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REMAINS OF CANIDAE FROM THE LOWER PLEISTOCENE SITE OF UNTERMASSFELD

1. Introduction

Finds of a small wolf in association with the large *Canis (Xenocyon) lycaonoides* Kretzoi are rather common for Eurasian faunas of the end of the Early/beginning of the Middle Pleistocene. In Central Europe this group of canids is well documented from numerous mammal localities, but for the most part it is represented by relatively incomplete material. The discovery of the new Untermaßfeld locality near Meiningen in Southern Thuringia (Germany) in the late 1970s and its excavations conducted during several years, provided a rich fossil material of this carnivore group.

Canis (Xenocyon) lycaonoides is represented in the locality by three lower mandibles from three individuals, upper teeth fragments, and an incomplete humerus. This material is not large, but it is rather informative. Morphological variations of the lower carnassial of the Untermaßfeld form made it possible to trace the development of a hypercarnivorous trend in M_1 of large canids.

Samples of a small wolf in the Untermaßfeld collection include more than 300 remains of incomplete skulls, mandibles, and skeletal elements.

Bones appear not to have experienced any substantial displacement both before and after the burial. The collection yields associated vertebrae and almost complete fore and hind feet with small carpal and tarsal bones, which are very few in mammal localities. Skeletal elements of one individual with twin fore and hind limb bones also occur. Twenty eight mandibles of 15 individuals, among which are five males and ten females, give the most complete idea of the character of the Untermaßfeld population of small wolf. More than half of the remains belong to adult animals, whereas the rest are old individuals with strongly worn teeth. Old individuals have pathologic changes, such as the healed anterior and posterior alveoli in a teeth series, and porous growth of bony tissue around carnassials. The Untermaßfeld material includes fragments of 6 skulls among which are complete tooth series and the almost uncrushed and undeformed dorsal part of a skull.

Owing to the lack of enough data on skulls, modern taxonomy of Pleistocene European medium-sized canids close in size to the Untermaßfeld form, is based mainly on tooth evidence of these carnivores. Skulls of these canids were known up to now mainly from southern regions of Europe (Italy, France). In central Europe, from where *Canis mosbachensis* Soergel was described, no one more or less complete skull of small wolf has previously been found.

Abundant Untermaßfeld material permitted the study of more satisfactory cranial features of small wolf and the tracing of variation limits of separate features within the population. The comparative analysis of the Untermaßfeld Canidae-association was made using the data on large and medium-sized canids studied during my visits to the Museum of Geology and Palaeontology, Florence; Institute of Palaeontology »M. Crusafont«, Sabadell and American Museum of Natural History, New York. Three skulls of *Canis pallipes* Sykes were investigated in the Museum of Natural Science, Berlin. For comparison, collections of recent Canidae from the Zoological Institute, St. Petersburg, and Zoological Museum, Moscow, as well as the collection of the Early and Middle Pleistocene large [*C. (Xenocyon) lycaonoides*] and medium-sized (*C.* ex gr. *mosbachensis-variabilis*) canids from Russia (Siberia), Tadjikistan and Mongolia, were examined.

The paper uses the stratigraphic scheme in which the Early-Middle Pleistocene boundary is placed at the base of Cromer s. l., and the Early Pleistocene is subdivided into two stages: late Early Pleistocene and early Early Pleistocene, where the latter corresponds to Olivola and Tasso faunal units.

1.1. Institutional Abbreviations

AMNH American Museum of Natural History, New York
F:AM Frick Collection, American Museum of Natural History, New York
GIN Geological Institute, Russian Academy of Sciences, Moscow
IGF Institute of Geology, Florence
IPS Institute of Palaeontology »M. Crusafont«, Sabadell
IQW Institute of Quaternary Palaeontology, Weimar (now part of the Senckenberg Institute)
MNB Museum of Natural Science, Berlin
PIN Palaeontological Institute, Russian Academy of Sciences, Moscow
VM Venta Micena Collection
ZIN Zoological Institute, Russian Academy of Sciences

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2. Description of fossil Canidae from Untermaßfeld

