

Ecomorphological study of large canids from the lower Pleistocene of southeastern Spain

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An ecomorphological analysis of the skeletal remains of large canids, *Canis (Xenocyon) falconeri* and *Canis etruscus* (Mammalia, Carnivora, Canidae), preserved in an assemblage of large mammals from the lower Pleistocene site at Venta Micena (Guadix–Baza Basin, Orce, Granada, southeastern Spain) is reported. Mean body mass of adult individuals was estimated to be around 10 kg for *C. etruscus* and approximately 28 kg for *C. falconeri* using multiple regression. A comparative study of tooth measurements in modern canids, using principal components and discriminant function analysis, infers quite different ecomorphological adaptations and feeding behavior for both fossil species. The craniodental morphology of *C. falconeri* is similar to that shown by extant hypercarnivorous canids whose diet include more than 70% of vertebrate meat, whereas *C. etruscus* shows a cranial morphology similar to those of modern omnivorous species, thus indicating a dietary niche in which vertebrate meat represented less than 70% of its diet, with other feeding resources making up the balance. These results suggest that there was a marked ecological segregation between both sympatric species of large canids. The find of a complete skull of *C. falconeri* showing bilateral asymmetry and marked dental anomalies could suggest high levels of genetic homozygosity in the population which inhabited this region during early Pleistocene times, possibly as a consequence of isolation and the low number of individuals. This may have subsequently led to the extinction of *C. falconeri* in the Western fringe of Europe. The survival of this pathological individual to adulthood indicates that this species may have developed cooperative behavior similar to that of modern African wild dogs. □ *CANIS (XENOCYON) FALCONERI, CANIS ETRUSCUS, ecomorphology, principal component analysis, discriminant analysis, cranial fluctuating asymmetry, Venta Micena, lower Pleistocene.*

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The Venta Micena site lies near the village of Orce, in the eastern sector of the Guadix–Baza Basin (province of Granada, southeastern Spain). The biochronologic study of the faunal assemblage indicates an early Pleistocene age, below the lower limit of the Jaramillo Normal Subchron (i.e. >1.07 Ma), according to the indications of paleomagnetic analysis (Martínez-Navarro *et al.* 1997). The assemblage is preserved in 98–99% pure micritic limestone precipitated in freshwater ponds, which was emplaced on a caliche paleosol of diagenetic origin and surrounded by a shallow lake with swampy marginal zones that existed in the paleovalley of Orce (Arribas & Palmqvist 1998).

The macrovertebrate assemblage from Venta Micena is comprised of a number of identifiable specimens (*NISP*)

of approximately 6,500, which allows the calculation of a minimum number of individuals (*MNI*) of ~300. The fossils preserved belong to 19 species of large mammals, ranging in body mass from less than 5 kg to more than 6000 kg (Palmqvist *et al.* 1996). Carnivores are represented in the assemblage by 289 skeletal remains (*MNI* = 28) with 66 (i.e. approximately 23%) belonging to the large canid *Canis (Xenocyon) falconeri* (40 bones from the postcranial skeleton, 25 teeth and cranial fragments, and one complete cranium), and the calculation of a minimum number of four adults. Canids are also represented by two other species, *Canis etruscus* (*NISP* = 33, *MNI* = 4) and *Vulpes praeglacialis* (*NISP* = 24, *MNI* = 1). However, the preservation of skeletal remains from carnivores is very fragmentary, since only two other relatively well-pre-

served crania have been unearthed so far. One skull lacking the mandible is of the large saber-tooth, *Homotherium latidens*, and is slightly deformed due to sediment compression. The other cranium with complete dentition is of the bear *Ursus etruscus* and probably belonged to an old female, given the heavily worn surface of the carnassials and the relatively small size of the upper canines.

This assemblage was formed by the transport and accumulation by the giant hyaena, *Pachycrocuta brevirostris*, of carcasses and bone remains of ungulates selectively preyed upon by saber-toothed felids (*H. latidens* and *Megantereon whitei*) and canids (*C. falconeri*) close to the entries of shallow dens dug by hyaenas in the plains that surrounded the Pleistocene lake (Palmqvist *et al.* 1996). Major taphonomic biases are related to the preferential consumption by hyaenas of low-density skeletal parts, and with differential fragmentation of limb bones for the extraction of their marrow content. Subaerial weathering was relatively insignificant, since most bones (89.3%) show weathering stage 0, and only a small fraction (10.7%) indicate weathering stage 1, with few, shallow and small split-line cracks due to sunshine, and without flaking of their outer surface. These results indicate that most bones were buried shortly after the death of the individuals (Arribas & Palmqvist 1998).

The excavation made in Venta Micena during the summer of 1995 yielded an unusually well preserved skull of the large canid *C. falconeri*. This skull (VM-7000) has the mandible in anatomical connection and belonged to an adult individual with moderately worn, full, permanent dentition. The importance of the find lies in the fact that this skull presents several bone and tooth anomalies, as well as a marked bilateral asymmetry. The find of a complete cranium of a canid, the osseous architecture of which is clearly weaker than those of any ungulate species preserved in Venta Micena, constitutes an exceptional event in an assemblage collected by the bone-cracking hyaenid *P. brevirostris*. Apart from the two other skulls of carnivores cited above, the preserved cranial remains from carnivores only encompass isolated teeth, maxillary fragments with the carnassial and molars, and hemimandibles in various states of preservation. All cranial elements from ungulates (>200) are composed of hemimandibles, hemimaxillae and/or complete maxillae of perissodactyls and artiodactyls, and also of calvarii of artiodactyls, which are in all cases not well preserved due to the activity of hyaenids (Arribas & Palmqvist 1998).

The assemblage also comprises mandibles from two other adult individuals of *C. falconeri*; one mandible is complete (left hemimandible: VM-2255, right: VM-2256) and the other is only represented by the left hemimandible (VM-2257). These fossils (Martínez-Navarro 1992, Pls. 6 and 7) preserve all elements of the dental formulae typical of canids (i.e. I_1-I_3 , C_1 , P_1-P_4 , M_1-M_3) in the case of the complete mandible, while the isolated left mandible

lacks the second premolar (P_2). Both individuals display unworn teeth and show no evidence of pathologies or osseous alterations produced during the life of the animal. The left side of the complete mandible shows clear marks of the activity of hyaenids, since both the mandibular condyle and the coronoid process have been destroyed, in part, by chewing.

The fossil record of lower Pleistocene carnivores in Spain consists mainly of small cranial fragments and isolated dentition preserved in fluvial, swampy and/or lacustrine sediments. However, there are two exceptions: (1) an assemblage accumulated in a death trap at Incarcàl (Gerona), which has provided two complete crania of *H. latidens* (Galobart *et al.* 1996); and (2) the karstic site at Cueva Victoria (Murcia) in which a complete cranium of *C. etruscus* has been reported (Pons-Moyà 1981). Finally, it should be emphasized that although more than twenty paleontological sites with large mammals of lower Pleistocene age are known in the Iberian Peninsula, the only available fossils of *C. falconeri* come from Venta Micena and Cueva Victoria, where the specimens were described by Pons-Moyà (1987) as belonging to *Canis (Xenocyon) rossii*, but Martínez-Navarro (1991) reassigned them to *C. falconeri*.

Systematic paleontology

The systematics of the genus *Canis* in the late Pliocene and early Pleistocene of Europe considers traditionally only three different species: *Canis arnensis*, *C. etruscus*, and *C. (Xenocyon) falconeri* (Torre 1967; Rook 1993, 1994). However, this integrative point of view is not always accepted, owing to differences in the interpretation of anatomical evidence. For example, Koufos & Kostopoulos (1997) recently described at Apollonia-1 (Mygdonia Basin, Macedonia, Greece) a new species, *C. apolloniensis*, as an evolved form derived from *C. etruscus*, but of smaller size and showing slight structural differences in the talonid basin of the lower carnassial. These authors also cited the presence of the species *Canis (Xenocyon) sp.*, described as a hypercarnivorous form differing from *C. falconeri* in its smaller size and the anatomy of the upper first molar.

