegensis* in TD3/4 and TD5. *C. crocuta* inhabited the Sierra since the Early Pleistocene levels at TD3/4 and was co-existing with *H. antecessor* (in TD6 level) and in the TD8 Middle Pleistocene level. (AS=Aurora Stratum). (?=uncertain occurence for *P. gombaszoegensis* in TD8, and uncertain level TD4–TD5 for *C. crocuta*). The TD5 level is still in the process of excavation (in the 8 m² test trench).

possibility is via the Caucasus. Although it probably functioned as an ice barrier during cold periods, Vekua (1986) reports the occurrence of *C*. cf. *sinensis* at the Early Pleistocene site of Akhalkalaki (Georgia; ∼50 km from Dmanisi). The existence of late Early Pleistocene sites with possible

Crocuta remains in Georgia, Romania, Italy and Spain supports the hypothesis of a migration route through East Europe around one Ma. The same route could also have been used by the first hominids (*H. antecessor*) which arrived in Europe at roughly the same period. A land bridge
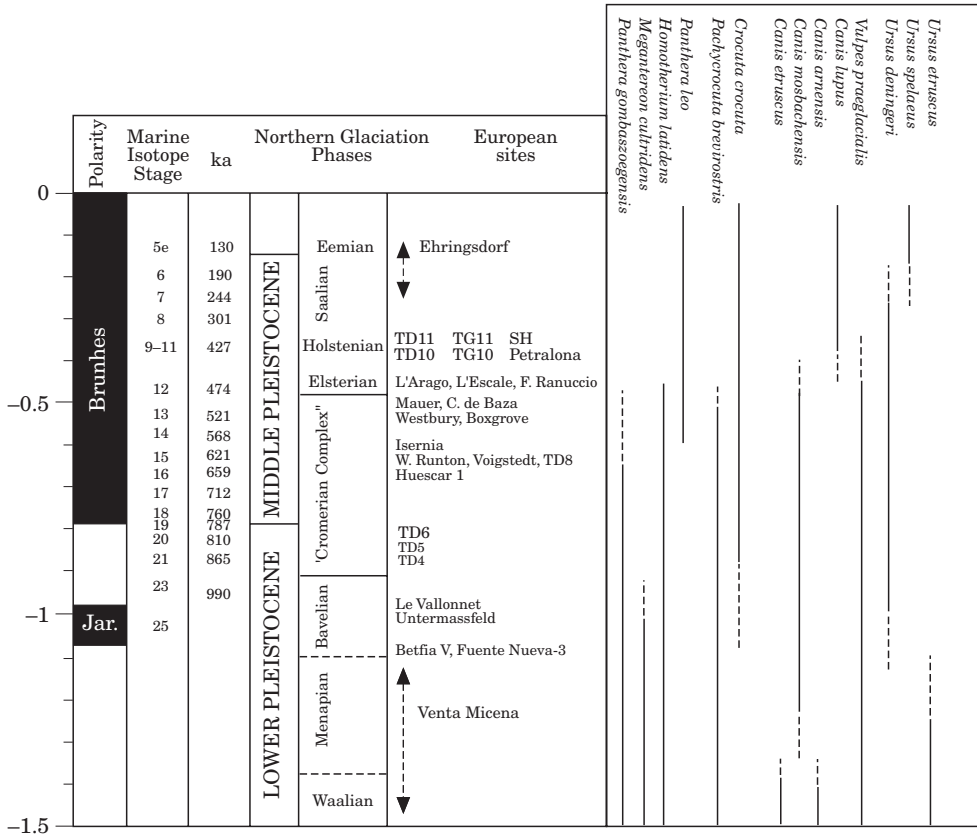
Figure 6. Biochronological position of some European sites and the temporal distribution of carnivore taxa. Different methods were employed for correlation: paleomagnetism, ESR, amino-acid racemization, U-series, and palaeontological (micro- and macromammal) evidence. The source of o.i.s. data is Aitken & Stokes (1997), and specifically for stages 17 to 21 Bassinot *et al.* (1994). Geomagnetic polarity timescale from Cande & Kent (1995). Faunas from Süssenborn, Voigtstedt, Huescar 1, Cúllar de Baza, Le Vallonnet, Petralona, Sima de los Huesos, TG11, TG10, TD11, TD10, TD8, TD6, TD5 and TD4 were studied by the authors. Data obtained from literature: Mauer (Koenigswald, 1995; Kolfschoten, 1996), Untermassfeld (Kahlke, 1995b), Isernia (Roebroeks & Kolfschoten, 1994; Sala, 1990; Gagnepain, 1996; Gagnepain *et al.* 1998), Boxgrove (Bowen & Sykes, 1994; Roberts, 1995), Westbury (Stringer *et al.*, 1996), L'Arago (Crégut, 1979; Montuire & Desclaux, 1997), L'Escale (Bonifay, 1971), West Runton (Rink *et al.*, 1996), Betfia V (Terzea, 1996), Fontana Ranuccio (Gliozzi et al., 1997) Venta Micena (Martínez, 1992; Agustí & Moyá-Solá, 1998).

between Africa and Europe 1·3 Ma. is considered possible by Agustí & Moyà-Solà (1998), based on the occurrence in southern Spain of *Theropithecus oswaldi* at Cueva Victoria and a gerbil tooth at El Higuerón. However, the rodent tooth could have been transported in the stomach of a raptor from Africa and regurgitated in a pellet in Spain (thousands of migratory raptors cross the Gibraltar Strait twice every year). Although

it is true that no other *Theropithecus* fossils have been found elsewhere in Europe, there are no occurrences of the genus in North Africa in the Early Pleistocene either; the earliest occurrence is at the Algerian site of Tighenif, an early Middle Pleistocene locality.