2.1. Methods

In studies of fossil canids from Untermaßfeld emphasis was placed on the examination of skulls, mandibles and teeth. I used mainly the system of cranial measurements by Nowak (1979), whereas teeth dimensions were taken in a standard way. The cusp terminology of Berta (1988, Fig. 8) with some appendices was used in the description. Measurements of skeletal elements were made chiefly according to the procedure of Hue (1907).
Features selected by Bonifay (1971), Torre (1974), Kurtén (1974), Nowak (1979), and Berta (1988) for better understanding of evolutionary changes in the *Canis* lineage were used for the investigation. In the interpretation of the polarity of character-states (primitive or derived) I followed to a greater or lesser extent the system of character analysis suggested by Berta (1988) for large South American Canidae. The system is based on the fundamental research of the North American Canini (Tedford and Taylor, unpublished MS).
There are some common abbreviations used in the tables of measurements of teeth and bones.

Abbreviations for measurements:
L - length; W - width; Lb - length of blade; La - alveolar length; Lm - length of mandible from canine to condyle; Trl - length of trigonid; D - depth; GL - greatest length; GW - greatest width; AP - antero-posterior diameter of proximal end; WP - greatest width of proximal end; WS - shaft width in the middle; TS - transverse shaft diameter in the middle; AD - antero-posterior diameter of distal end; WD - greatest width of distal end; N - number of measurements; r - right; l - left; av. - average; Mc - metacarpal; Mt - metatarsal.
All measurements in tables are in mm.

2.2. *Canis mosbachensis* Soergel, 1925

2.2.1. Cranium and upper teeth

The collection yields fragments of six skulls. The incomplete skull lacking basioccipital and bulla areas, as well as zygomatic archs, is of a large adult male [IQW 1982/18052 (Mei. 17572) (Taf. 102, 1; Taf. 103, 1; Taf. 104, 1)]. The left part of a muzzle of a young individual IQW 1984/20177 (Mei. 19697) is shown

in Taf. 102, 3. The incomplete occipital area of this skull and right side of the muzzle with C-M^2 also occur. Fragments of two other medium-sized skulls evidently refer to females: IQW 1982/18249 (Mei. 17769) (Taf. 104, 2) and IQW 1980/15328 (Mei. 14840) (Taf. 102, 2.)
Additionally, the collection yields maxillary fragments of very old individuals with worn teeth: IQW 1980/16077 (Mei. 15588), IQW 1983/19214 (Mei. 18734), IQW 1983/19215 (Mei. 18735), IQW 1983/19113 (Mei. 18633) and separate upper canines and incisors (10 specimens).
Dimensions are typical for the genus *Canis*. Cranium proportions are relatively narrow, the rostrum is elongated, the maximum length of the nasal bone along the suture is 75.2 mm on the specimen IQW 1982/18052 (Mei. 17572). The maxilla is moderately curved in the area of the infraorbital foramen. Frontals are not prominently convex and are moderately elevated above the rostrum. A relatively narrow frontal shield is surrounded by well-developed, sharp temporal ridges. The sagittal crest is prominent, with a maximum length of 77.0 mm and a maximum height of 17.0 mm in the specimen IQW 1982/18052 (Mei. 17572). The postorbital constriction area is moderately elongated and is relatively narrow lateromedially. The braincase is not elongated and is little inflated. Choanae are oval shaped and their frontal margin is at the level of the M^2 centre. The infraorbital foramen is above the posterior root of P^4. Cranial measurements are listed in Tab. 1.

	IQW 1982/18052 (Mei. 17572)	IQW 1982/18249 (Mei. 17769)	IQW 1984/20177 (Mei. 19697)
Greatest length	217.0	–	–
Braincase width	57.0	–	58.4
Alveolar length of P^1-M^2	80.0	75.0	69.4
Maximum width across M^1	70.0	–	–
Width across canines	37.0	–	–
Width of frontal shield	50.0	54.0	54.0
Least width at postorbital constriction	36.2	–	39.7
Greatest palatal length	100.5	93.5	–
Greatest nasal length	75.2	–	–
Greatest sagittal crest length	77.0	–	–

Tab. 1 *Canis mosbachensis*, Untermaßfeld. Measurements of skull (mm).