The fossil remains of canids preserved at Venta Micena were first described by Pons-Moyà (1987). This author cited the presence of two species, *Xenocyon sp.*, based on one mandibular fragment (VM-2257), and *Canis etruscus mosbachensis*, based on two hemimandibles from the same individual (VM-2255 and VM-2256) as well as other teeth. This author also cited the species *Cuon priscus* based on a right lower carnassial (VM-84-C3-2C10-73) which shows the main cusplet of the talonid in a central position. However, the systematic revision of the assemblage of large mammals from Venta Micena made by Martínez-

Navarro (1991, 1992) revealed the presence of only two species: (1) *C. falconeri*, which is represented by the specimens attributed by Pons-Moyà to both *C. etruscus mosbachensis* and *Xenocyon sp.*; and (2) *C. etruscus*, which was identified using unpublished specimens with the lower carnassial erroneously determined by Pons-Moyà as belonging to *C. priscus*. The determination of *C. falconeri* at Venta Micena was assumed to be *C. (Xenocyon) falconeri* in Rook (1993), who considered that the specimens of *C. etruscus* described by Martínez-Navarro (1991, 1992) correspond to the somewhat smaller form *Canis ex gr. arnensis*, according to measurements of the dentition. However, we reassess the first determination of *Canis ex gr. etruscus* on grounds of anatomical features, which are more significant than the metric data. Finally, Sotnikova (1998), in her work on the canids from the late lower Pleistocene site at Untermassfeld (Germany), describes the species *C. mosbachensis* and *C. (Xenocyon) lycanoides*. Sotnikova (1998) also reports the presence of the same species of *C. falconeri* as that described from Venta Micena and Cueva Victoria, and regards it as a typical evolved species of the middle Pleistocene.

According to the systematic revision made by Rook (1993, 1994), *Canis (Xenocyon) ex gr. falconeri* includes all the large hypercarnivorous canids that inhabited the Old World during the late Pliocene – early Pleistocene (*C. falconeri* Forsyth Major in Europe, *C. antonii* Zdansky in Asia, and *C. africanus* Pohle in Africa). This species had a large body size, comparable with that of the northern populations of gray wolf (*Canis lupus*), and was characterized by a relatively short neural cranium and a narrow muzzle. The sagittal crest is strong and the bullae are inflated. Features of the dentition include a relatively reduced metaconid in the second lower molar (M_2), and the lower carnassial (M_1) with a stoutly built talonid, consisting of a preminent hypoconid relative to the entoconid. The lower premolars usually show accessory cusplets and the mandibular ramus is high and heavy. The upper molars, and especially the upper carnassials (P^4), show a marked tendency towards brachydonty; a wide occlusal basin is present at the base of the metacone and paracone in the first upper molar (M^1), and the second upper molar (M^2) is large. The two cusplets of the talonid of the lower carnassial (i.e. hypoconid and entoconid) are independent, since they are neither joined to each other by any crest or to the trigonid (a condition which is found in *C. etruscus*). The metacarpal II has a very reduced articular facet to the metacarpal I, which indicates that the latter bone was vestigial, if not absent, and is a condition similar to that of *Lycaon pictus*, the only living canid with a tetradactyl forelimb, which suggests increased cursoriality.

C. falconeri was first recorded in China, at the upper Pliocene locality at Fan Tsun (2.5 Ma) (Rook 1994; Sotnikova *et al.* 1997). The arrival of this species in East Africa is recorded at Olduvai Bed I (1.9 Ma) and coincides with

the earliest evidence of human presence in East Asia (Swisher *et al.* 1994), thus opening the possibility of faunal interchange between both continents. *C. falconeri* spread in the austral continent between 1.5 and 1.4 Ma (Kromdraai A and Olduvai Bed II, respectively). The first record of this species in Western Europe is in the Tasso faunal unit, Upper Valdarno (Rook & Torre 1986), which, according to paleomagnetic data by Torre *et al.* (1996), is tentatively included in the upper part of the Olduvai Subchron (1.8–1.7 Ma). In spite of the Asian origin of this species, we cannot rule out that it reached Europe from Africa, since its first record is simultaneous with that of other African immigrants, such as *Hippopotamus antiquus* and *Equus altidens* (Martínez-Navarro & Palmqvist 1995; Guerrero-Alba & Palmqvist 1998) and also coincides with the first human dispersal in Eurasia (Martínez-Navarro *et al.* 1997). However, the arrival in Europe of both species is simultaneous with those of other Asian immigrants, such as the jackal-sized species *C. arnensis* and the first representatives of the genus *Praevivobos* (Arribas & Palmqvist 1999).

Morpho-functional analysis and size estimates

Among living canids, 4 out of 36 species are considered hypercarnivorous (i.e. vertebrate meat constitutes more than 70% of their diet): the Eurasian and North American gray wolf, the African wild dog, the Indian dhole (*Cuon alpinus*), and the South American bush dog (*Speothos venaticus*) (Van Valkenburgh 1989, 1991). Three species, the dhole, hunting dog, and bush dog, share a trenchant-heeled condition in their lower first molar (M_1), in which the talonid basin bears a single, large and centrally positioned, blade-like cusp (hypoconid). This condition seems to have evolved convergently in the three lineages, as well as in other fossil canids (e.g., *Cerdocyon sarcbus*). The wolf shows a moderately trenchant talonid, asymmetrically bicuspid, with a large, buccally positioned hypoconid and a reduced entoconid (Van Valkenburgh 1991). Associated with the appearance of the trenchant heel on the lower M_1 are other dental modifications in hypercarnivorous canids, including the reduction of the M_1 metaconid and the M^1 hypocone, as well as size reduction (M_2) or complete loss (M_3) of the postcarnassial molars.

The functional significance of the trenchant condition of the M_1 is a lengthening of the effective cutting blade of the carnassial. The relative length of the trigonid blade (i.e. $[L_{\text{trigonid}}/LM_1] \times 100$) in hypercarnivorous canids is comprised of between 72% of the total length of the carnassial in the gray wolf, wild dog and bush dog, and 74% in the dhole (Van Valkenburgh 1989). In other canid spe-

cies, which are more omnivorous (i.e. vertebrate meat represents less than 70% of their diet, with fruits and/or insects making up the balance), the talonid basin of the M_1 bears two subequal cusps, one buccal (the hypoconid) and one lingual (the entoconid). The relative length of the carnassial blade is shorter than in the hypercarnivorous canids, representing between 57% of the total length of M_1 in the maned wolf (*Chrysocyon brachyurus*) and 68% in the Chilean fox (*Dusicyon culpaeus*). On the contrary, the relative grinding area (estimated by dividing the square root of the total grinding area of the molars [i.e. occlusal surface of the talonid, M_2 and M_3] by the total length of the carnassial blade [i.e. trigonid length]; Van Valkenburgh 1989) is greater in the omnivorous species, ranging from 0.75 in the black-backed jackal (*Canis mesomelas*) to 1.08 in the maned wolf, while in the hypercarnivorous canids the range of values is between 0.55 in the bush dog and 0.66 in both the wolf and the dhole.

Body mass estimation. – Van Valkenburgh (1990) used single least squares regressions of log-transformed data to estimate body mass from skeletal measurements in carnivores. The osteometric variables used in her analysis included head–body length (which is impossible to estimate in many fossil species, given the incompleteness of the record for most postcranial elements), skull length, occiput-to-orbit length (measured from occipital condyles to anterior edge of orbit), and lower first-molar length. The predictive power of the single regression models adjusted for canid species (Van Valkenburgh 1990; Table 10.2), as evaluated from the standard error of the estimates, is comprised between ± 1.30 kg (22% prediction error) for occiput-to-orbit length ($r^2 = 0.88$), and ± 1.44 kg (27% prediction error) for lower carnassial length ($r^2 = 0.76$). However, the first metric variable is often difficult to measure in fossil species since it requires a well-preserved skull. The second variable, car-

nassial length, tends to overestimate the mass of several species of small size by a factor of 100% or even more (i.e. estimated mass of 5.8 kg for *Vulpes velox*, actual mass of 2.6 kg), and underestimates those of larger size (i.e. estimated mass of 24.2 kg for the gray wolf, actual mass of 42.7 kg). These divergences are related to the fact that hypercarnivorous species show a reduced talonid basin in their lower carnassial.

The values obtained for *C. falconeri* from Venta Micena using these equations were the following: 56.2 kg for skull length, 37.3 kg for occiput-to-orbit length, and 22.8 kg for M_1 length (the first two values were calculated using the complete skull VM-7000, while the third estimate was obtained from the mean value of M_1 length in four specimens). These estimates differ widely (i.e. the first value is 246% greater than the third one), thus representing a high uncertainty for mass estimation in a fossil species. Because of such problems, a multiple regression approach was used, with seven independent craniodental variables as estimators for body mass, which can be easily measured in most fossil species: length and width of the upper canine (C^1), length of the mandible, length and width of the fourth lower premolar (P_4), and length of trigonid and talonid in the lower carnassial (M_1) (Table 1; average measurements for modern species obtained from data in Van Valkenburgh and Ruff 1987; Van Valkenburgh 1989, 1990).