The fact that no large felids have been found in TD6 may be due to the small size of the excavation trench. However,

the occurrence of *Homotherium latidens* is confirmed in level TD5. This is a frequent taxon in Early Pleistocene sites. The last occurrence of this felid in Western Europe seems to correspond to Fontana Ranuccio (Italy) dated to 458 ka (Gliozzi *et al.*, 1997). *H. latidens* was one of the longest-lived of the larger carnivores, occurring throughout the Villafranchian and into the Middle Pleistocene.

Formerly it was accepted that *Panthera leo* immigrated from Africa into Europe around one Ma (Turner, 1992; Turner & Antón, 1996), based on evidence from Le Vallonnet (Lumley *et al.*, 1988). However, a subsequent revision of the fauna by Moullé (1992) disproved the existence of *P. leo* at that site. The oldest currently accepted record for this species is at Isernia (Sala, 1990), which is placed in the Middle Pleistocene between 783 ka and 500 ka (Gagnepain, 1996). Based on faunal evidence, it cannot be older than around 600 ka (Kolfschoten, 1996). *Homotherium* survived in Europe until the end of the Cromerian, coinciding with the first occurrences of the African lion (with a short coexistence of both species at some late Cromerian sites, such as Mauer, Westbury, Mosbach and Vértesszölös). Their similarity in size and resource competition (Hutchinson, 1959) could explain the extinction of *Homotherium*. In the Sierra de Atapuerca, *P. leo* is first recorded in the uppermost levels of TD (TD10–TD11) and at SH and TG (GII and GIII), placed between o.i.s. 9 and 11, when *Homotherium* was already extinct. It seems that *P. leo* either had not arrived in Europe prior to the Cromerian III–IV interglacials or was very rare; *Homotherium* was still the principal large felid predator in the ecosystem.

C. mosbachensis is present at Early Pleistocene sites, such as Dmanisi, Betfia V, Untermassfeld, VM and Le Vallonnet. During the Middle Pleistocene it becomes common, surviving to the Elsterian, where

its last occurrence is at L'Escale and L'Arago. At TD, *C. mosbachensis* is present in Early Pleistocene levels (TD4, TD5 and TD6), and also in TD8, which is correlated with Cromer III (Figure 6), based on the micromammals (Cuenca Bescós *et al.*, 1999) and ESR and U/Th dating (Falguères *et al.*, 1999). In TD10, TD11, TG and SH the first populations of *C. lupus* occur, although their size is not very large.

Le Vallonnet and Untermassfeld are placed in the Jaramillo subchron. Torres *et al.* (1997) obtained dates for VM (with aminostratigraphy) of around 1 Ma. As Fuente Nueva-3 has negative polarity it could be placed prior to or later than the Jaramillo subchron. However, based on faunal evidence it is most probably situated below the lowermost levels of TD (Martínez *et al.*, 1997). The TD4–6 and Le Vallonnet carnivore assemblages do not contain *U. etruscus* or *Megantereon*, which did not survive the Villafranchian; the latter being present in FN-3 and Untermassfeld. *C. mosbachensis*, *Homotherium*, *P. gombaszoegensis* and *V. praeglacialis* survived the Villafranchian, and are present at many Cromerian sites. The lack of *P. leo* at TD4–6, which first occurs at Isernia, is consistent with an early Cromerian age, when the African lion had not yet arrived in Europe. However, if lion remains are found in future excavations at TD4–6 (or at other sites of that period) the time of arrival for this taxon will have to be revised.

The idea of a "Terminal-Villafranchian" event as a single and abrupt faunal turnover at 900 ka proposed by several authors is now being critically reviewed. *Pachycrocuta* was still present at the Jaramillo Event (and during the Cromerian complex) while the first occurrence of *Crocuta* is at TD3–4 (at a minimum age of 800 ka, and probably around 900 ka). *Homotherium* also persisted up to the end of the Cromerian, where it coexisted with the recently immigrated African lion. *C. mosbachensis*, which

characterizes the Cromerian period, was already inhabiting Spain during the Early Pleistocene. The last occurrence of *U. etruscus* seems to be at the Italian Late Villafranchian site of Pietrafita, and *Megantereon cultridens* persists until the Jaramillo event at Untermassfeld. The evidence from the TD4–6 assemblage suggests a gradual turnover in Europe.

The co-occurence of *C. crocuta* and *H. antecessor* in TD6-AS is of relevance for the taphonomic interpretation of the human remains in this layer because the hyaenas could have contributed, at least partially, to the breakage pattern seen in the human material.

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