The arrangement of incisors is semicircular. Width of incisor toothrow is 25.0-28.8 mm. I^1 and I^2 are relatively large with two basal cusps on each side of the main cusp. The canine-form I^3 has well-developed posterolateral cingulum. Canines are flattened laterally and relatively thin anteroposteriorly.
Premolars are separated by diastemas in the specimen IQW 1982/18052 (Mei. 17572) and set closely together in the specimen IQW 1984/20177 (Mei. 19697). Main axes of P^3 and P^4 coincide. P^1 is single-rooted and single-cusped. P^2 is double-rooted, elongated posteriorly with a single, poorly pronounced accessory cusp behind the main cusp. P^3 is elongated posteriorly with two posterior cusplets. P^4 has a well-developed and slightly anteriorly situated protocone. A prominent ridge rises from the base of anterior part of P^4 crown. All specimens of P^4 have a strong lingual cingulum.
Upper molars are large and broad. The first molar is closer in size to M^1 of *Canis etruscus* Forsyth Major from Valdarno and Olivola, whereas its proportions are closer to those of medium-sized canids from the Petralona Cave, L'Escale, Stránská Skála, and Hundsheim (Fig. 1). M^1 of the Untermaßfeld wolf has a complete buccal cingulum. Its paracone and metacone are normally developed, metaconule and paraconule are present. The protocone basin is deep. The large hypocone basin is surrounded by a prominent protocone and large hypocone. M^2 is large, with a paracone distinctly greater than metacone, with well-developed hypocone basin and complete buccal cingulum. The Untermaßfeld wolf has LP^4: LM^{1+2}

		IQW 1982/18052 (Mei. 17572)		IQW 1982/18249 (Mei. 17769)		IQW 1980/15328 (Mei. 14840)		IQW 1984/20177 (Mei. 19697)		IQW 1980/16077 (Mei. 15588)	
		r	l	r	l	r	l	r	l	r	l
I^1	L	5.1	–	4.7	–	–	–	–	–	–	–
	W	4.0	–	4.1	–	–	–	–	–	–	–
I^2	L	6.2	6.2	5.8	–	6.1	6.0	–	6.0	–	6.0
	W	5.0	5.1	5.0	–	5.5	5.5	–	5.7	–	5.4
I^3	L	7.2	7.2	6.8	–	6.9	7.1	–	6.7	–	7.4
	W	5.8	5.9	5.4	–	4.9	4.9	–	5.8	–	5.1
C	L	11.6	–	–	9.0	–	–	9.8	10.0	–	9.9
	W	6.7	6.7	5.3	–	–	–	6.1	6.1	–	6.8
P^1	L	6.1	6.1	6.8	6.9	6.6	6.7	–	6.8	6.5	6.5
	W	4.3	4.3	4.0	4.1	4.4	4.4	–	4.5	4.3	4.3
P^2	L	11.8	11.9	11.3	11.2	–	–	11.8	11.5	12.4	11.2
	W	4.5	4.4	4.1	4.1	–	–	4.55	4.4	4.4	4.4
P^3	L	13.5	13.2	12.5	–	–	–	13.3	13.4	14.2	–
	W	5.4	5.4	4.5	–	–	–	5.4	5.4	5.5	–
P^4	L	23.0	23.0	20.7	–	20.4	20.5	21.2	21.2	22.9	22.4
	W	11.2	11.5	9.6	–	11.3	11.2	11.0	11.1	10.8	11.4
	Lb	8.3	8.4	7.9	–	7.6	7.5	8.2	8.1	8.4	8.0
M^1	L	14.6	15.1	13.7	–	13.4	–	14.4	14.2	–	–
	W	19.1	19.3	18.0	–	19.5	–	18.7	18.9	–	–
M^2	L	8.5	8.6	7.9	–	7.5	–	7.9	7.6	–	–
	W	14.0	14.0	11.8	–	12.6	–	12.2	12.2	–	–

Tab. 2 *Canis mosbachensis*, Untermaßfeld. Measurements of upper teeth (mm).

(length of P^4 to the length of M^{1+2}) ratio of 94.0-96.2%. This value agrees with that of Late Villafranchian *Canis etruscus* from Italy, whereas the Middle Pleistocene population of small wolf from L'Escale yields more individuals with the ratio higher than 100% (Bonifay 1971). Measurements of upper teeth are listed in Tab. 2.