The results obtained from the multiple regression permit body mass in fossil canids to be estimated with higher accuracy than using single regressions, given the higher value obtained for the coefficient of determination ($r^2 = 0.97$) in this adjustment, as well as the lower standard error of the estimates (± 1.099 kg):

$$\log_{10}(\text{body mass}) = 0.12 - 0.61\log_{10}(L_{\text{mandible}}) + 1.15\log_{10}(LC^1) + 0.08\log_{10}(WC^1) - 0.13\log_{10}(LP_4) + 0.86\log_{10}(WP_4) + 0.33\log_{10}(L_{\text{trigonid}}) + 0.36\log_{10}(L_{\text{talonid}}),$$

Table 1. Mean values of different craniodental variables in modern canids and in the species of large canids preserved at Venta Micena (a: data from Van Valkenburgh 1988a, 1989, 1990, 1991; Van Valkenburgh & Ruff 1987; b: data from Martínez-Navarro 1991, 1992). Asterisks indicate the mass estimated for *C. falconeri* and *C. etruscus* using the multiple regression approach. Body mass in kg, craniodental variables measured in millimeters.

Species	Weight (kg)	L_{mand}	LC^1	WC^1	LP_4	WP_4	$LM_1 \text{ trig}$	$LM_1 \text{ tal}$
a <i>Canis lupus</i>	44.7	133.0	14.2	7.6	14.6	8.5	19.4	7.6
<i>Cuon alpinus</i>	17.0	114.6	10.1	5.8	10.8	5.2	14.4	5.4
<i>Lycan pictus</i>	21.9	175.8	10.9	7.0	14.4	7.1	18.0	7.0
<i>Speothos venaticus</i>	8.9	84.1	7.4	5.3	8.4	4.1	10.0	3.9
<i>Dusicyon culpaeus</i>	12.6	105.9	8.4	5.4	11.4	5.1	11.5	5.4
<i>Cerdocyon thous</i>	7.1	89.1	6.0	3.5	8.2	3.8	8.2	5.7
<i>Chrysocyon brachyurus</i>	22.9	149.6	11.3	7.2	13.3	6.7	12.9	9.7
<i>Canis mesomelas</i>	7.1	93.1	6.4	3.8	9.2	4.3	11.2	5.8
<i>Canis latrans</i>	11.5	130.6	8.1	5.0	11.4	5.0	14.5	7.5
<i>Vulpes vulpes</i>	7.2	92.7	5.7	4.2	9.8	4.3	9.8	4.9
b <i>Canis (Xenocyon) falconeri</i>	* 27.8	162.8	13.1	8.2	15.7	7.3	19.7	6.4
<i>Canis etruscus</i>	* 10.3	134.8	6.5	4.0	12.9	5.7	16.2	6.6

with $r^2 = 0.99$, $s.e. = 0.04$, $F_{9,5} = 49.50$ ($p < 0.02$). When this function is applied to the mean values obtained from measurements on the specimens of *C. etruscus* and *C. falconeri* from Venta Micena (data from Martínez-Navarro 1991, 1992), an estimated mass of ~10 kg is obtained for the former species and ~28 kg for the latter (see Table 1).

Morphometric analysis and ecomorphological considerations. The diversity of locomotor and trophic types in past and present guilds of large carnivores has been applied using several morphometric indices (i.e. ratios between variables) and three-dimensional graphs (Van Valkenburgh 1985, 1989). Van Valkenburgh (1991) studied the diversity of dental morphologies and body sizes in paleoguilds of hypercarnivorous canids using as ratios premolar shape (maximum width/maximum length of largest lower premolar), relative premolar size (maximum width of largest lower premolar/cube root of body mass), and relative molar grinding area of the lower molars (square root of total grinding area/length of M_1 trigonid). These ratios (standardized to z-scores) defined a theoretical three-dimensional morphospace of the family Canidae. Although this approach seemed very useful for evaluating and comparing patterns of dental diversity among different assemblages (including members of other carnivore families, such as Felidae, Hyaenidae and Ursidae), it is rather limited in the number of variables used to describe the morphospace, and takes no account of size differences. If body mass (actual size in extant species and estimated mass for extinct ones) is included in the analysis (e.g., Van Valkenburgh 1988a; Lewis 1997) the number of morphometric indices which can be used with this approach is then reduced to only two dimensions.

However, although ratios of characters have a long tradition in vertebrate paleontology (e.g., Simpson's ratio diagrams), their use in morphometric studies is discouraged by many authors (see Reyment *et al.* 1984) because

(1) ratios are rarely normally distributed and tend to produce outliers; (2) as generally used, ratios contain only two characters and thus afford a poor appreciation of shape differences (i.e. to compound two characters into a ratio implies that there is only one contrast of form to be studied, and that this unique contrast is well assessed in terms of two characters of equal weights, but opposite in sign); and (3) ratios will not be constant for organisms of the same species unless they are also of the same size, because of the effects of allometric growth.

In order to avoid such limitations, we have made a multidimensional study of craniodental adaptations in extant canids, using as morphometric descriptors the seven variables defined in the previous section. The analysis of size and shape variation among canids was defined by *R*-mode principal component analysis (PCA) of log-transformed data (Reyment 1991). Logarithmic transformation ensured that all variables were normally distributed, according to the Kolmogorov–Smirnov test. Linear discriminant analysis was used to investigate shape differences between hypercarnivorous and omnivorous species, and also to allocate the fossil canids from Venta Micena (*C. falconeri* and *C. etruscus*) to one of these groups.

Table 2 summarizes the results obtained by PCA analysis. The first principal component (*PC I*) accounts for more than 80% of the total variance explained by the seven original variables. All variables show positive factor loadings of similar value on this eigenvector. Given the fact that the variables were logarithmically transformed prior to analysis, this axis may be interpreted in an *ad hoc* manner as a size vector (see Reyment 1991), which approximately disperses the analysed species as a function of their body mass. *PC II* explains nearly 10% of the total variance, and the variables obtain positive and negative factor loading values on this axis, which indicates that it is an *ad hoc* shape vector. The variable which takes the highest positive loading is talonid length, while the length and

Table 2. Results obtained in principal component analysis: upper triangular matrix with Pearson *r*-values for correlations among the analysed variables, factor loadings for the variables on the first three principal components (*PC I*, *PC II*, and *PC III*), and eigenvalues of each eigenvector translated into percentages of variance explained.

	$L_{tal.}$	$L_{trig.}$	WP_4	LP_4	WC^1	L_{C1}	$L_{mand.}$	<i>PC I</i>	<i>PC II</i>	<i>PC III</i>
Mandible length	0.722	0.857	0.875	0.937	0.72	0.736	1.000	0.391	0.245	0.271
C^1 length	0.540	0.786	0.890	0.797	0.960	1.000		0.383	-0.328	-0.421
C^1 width	0.465	0.722	0.848	0.779	1.000			0.369	-0.410	-0.460
P_4 length	0.649	0.913	0.957	1.000				0.405	0.060	0.299
P_4 width	0.664	0.906	1.000					0.411	-0.035	0.048
M_1 trigonid length	0.468	1.000						0.381	-0.165	0.532
M_1 talonid length	1.000							0.294	0.795	-0.404
Eigenvalues								-5.675	0.683	0.431
percent of variance explained								81.1	9.7	6.2

$$\Phi = 7.8 L_{\text{mandible}} + 26 L_{C^1} + 116.7 W_{C^1} - 240.0 L_{P_4} + 169.7 W_{P_4} + 37.5 L_{\text{trigonid}} - 123.2 L_{\text{talonid}}$$

$$D = 482.5, F_{7,2} = 41.1 (p < 0.001)$$

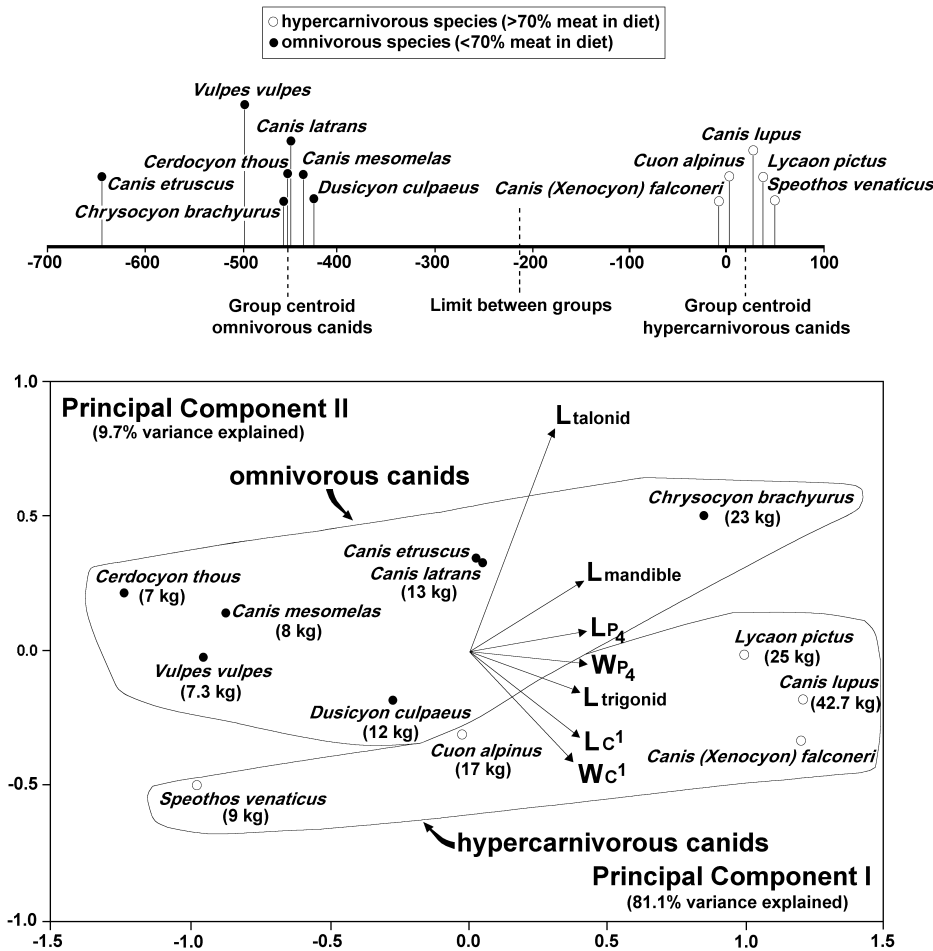


Fig. 1. Discriminant analysis between hypercarnivorous and omnivorous species of extant canids, and R-mode principal component analysis of craniodental variables in canids.

width of the upper canine have the lowest values among those variables which show negative loadings. *PCIII*, which explains more than 6% of the original variance, can be also interpreted as a shape vector. The most contributing variables according with their factor loadings are trigonid and talonid length, which are inversely related, and again the mesiodistal and labiolingual dimensions of the upper canine, both with negative loadings.

Fig. 1 shows the scores of both extant and fossil canid species projected on the morphospace defined by the first two principal components, which jointly account for more than 90% of the original variance explained by the seven variables used in this study. The first axis distributes the species according to their size, while the second component arranges them as a function of their tooth shape. Omnivorous species show a well-developed mandible and a stoutly built talonid basin in their lower carnassial, which are longer in relation to their body mass than in the

hypercarnivorous species. The upper canines in hypercarnivorous species are comparatively stronger, and the trigonid blade of the lower carnassial is more developed. As a consequence, omnivorous species tend to obtain more positive scores on the second principal component, while hypercarnivorous canids are projected on the negative values of this eigenvector.

Quite different ecomorphological inferences may be extracted for those species of large canids preserved at Venta Micena, according to their scores on these components. *C. etruscus* is projected within the region of the morphospace occupied by the omnivorous species, in a position very close to that of the extant coyote, *C. latrans*, thus indicating similar size and feeding ecology for both species. *C. falconeri* records a high positive score on the first axis and is projected on the negative values of the second one near the gray wolf, *C. lupus*, which suggests this fossil species was hypercarnivorous.

The results obtained in the discriminant analysis between hypercarnivorous and omnivorous canids are also shown in Fig. 1. The graph illustrates the scores of the species analysed, while the linear discriminant function (ϕ) correctly assigns all canids to their respective group (i.e. 100% correct reclassifications) with no overlap between omnivores and hypercarnivores. The Mahalanobis distance between the centroids of both groups ($D^2 = 482.5$) indicates, on the basis of Hotelling's T -test and its associated F statistic (see Reyment *et al.* 1984), that the difference between the multivariate means of these trophic groups is highly significant ($F = 41.36, p < 0.001$). The value obtained for *C. falconeri* in the discriminant function clearly shows this fossil species to be within the hypercarnivorous canids, while *C. etruscus* is placed within the group of omnivorous species. These results confirm those obtained with *PCA*, indicating an ecological segregation between both sympatric species of large canids from Venta Micena.

Description of the cranium

The cranium of *C. falconeri* (VM-7000) belonged to an adult individual with moderately worn full permanent dentition (Fig. 2). The most significant measurements are the following (in mm): greatest length of the skull, 246.5; braincase width, 73.2; bizygomatic width, 149.8; maximum width across M^1 , 89.5; width across C^1 , 48.7; alveolar length P^1 – M^2 , 82.4 (right), 83.3 (left); width of frontal shield, 84.0; minimum width at postorbital constriction, 50.2; greatest palatal length, 117.0; greatest nasal length, 53.0; greatest sagittal length, 71.5; maximum length of the mandibles, 191.0 (right), 187.2 (left); length I_1 -condyle, 186.0 (right), 185.0 (left); length P_1 – M_2 , 93.6 (right), 91.4 (left); mandibular depth behind M_1 , 32.5 (right), 32.1 (left); and mandibular depth behind P_4 , 32.0 (right), 31.4 (left).

This specimen presents several bone and tooth anomalies, which are related with an important degree of cranial bilateral asymmetry, as may be seen in an upper view of the skull (Fig. 2A). Both the skull and the mandible are lacking several teeth (Fig. 2B, C), specifically the upper right I^1 , I^2 , C^1 and P^2 , and the lower right M_2 and M_3 , while the upper right I^3 and P^1 are partially fractured. The upper canine and the lower third molar never erupted during the individual's life, and their tooth germs are not inside the skull or the mandibular ramus, respectively, as revealed by radiographs and computer assisted tomographs (Fig. 3). The remaining teeth (i.e. I^1 , I^2 , P^2 , and M_2) were fractured and completely lost during the life of this individual. In the case of M_2 , its roots are clearly visible in the occlusal view of the mandible but the crown is lost (Fig. 2C). The dental alveoli of I^1 , I^2 and P^2 were subsequently filled by porous bony tissue, once the teeth were

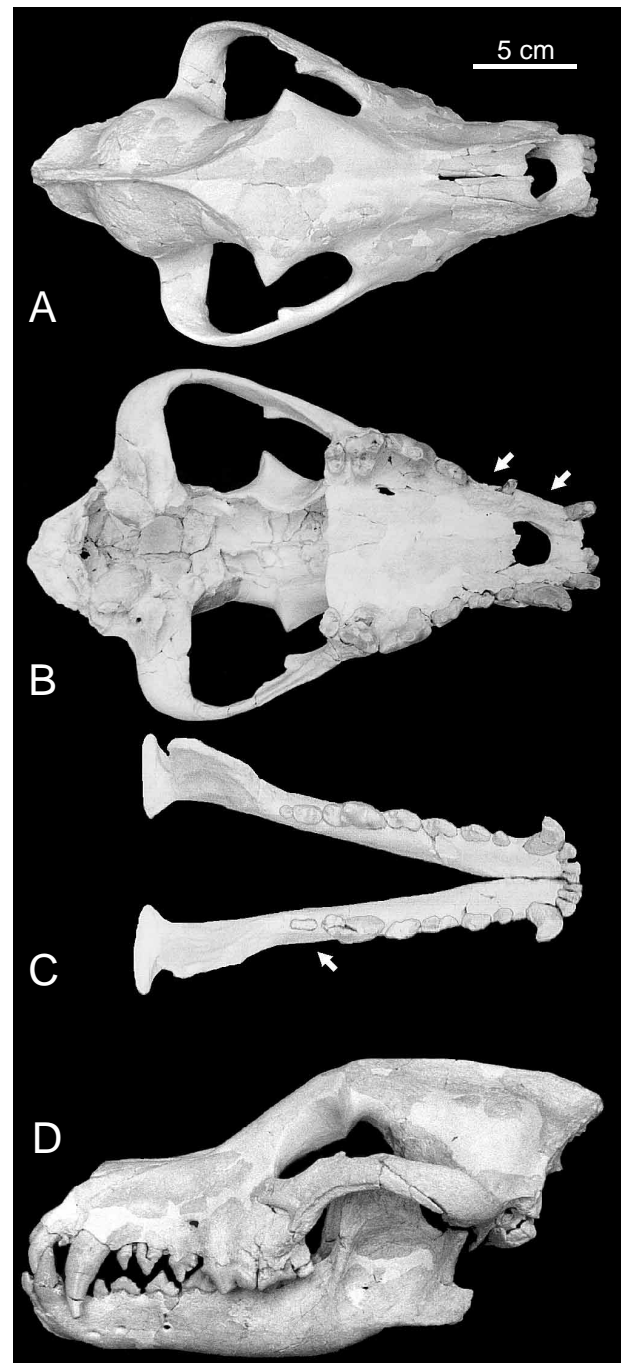
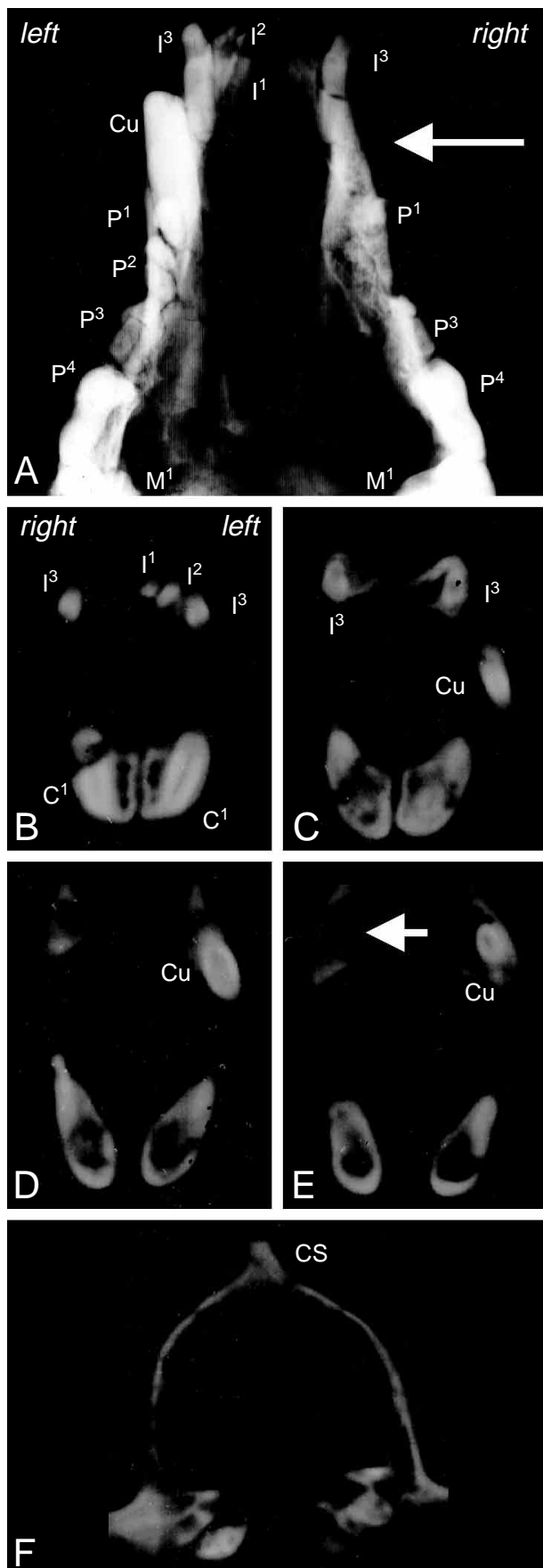