Comparison of cranium and upper teeth

Dimensions of the small wolf from Untermaßfeld correspond to those of fossil medium-sized canids *Canis etruscus* and *Canis mosbachensis* in Europe, *Canis chihliensis* and *Canis variabilis* from Asia, as well as to the recent small wolf *Canis pallipes* from India and Pakistan. Its dimensions also overlap with the lower limits of gray wolf size from southern parts of the distribution area. According to the upper teeth morphology, Untermaßfeld specimens are also similar to *Canis arnensis*, although, cranial features of these two forms differ greatly (Fig. 2).

Compared with *C. arnensis*, the Untermaßfeld skull has larger and broader muzzle and its frontals are more elevated above the rostrum. The postorbital constriction and braincase are narrower and the toothrow is relatively shorter. Temporal ridges are more sharp and the sagittal crest is stronger. These characters make the Untermaßfeld form closer to medium-sized wolves, whereas *C. arnensis*, according to cranial features, is more similar to coyote-like dogs.

The Untermaßfeld wolf differs from *Canis lupus* by averagely smaller dimensions and narrower skull, especially in the rostrum and carnassials. The frontals of a small wolf are less elevated above the rostrum

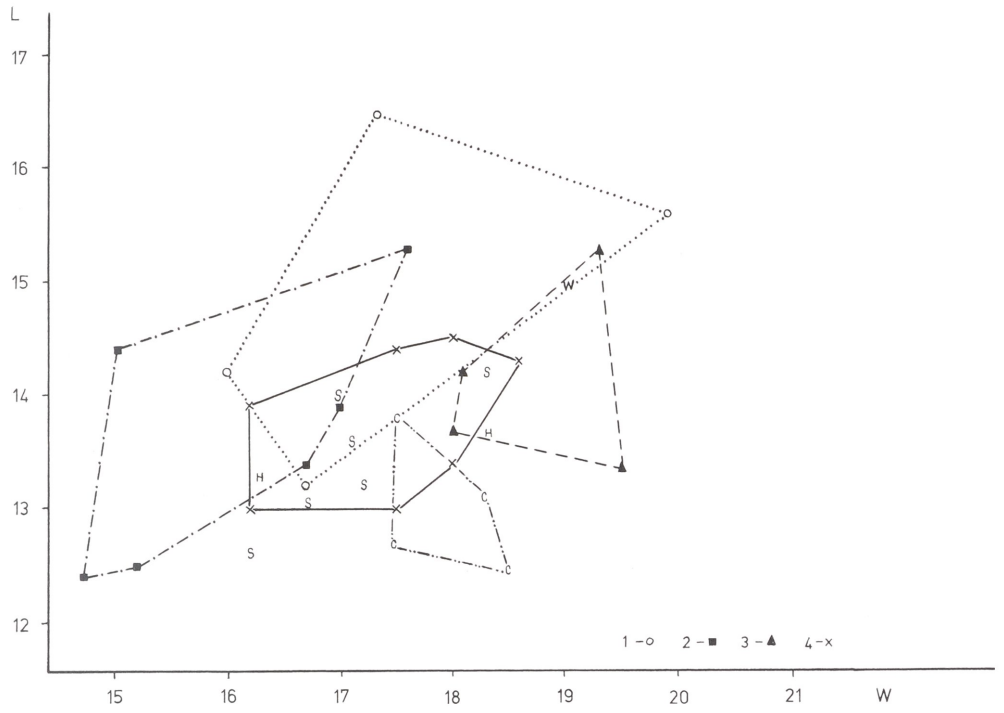

Fig. 1 Relationships between width and length of M^1 (mm) in various samples of medium-sized *Canis*. – 1 *C. etruscus* (after Rook 1993). – 2 *C. arnensis* (after Rook 1993). – 3 *C. mosbachensis*, Untermaßfeld. – 4 *C. mosbachensis*, L'Escale (after Bonifay 1971). – Further: Canidae from various localities: S Stránská Skála, H Hundsheim, C Petralona Cave, W Würzburg-Schalksberg (after Musil 1972; Thenius 1954; Kurtén and Poulianos 1981; Schütt 1974).

and are more flat. Postorbital constriction is relatively shorter and the toothrow is on the average longer and less curved in the junction of P^4 and P^3. The upper premolars are more elongated anteroposteriorly and are narrower. The upper carnassial has a prominent protocone located slightly anteriorly, and a strong lingual cingulum. The first molar has a more developed buccal cingulum, as well as a deeper and larger hypocone basin. M^2 is larger.