Fig. 2. Skull and mandible of *Canis (Xenocyon) falconeri* from Venta Micena (VM-7000), in upper (A, skull; C, mandible), lower (B), and lateral (D) views. Arrows indicate missing teeth.

lost. According to Vilà *et al.* (1993), when adult teeth of *C. lupus* break off at the root the alveolus is then filled by porous bony tissue in a process of reossification. Loss of a tooth from a mechanical cause can be thus recognized by the presence of porous tissue resulting from obliteration of the alveolus by bony overgrowth. This is the case in the



first and second right upper incisors and the second right upper premolar of the skull of *C. falconeri* studied here.

The wearing patterns of the occlusal surfaces of both the upper and lower tooth rows are also strongly asymmetrical; the crowns of the teeth which constitute the right tooth row showing more wear, which is particularly evident when the blades of the upper right and left carnassials (P^4) are compared (Fig. 2B). Such asymmetries were not produced during the restoration of the fossil, since several measurements of the skull, obtained before extracting it completely from the surrounding micrite sediment and later, once the restoration process was concluded, have shown noteworthy correspondence (less than 5% of differences between both sets of measurements). On the other hand, since the skull was originally in horizontal position, resting on the mandible in anatomical connection, the observed asymmetry could not have been produced by crushing because of the slight diagenetic compaction of the sediment.

The malformations observed in this cranium cannot be attributed to any biostratinomic process and could only be due to genetic abnormalities, accidents or diseases experienced by the animal during its life. Given the fact that neither the skull nor the mandible show any type of fractures with evidence of bone regeneration processes (which would indicate accidents during the life of this individual), and that there is no disease known in modern canids the ethology of which coincides with all the features shown by this cranium (i.e. marked bilateral asymmetry and, if we consider a pathologic origin, intense resorption of the alveoli), diseases should then be discarded as a cause of these anomalies, at least for the moment.

This specimen was unearthed in a square of the Venta Micena quarry (Fig. 4) which shows a very high density of bones, as is usual all over the surface of this paleontological site. However, no bones were in close contact with the cranium, and edaphic carbonate nodules were absent (if present, they could have produced a mechanical deforma-

Fig. 3. Radiograph and serial tomographs of the cranium of *Canis* (*Xenocyon*) *falconeri* from Venta Micena (VM-7000). □A. Radiograph of the splanchnocranium (occlusal view) in which the teeth present in the premaxillary and maxillary bones are observed (up to M^1). The arrow indicates the absence of the right upper canine (*Cu*). □B–F. Serial tomographs of the cranium (skull articulated with the mandible). □B–E. Sections of the premaxillary bones, maxillary bones and mandible, from the level of the upper incisors (B) to the base of the upper canine (E). The crowns and roots of the preserved teeth stand out in this sequence, and the arrow indicates the absence of both the right upper canine and the dental alveoli of this tooth, and of any sign of osseous regeneration in this region of the maxilla. □F. Transverse section of the neurocranium, in which an evident asymmetry between both sides can be observed (*Cu*: upper canine, *Cs*: sagittal crest).

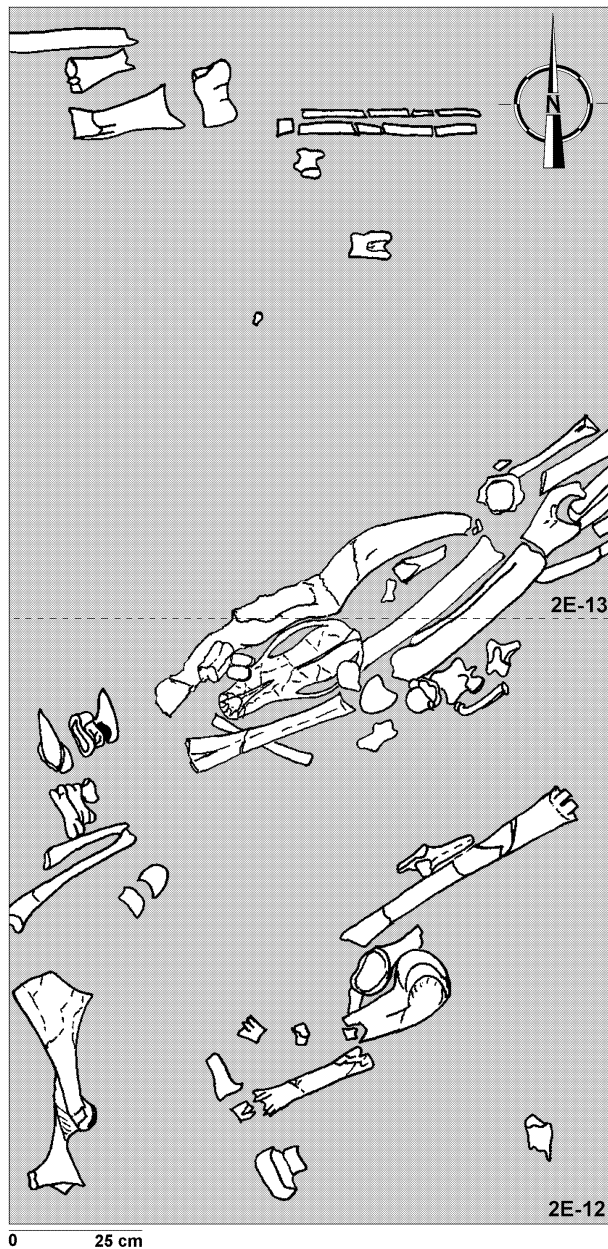


Fig. 4. Surface of the Venta Micena quarry where the cranium of *Canis (Xenocyon) falconeri* (VM-7000) was unearthed (grids 2E-12 and 2E-13).

tion of the skull during the diagenetic compaction of the micrite sediment). The cranium was covered in part by a very large calvarium of buffalo (*Bovini* cf. *Dmanisibos*), which protected it from sediment pressure. The surface of the skull bones is undamaged and shows no biostratigraphic fractures or alteration of the cortical. There are no split line cracks (i.e. weathering stage 0) and the surface of the skull bones shows no evidence of abrasion or polish, no traces of attack by insect larvae, or gnawing marks by

rodents. There is no evidence of carnivore damage such as striations and bite marks, which are very frequent in all the bones preserved in the assemblage (the remaining cranial fragments and complete skulls have furrows and punctures, showing dense scoring and pitting; Arribas & Palmqvist 1998). The cranium shows rootmarks on the right side: the premaxillary bone, the basal margin of the maxilla and the right hemimandible all have the outer cortical bone intensely altered owing to chemical attack by plant roots, and the crown enamel of both right I^3 and C_1 shows the same effect. The concentration of these traces on the right side of the cranium may be related to the location on this side of some bones which experienced osseous regeneration and/or which are lacking several teeth. Such skeletal parts would then be more vulnerable to the chemical activity of roots, since they present a volume of porous bony tissue which is atypical in such smooth regions.

The original horizontal position of the cranium, the articulation between the skull and the mandible, and the anatomical position of teeth (which are located inside their respective alveoli), indicate that the cranium was buried in a very short period of time after the death of the individual, and that it was not subject to transportation. All the bones of the neurocranium and the splanchnocranium are preserved in anatomical connection, as well as both hemimandibles. The latter present the mandibular condyles inside the glenoid fossae, with both upper and lower dental rows occluded. All teeth and dental structures (such as accessory cusplets) are well preserved, with no destruction or enamel losses due to diagenetic compaction, as is typical in other types of assemblages, from karstic sites. The hemimandibles are joined by the symphysis.

Cranial asymmetry is basically due to the slight deviation (approximately 3°) of the nasal plane of the splanchnocranium with respect to the sagittal plane of the neurocranium. This deviation predominantly affects the nasal, premaxillary, maxillary, frontal and temporal bones. The asymmetry is especially marked in the frontal region, where the orbital apophysis of the right frontal bone is displaced approximately 10 mm backwards in respect to the corresponding structure on the left side, according with the nasal plane (the nasal and frontal sutures coincide in the same plane, which differs in this skull from the sagittal plane). A large portion of the neurocranium, the parietal bones and the occipital show no evidence of asymmetry. The sagittal crest is well developed and the nuchal crest is wide and strong. Cranial sutures are partially sinostosed.

The oligodont condition for several teeth merits comment. The absence of P^1 or M_3 is relatively frequent in modern populations of *C. lupus* (see below), and the anodont condition of P^2 is not uncommon in both extant and Pleistocene felids (*Panthera pardus*, *Felis sylvestris*).

However, the absence of the upper canine and incisors has not been previously reported for any Pleistocene carnivore. In fact, dental anomalies are poorly represented in the mammalian fossil record (Ducrocq *et al.* 1995), given the rarity of the phenomenon at the individual scale and also because of the generally small number of fossil remains available for a single species. There are several examples of supernumerary teeth and absence of teeth in fossil mammals (Wilson 1955; Wang & Wu 1976; Fordyce 1982; Lucas & Schoch 1987). Other types of abnormal dental development include aberrant cusp morphologies due to the fusion or division of tooth germs, which have also been reported in fossil mammals (Rose & Smith 1979; Suseethorn *et al.* 1988). In canids, Sotnikova (1998) described in the population of *C. mosbachensis* the presence of two old individuals with strongly worn teeth and pathologic changes, including the healed anterior and posterior alveoli in a tooth series and a porous overgrowth of bony tissue around the carnassials.

If we consider the absence of several teeth shown by this individual together with the marked asymmetry of the skull, the case studied here would be unique in the fossil record of Pleistocene carnivores. On the other hand, it is really remarkable that the oligodont condition affects teeth (C^1 and M_3) that are not located on a single bone, but involve two different bones of the right side of the cranium: maxilla (canine) and dentarium (molar). If tooth losses resulted as a consequence of infection or breakage, evidence of osseous regeneration or resorption should be clear, as for I^1 , I^2 and P^2 ; this is not seen in the case of C^1 and M_3 . According to Miles & Grigson (1990), the variation in the number, size and shape of teeth tends to be largely of genetic origin. Therefore, the cranial asymmetry and the absence of teeth found in this individual of *C. falconeri* must have arisen from intrinsic or genetic factors.

Tooth losses and anomalies in modern canids

In an analysis of wolf skulls from Poland and Russia, Buchalczyk *et al.* (1981) found that deviations from typical tooth pattern included increased supernumerary teeth (polydonty) in 16 out of 234 individuals (6.8% of analysed cases), decreased number of teeth (oligodonty) in nine individuals (3.9%), and other types of tooth anomalies occurring when the normal number of teeth are present, such as one case of oblique situation of both P^3 . Asymmetries of the skull were found in two cases (0.9%) with several deformed bones in the splanchno- and neurocranium. Changes in the bones were accompanied by distortion of the skull in the sagittal plane, which in one specimen was also connected with a slight turn of the

braincase to the left in relation to the facial part. It is interesting to note that in oligodont dentition Buchalczyk *et al.* (1981) observed repeated cases of unilateral and bilateral absence of the last molars (M_3) in six individuals (i.e. the same anomaly found in the case study shown here), which represented 2.6% of analysed cases. Two specimens were determined to be the result of breeding between a wolf and a dog.

Similarly, in a study of wolf skulls from Central Europe and Russia, Vilà *et al.* (1993) found nine cases of oligodonty (1.8% of 467 individuals), in which the missing tooth from six cases was the lower third molar (M_3). Twenty-three tooth duplications were noted in 19 individuals (which represents 3.8% of 500 skulls studied), in which 16 involved the premolars (70% of all duplications). These anomalies seem to have affected the survival of individuals, since polydonty was noted in 4.4% of the group less than four years old, but in only 2.4% of individuals older than this. In 15 skulls (3.0% of cases) some form of malocclusion like prognathism was found. Three individuals (0.6%) showed anomalies in either tooth shape or placement.

In their study of wolf skulls, Vilà *et al.* (1993) also observed 38 individuals (12.4% of 306 skulls analysed) with 101 cases of alveolar resorption, 12 of them only partial (i.e. resorption of a tooth fragment). These resorptions predominantly affected the premolars (59.4% of cases). No resorptions were found in the canines or in I^2 and I^3 , the largest incisors in contact with canines. These results indicate that fracture at the base or loss of any tooth is a rather common phenomenon in wolves, being found in approximately one-eighth of the population, and its incidence increases with age until half of the older population is affected, but in most cases tooth losses are not a serious impediment to individual survival.

Comparative studies of the incidence of tooth breakage among large extant carnivores (Van Valkenburgh 1988b; Van Valkenburgh & Hertel 1993) have revealed that the percentage of broken teeth is 0.54% in the African wild dog, 1.04% in the gray wolf, and 2.7% in the coyote. The higher incidence of tooth breakage in wolves and coyotes as compared to wild dogs is due to the fact that wolves and coyotes include more bone in their diet. The most commonly broken teeth in wild dogs are canines (70% of all broken teeth), and premolars and canines in wolves (46.8% and 42.6%) and coyotes (57% and 17.2%), respectively. Tooth fracture frequencies among canids preserved in several late Pleistocene deposits, including the Rancho La Brea tar pits in Los Angeles, California, are even greater with 5.16% in the coyote and 4.5% in the dire wolf, *Canis dirus*, which suggests that dietary competence was greater in this carnivore paleoguild (Van Valkenburgh & Hertel 1993).

Cranial fluctuating asymmetry: implications for developmental instabilities and genetic homozygosity

Fluctuating asymmetries (*FA*) are small, random developmental accidents during ontogeny in morphological traits that would otherwise be described as bilaterally symmetric. Many empirical studies in remarkably different groups of animals and plants have shown that the degree of *FA* increases with the homozygosity of enzyme polymorphisms. This causes developmental instabilities as a consequence of low genetic homeostasis. *FA* increases also under stressful conditions and/or environmental perturbations experienced by the organism (e.g., Bouza *et al.* 1997; Hallgrímsson 1998; Imasheva *et al.* 1997; Möller 1997). Experimental evidence shows that *FA* is an indirect measure of fitness and reproductive quality, since individuals with asymmetries in the size of secondary sexual characters and ornaments have reduced mating opportunities and breeding success, and show diminished resistance to stress, environmental contamination, interspecific and intraspecific competition, and parasites (for review and references see Möller & Thornhill 1998).

Recent studies in mammals have shown an inverse correlation between the level of genetic heterozygosity of a population, estimated by allozyme variability of polymorphic loci, and departures from perfect bilateral symmetry. *FA* was estimated by: (1) the mean cranial asymmetry of individuals; (2) the difference in the number of foramina in both sides of the skull and mandible; (3) the frequency of reductions in tooth size; and (4) the asymmetry of the postcranial skeleton (Alados *et al.* 1995; Hartl *et al.* 1995; Hutchinson & Cheverud 1995; Lacy & Horner 1996; Leamy *et al.* 1997, 1998; Schalkvanderweide *et al.* 1994). These studies show that the level of asymmetry measured in the population increased significantly with inbreeding.