According to many cranial parameters, the skull from Untermaßfeld is close to that of the recent small wolf *Canis pallipes* (Fig. 2), which has a number of primitive characters distinguishing it from large gray wolves and making it similar to fossil medium-sized canids. Its primitive features are small size, frontals moderately elevated above the rostrum, relatively straight toothrows without a sharp curve in the junction of P^4 and P^3, prominent protocone of P^4 and a complete buccal cingulum at M^1. According to its dimensions, cranial proportions, and teeth features mentioned above, this recent small wolf is united with *Canis* from Untermaßfeld.

The Untermaßfeld wolf differs from *Canis pallipes* by having on average a narrower skull, especially in the canine area, by having a more elongated muzzle, by the greater length of the toothrow, weaker canines, and larger upper molars. Additionally, the recent small wolf shows a difference in the value of ratio $LP^4:LM^{1+2}$. This index ranges in *C. pallipes* from 93.1% to 105.4% against 94.0-96.2% in the Untermaßfeld wolf.

Finds of canid skulls of the same size range as the Untermaßfeld specimens, are known from the Early-Middle Pleistocene deposits of Eurasia.

In China, medium-sized canids from Nihowan were described as *Canis chihliensis* (var. *palmidens* and var. *chihliensis*) (Teilhard de Chardin and Piveteau 1930), whereas the Middle Pleistocene *Canis* of the same size from Choukoutien Locality 1 was identified as *Canis lupus* var. *variabilis* (Pei 1934). How-