In carnivores, an early study made on 55 cheetahs (*Acinonyx jubatus*) from South Africa showed no heterozygosity (*H*) at any of >60 allozyme loci (O'Brien *et al.* 1983). Subsequent analysis by two-dimensional electrophoresis of >150 soluble proteins reported a mean heterozygosity of $H \approx 0$ for South African populations and $H = 0.014$ for East Africa; a figure in direct contrast with the average value for mammalian species ($H = 0.067$). Possibly even more unusual was the finding that cheetahs were apparently monomorphic at the major histocompatibility complex, an abundantly polymorphic locus in nearly all mammals (O'Brien *et al.* 1985; Yuhki & O'Brien 1990). Recent studies on short tandem repeat

polymorphisms, or microsatellites, have shown that the cheetah exhibits the lowest level of polymorphism among felid species (Menotti-Raymond & O'Brien 1995).

The near absence of genetic variability found in the cheetah was presumably produced as a consequence of the reduction in population numbers during the late Pleistocene, near the end of the last ice age (Menotti-Raymond & O'Brien 1993; May 1995). Many large specialized carnivores became extinct during this period, including several species of the genus *Acinonyx*. The modern cheetah is now clearly in the process of a severe range contraction since its distribution was worldwide 20 ka ago, but today the species is restricted to isolated populations between 1500 and 5000 individuals in South and East Africa. The interpretation most compatible with all data suggests that the cheetah experienced a severe bottleneck, which reduced the amount of genetic variation in the populations owing to the combined forces of natural selection and genetic drift, followed by intense inbreeding in its recent history. Significant consequences of this homozygosity are (1) the acceptance of reciprocal skin grafts between unrelated individuals, a phenomenon not previously observed in wild mammals (O'Brien *et al.* 1985; Sanjayan & Crooks 1996); and (2) the small number of sperm counts (ten times lower than in related felid species) and the high number of morphologically aberrant spermatozoa (approximately 70%), which is a characteristic only seen previously in inbred livestock and inbred mice (see references in O'Brien *et al.* 1983; Donoghue *et al.* 1992). Similar effects have been reported recently in wild populations of *Gazella cuvieri* which are endangered by inbreeding (Roldan *et al.* 1998). Of particular interest for our study is that the paucity in genetic variation of the cheetah results in a high level of fluctuating cranial asymmetry which is significantly greater than in other felid species. Wayne *et al.* (1986) found a statistically significant inverse relationship between *H* and cranial *FA* in modern felid species, with the lowest values of *H* and the highest score of *FA* in the cheetah. A similar effect of population bottlenecks on cranial asymmetry has been detected in the Eurasian otter (Pertoldi *et al.* 1997).

There are few studies applying the *FA*/homozygosity correlation to the fossil record (see review in Palmer 1986). However, several examples include the examination of *FA* in Pliocene horses (Van Valen 1962), the analysis of patterns of antisymmetry in Jurassic brachiopods (Fürsich & Palmer 1984), the measurement of *FA* in lower Paleozoic trilobites (Smith 1998), and the study of dental anomalies in upper Eocene anthracoteriids related to inbreeding (Ducrocq *et al.* 1995).

Inbreeding and population size in *Canis (Xenocyon) falconeri*

Fluctuating asymmetry can be used to infer general conditions such as inbreeding or environmental stress on a population whenever it is measured in a population sample with a relatively large number of well-preserved specimens. This clearly excludes the situation discussed here, although in some cases it has been proposed for limited sets of fossil specimens (see Ducrocq *et al.* 1995 and references therein). Even in such cases it would be impossible, by looking at asymmetry alone, to distinguish between asymmetries originating from genetic homozygosity due to inbreeding and those resulting from environmental stress.

However, the high degree of cranial asymmetry observed in the fossil cranium of *C. falconeri* associated with severe tooth anomalies which are clearly related to genetic disturbances in mammals (e.g., Buchalczyk *et al.* 1981; Miles & Grigson 1990; Schalkvanderweide *et al.* 1994), may suggest a high level of genetic homozygosity in the populations of this species living in southeastern Spain during the early Pleistocene. This would cause a lack of genetic homeostasis and the emergence of developmental instabilities. This homozygosity may be explained as a consequence of the presumably small population of wild dogs that inhabited the Guadix-Baza intramontane basin, which was isolated from other similar ecosystems and, thus conditions that would promote inbreeding. In fact, the fossil record of *C. falconeri* in the Iberian Peninsula comprises only this population. Such endemic conditions promoting genetic isolation from other European populations could be the main cause behind the presence of this anomalous individual and the disappearance of *C. falconeri* in the Western fringe of Europe. If this explanation holds, the case study reported here would be the first documented example for the Pleistocene record in which geographic and genetic isolation were the causal factors of a local extinction of large mammals.

On the other hand, the pathologies found in this specimen indicate that conditions were such that the individual was able to survive to adulthood in spite of severe developmental handicaps. This might suggest a very benign environment, but more probably that social behavior and assistance from other members of the hunting group may have helped this individual to survive. This would imply that the high level of cooperative behavior shown by modern African wild dogs was fully evolved in *C. falconeri* during early Pleistocene times.

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References

- Alados, C.L., Escós, J. & Emlen, J.M. 1995: Fluctuating asymmetry and fractal dimension of the sagittal suture as indicators of inbreeding depression in dama and dorcas gazelles. *Canadian Journal of Zoology* 739, 1967–1974.
- Arribas, A. & Palmqvist, P. 1998: Taphonomy and paleoecology of an assemblage of large mammals: hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios* 31 (Suppl. 3), 3–47.
- Arribas, A. & Palmqvist, P. 1999: On the ecological connection between sabre-tooths and hominids: faunal dispersal events in the lower Pleistocene and a review of the evidence for the first human arrival in Europe. *Journal of Archaeological Science* 26 (in press).
- Bouza, C., Sánchez, L. & Martínez, P. 1997: Gene diversity analysis in natural populations and cultured stocks of turbot (*Scophthalmus maximus* Linné). *Animal Genetics* 28, 28–36.
- Buchalczyk, T., Dynowski, J. & Sztayn, S. 1981: Variations in number of teeth and asymmetry of the skull in the wolf. *Acta Theriologica* 26, 23–30.
- Donoghue, A.M., Howard, J.G., Byers, A.P., Goodrowe, K.L., Bush, M., Blumer, E., Lukas, J., Stover, J., Snodgrass, K. & Wildt, D.E. 1992: Correlation of sperm viability with gamete interaction and fertilization in the cheetah (*Acinonyx jubatus*). *Biology of Reproduction* 46, 1047–1056.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J.J. 1995: Dental anomalies in Upper Eocene Anthracotheriidae: a possible case of inbreeding. *Lethaia* 28, 355–360.
- Fordyce, R.E. 1982: Dental anomaly in a fossil squalodont dolphin from New Zealand, and the evolution of polydonta in whales. *New Zealand Journal of Zoology* 9, 419–426.
- Fürsich, F.T. & Palmer, T. 1984: Commissural asymmetry in brachiopods. *Lethaia* 17, 251–265.
- Galobart, A., Maroto, J. & Ros, X. 1996: Las faunas cuaternarias de mamíferos de la cuenca de Banyoles-Besalú (Gerona). *Revista Española de Paleontología* N° Extraordinario, 248–255.
- Guerrero-Alba, S. & Palmqvist, P. 1998: Estudio morfométrico del caballo de Venta Micena (Orce, Granada) y su comparación con los équidos modernos y del Plió-Pleistoceno en el Viejo y Nuevo Mundo. *Paleontología i Evolucio* 30–31, 121–175.
- Hallgrímsson, B. 1998: Fluctuating asymmetry in the mammalian skeleton: evolutionary and developmental implications. *Evolutionary Biology* 30, 187–251.
- Hartl, G.B., Suchentrunk, F., Willing, R. & Petznek, R. 1995: Allozyme heterozygosity and fluctuating asymmetry in the brown hare (*Lepus europaeus*): a test of the developmental homeostasis hypothesis. *Philosophical Transactions of the Royal Society of London, Series B* 350, 313–323.
- Hutchison, D.W. & Cheverud, J.M. 1995: Fluctuating asymmetry in *Tamarin saguinus* cranial morphology: intraspecific and interspecific comparisons between taxa with varying levels of genetic heterozygosity. *Journal of Heredity* 86, 280–288.
- Imasheva, A.G., Loeschke, V., Zhivotovskiy, L.A. & Lazebny, O.E. 1997: Effects of extreme temperatures on phenotypic variation and developmental stability in *Drosophila melanogaster* and *Drosophila buzzatii*. *Biological Journal of the Linnean Society* 61, 117–126.
- Koufos, G. D. & Kostopoulos, D. 1997: New carnivore material from the Plió-Pleistocene of Macedonia (Greece) with description of a new canid. *Münchner Geowissenschaften, Abherdt (A)* 34, 33–63.

- Lacy, R.C. & Horner, B.E. 1996: Effects of inbreeding on skeletal development of *Rattus villosissimus*. *Journal of Heredity* 87, 277–287.
- Leamy, L.J., Routman, E.J. & Cheverud, J.M. 1997: A search for quantitative trait loci affecting asymmetry of mandibular characters in mice. *Evolution* 51, 957–969.
- Leamy, L.J., Routman, E.J. & Cheverud, J.M. 1998: Quantitative trait loci for fluctuating asymmetry of discrete skeletal characters in mice. *Heredity* 80, 509–518.
- Lewis, M.E. 1997: Carnivorous paleoguilds of Africa: implications for hominid food procurement strategies. *Journal of Human Evolution* 32, 257–288.
- Lucas, S.G. & Schoch, R.M. 1987: Paleopathology of early Cenozoic *Coryphodon* (Mammalia; Pantodontia). *Journal of Vertebrate Paleontology* 7, 145–154.
- [Martínez-Navarro, B. 1991: Revisión sistemática y estudio cuantitativo de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada). Ph.D. dissertation (unpublished). Universitat Autònoma de Barcelona, Spain.]
- Martínez-Navarro, B. 1992: Revisión sistemática y estudio cuantitativo de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada). In Gibert J. (ed.): *Proyecto Orce-Cueva Victoria (1988–1992). Presencia humana en el Pleistoceno inferior de Granada y Murcia*, 21–85. Ayuntamiento de Orce, Granada (Spain).
- Martínez-Navarro, B. & 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, 569–575.
- Martínez-Navarro, B., Turq, A., Agustí, J. & Oms, O. 1997: Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution* 33, 611–620.
- May, R.M. 1995: The cheetah controversy. *Nature* 374, 309–310.
- Menotti-Raymond, M.A. & O'Brien, S.J. 1993: Dating the genetic bottleneck of the African cheetah. *Proceedings of the National Academy of Sciences USA* 90, 3172–3176.
- Menotti-Raymond, M.A. & O'Brien, S.J. 1995: Evolutionary conservation of ten microsatellite loci in four species of Felidae. *Journal of Heredity* 86, 319–322.
- Miles, E.E.W. & Grigson, C. 1990: *Colyer's Variations and Diseases of the Teeth of Animals*. 672 pp. Cambridge University Press, Cambridge, Mass.
- Möller, A.P. 1997: Developmental stability and fitness: a review. *American Naturalist* 149, 916–932.
- Möller, A.P. & Thornhill, R. 1998: Bilateral symmetry and selection: a metaanalysis. *American Naturalist* 151, 174–192.
- O'Brien, S.J., Roelke, M.E., Marker, L., Newman, A., Winkler, C.A., Meltzer, D., Colly, L., Evermann, J.F., Bush, M. & Wildt, D.E. 1985: A genetic basis for species vulnerability in the cheetah. *Science* 227, 1428–1434.
- O'Brien, S.J., Wildt, D.E., Goldman, D., Merrill, C.R. & Bush, M. 1983: The cheetah is depauperate in genetic variation. *Science* 221, 459–462.
- Palmer, A.R. 1986: Inferring relative levels of genetic variability in fossils: the link between heterozygosity and fluctuating asymmetry. *Paleobiology* 12, 1–5.
- Palmqvist, P., Martínez-Navarro, B. & Arribas, A. 1996: Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. *Paleobiology* 22, 514–534.
- Pertoldi, C., Loeschcke, V., Madsen, A.B. & Randi, E. 1997: Developmental stability in the Eurasian otter (*Lutra lutra*) in Denmark. *Annales Zoologici Fennici* 34, 187–196.
- Pons-Moyà, J. 1981: El *Canis etruscus* Major (Carnivora, Mammalia) del Villafranchiense terminal de la Cueva Victoria (Murcia, España). *Endins* 8, 43–46.
- Pons-Moyà, J. 1987: Los carnívoros (Mammalia) de Venta Micena (Granada, España). *Paleontología i Evolució Mem. Espec.* 1, 109–128.
- Reyment, R.A. 1991. *Multidimensional Palaeobiology*. 377 pp. Pergamon Press, Oxford.
- Reyment, R.A., Blackith, R.E. & Campbell, N.A. 1984. *Multivariate Morphometrics*. 2nd Edition, 233 pp. Cambridge University Press, Cambridge.
- Roldan, E.R.S., Cassinello, J., Abaigar, T. & Gomendio, M. 1998: Inbreeding, fluctuating asymmetry, and ejaculate quality in an endangered ungulate. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 265, 243–248.
- [Rook, L. 1993: I cani dell'Eurasia dal Miocene superiore al Pleistocene medio. Ph.D. dissertation (unpublished), University of Firenze, Italy.]
- Rook, L. 1994: The Plio–Pleistocene Old World *Canis* (*Xenocyon*) ex. gr. *falconeri*. *Bollettino della Società Paleontologica Italiana* 33, 71–82.
- Rook, L. & Torre, D. 1986: The wolf-event in Western Europe and the beginning of the Late Villafranchian. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 8, 495–501.
- Rose, K.D. & Smith, B.H. 1979: Dental anomalies in the early Eocene condylarth *Ectocion*. *Journal of Paleontology* 53, 756–760.
- Sanjayan, M.A. & Crooks, K. 1996: Skin grafts and cheetahs. *Nature* 381, 566.
- Schalkvanderweide, Y., Steen, W.H.A., Beemer, F.A. & Bosman, F. 1994: Reductions in size and left-right asymmetry of teeth in human oligodontia. *Archives of Oral Biology* 39, 935–939.
- Smith, L.H. 1998: Asymmetry of early Paleozoic trilobites. *Lethaia* 31, 99–112.
- Sotnikova, M. 1998: 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.)
- Sotnikova, M.V., Dodonov, A.E. & Pen'kov, A. V. 1997: Upper Cenozoic bio-magnetic stratigraphy of Central Asian mammalian localities. *Palaeoecography, Palaoclimatology, Palaeoecology* 133, 243–258.
- Suseethorn, V., Buffertaut, E., Helmcke-Ingavat, R., Jaeger, J.-J. & Jongkanjanasontorn, Y. 1988: Oldest known Tertiary mammals from South-East Asia: middle Eocene primate and anthracotheres from Thailand. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 9, 563–570.
- Swisher, C.C., Curtis, G.H., Jacob, T., Getty, A.G., Suprijo, A. & Widiasmoro 1994: Age of the earliest known hominids in Java, Indonesia. *Science* 263, 1118–1121.
- Torre, D. 1967: I cani Villafranchiani della Toscana. *Paleontographica Italica* 64, 113–138
- Torre, D., Albanielli, A., Bertini, A., Ficarrelli, G., Massini, F. & Napoleone, G. 1996: Paleomagnetic calibration of Plio–Pleistocene mammal localities in central Italy. *Acta Zoologica Cracoviensis* 39, 559–570.
- Van Valen, L. 1962: A study of fluctuating asymmetry. *Evolution* 16, 125–142.
- Van Valkenburgh, B. 1985: Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* 11, 406–428.
- Van Valkenburgh, B. 1988a: Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14, 155–173.
- Van Valkenburgh, B. 1988b: Incidence of tooth breakage among large, predatory mammals. *American Naturalist* 131, 291–302.
- Van Valkenburgh, B. 1989: Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In Gittleman, J.L. (ed.): *Carnivore Behavior, Ecology, and Evolution*, 410–435. Cornell University Press, Ithaca, N.Y.
- Van Valkenburgh, B. 1990: Skeletal and dental predictors of body mass in carnivores. In Damuth, J. & MacFadden, B.J. (eds.): *Body size in Mammalian Paleobiology: Estimation and Biological Implications*, 181–205. Cambridge University Press, Cambridge.
- Van Valkenburgh, B. 1991: Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. *Paleobiology* 17, 340–362.

- Van Valkenburgh, B. & Hertel, F. 1993: Tough times at La Brea: tooth breakage in large carnivores of the Late Pleistocene. *Science* 261, 456–459.
- Van Valkenburgh, B. & Ruff, C.B. 1987: Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* 212, 379–397.
- Vilà, C., Urios, V. & Castroviejo, J. 1993: Tooth losses and anomalies in the wolf (*Canis lupus*). *Canadian Journal of Zoology* 71, 968–971.
- Wang, L. & Wu, M. 1976: A dental anomaly of *Ailuropoda melanolenca baconi*. *Vertebrata Palasiatica* 14, 263–266.
- Wayne, R.K., Modi, W.S. & O'Brien, S.J. 1986: Morphological variability and asymmetry in the cheetah (*Acinonyx jubatus*), a genetically uniform species. *Evolution* 40, 78–85.
- Wilson, R.W. 1955: Two cases of dental anomaly in early Tertiary mammals. *Transactions of the Kansas Academy of Sciences* 58, 514–518.
- Yuhki, N. & O'Brien, S.J. 1990: DNA variation of the mammalian major histocompatibility complex reflects genomic diversity and population history. *Proceedings of the National Academy of Sciences USA* 87, 836–840.