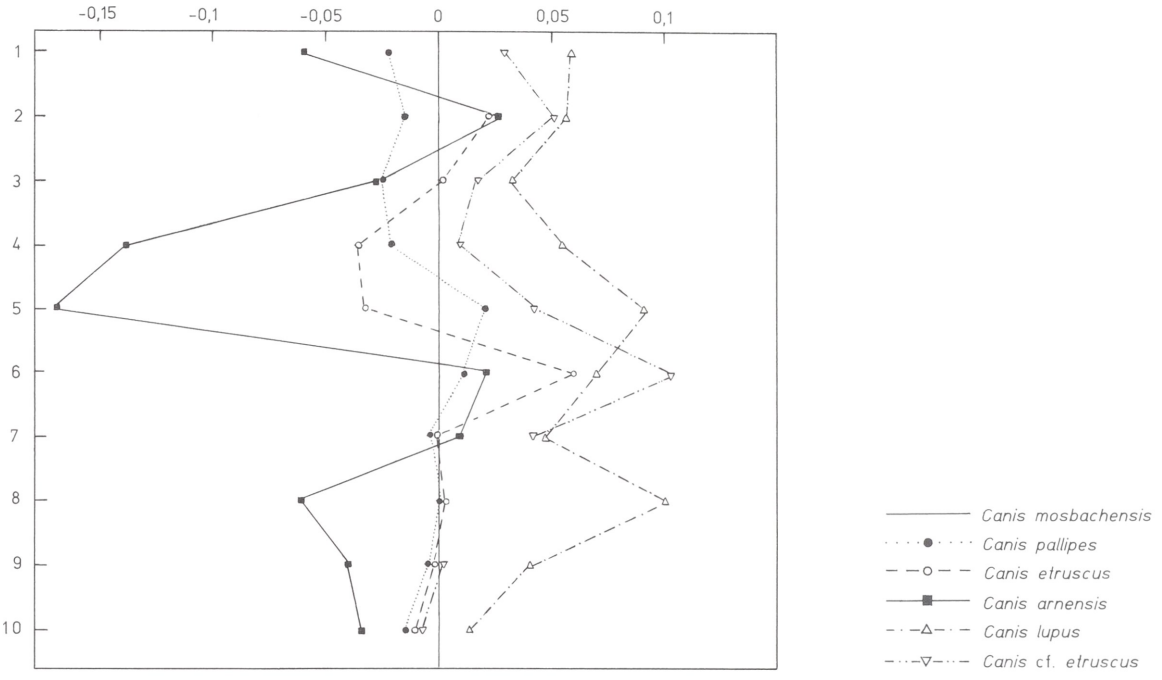

Fig. 2 Log-ratio diagram comparing the cranial proportions of *Canis mosbachensis* from Untermaßfeld (standard of comparison) using the following measurements: – 1 Length anterior tip of praemaxillare to posterior point of inion. – 2 Maximum breadth of braincase. – 3 Length of P^1-M^2. – 4 Maximum breadth between outer sides of P^4 or M^1. – 5 Greatest width across outer sides of alveoli of canines. – 6 Maximum width across postorbital processes of frontals. – 7 Least breadth of frontals in the postorbital constriction. – 8 Anteroposterior diameter of upper canine. – 9 Length of upper carnassial. – 10 Width of second molar. – *Canis mosbachensis* represented by Untermaßfeld samples (N=1-3); *Canis pallipes* represented by skulls (N=3) MNB 49997, MNB 49996, MNB A-5211; *Canis etruscus* from Valdarno represented by skulls (N=1-3) casts IGF 12333, IGF 12334 and F:AM 89779, cast IGF 12867; *Canis arnensis* represenred by skulls (N=2) cast IGF 869 from Tasso and skull GER-45 from Gerakorou, measurements of GER-45 were used after Koufos (1987); *Canis* cf. *etruscus* represented by skull (N=1) from Hsia Chwang (China) F:AM 97050; *Canis lupus* represented by skulls (N=7) from Kazakhstan, collection ZIN.

ever, skulls of these canids were not described in detail. According to Teilhard de Chardin (1940, 9), medium-sized *Canis* from those two localities, as well as *Canis* from Locality 13, »belong to a relatively small type, with rather elongated skull and decidedly strong carnassial teeth«. These features unite Chinese medium-sized canids with the Untermaßfeld wolf. Details of the teeth morphology seen in figures of *C. chihliensis* and *C. variabilis*, as well as the analysis of medium-sized canids from Middle Pleistocene deposits of Northern Siberia, on the whole coincide with the dental morphology of Untermaßfeld wolf. However, a special study of skulls from Asia is necessary for more detailed comparison.

In Europe, skulls of Early-Middle Pleistocene medium-sized canids are known from Italy and France (Torre 1967; Bonifay 1971). Unfortunately, the material from France (L'Escale) lacks the dorsal part of the skull. According to Bonifay's description (1971), the skull D-8 yields a strong sagittal crest also developed on skulls of recent large wolves. The anteroposterior elongation of the muzzle also occurs. These features make *Canis* from L'Escale similar to the group of medium-sized canids. A strong development of the sagittal crest, as well as rather large incisors, canines, and molars, indicate the greater similarity of L'Escale specimens to the fossil wolf group, including *Canis* from Untermaßfeld, than to the group of coyote-like dogs, in which they have been referred by Rook and Torre (1996).

I have not found a substantial morphological difference in the structure of upper teeth series of the small wolf from L'Escale, *Canis etruscus* from Upper Valdarno, and Untermaßfeld wolf, but they have pro-

portional differences in upper molars. According to proportions of M^1, *Canis* from Untermaßfeld is closer to the wolf from L'Escale, whereas its ratio LP^4:LM^{1+2} corresponds more to that of *C. etruscus*. Cranial features of the Untermaßfeld form differ from those of *Canis etruscus* (cast IGF 12867, F:AM 89779) by an averagely broader muzzle and narrower frontal shield. Within the genus *Canis* a broad frontal shield may evidently be considered as a primitive feature. *Canis* cf. *etruscus* F:AM 97050 from China (Hsia Chwang locality, Villafranchian), as well as, according to Nowak (1979), the North American Pliocene-Early Pleistocene *Canis lepophagus* and *Canis edwardii*, have a broad frontal shield, whereas recent representatives of large and medium-sized *Canis* have a narrower shield.

2.2.2. Mandible and lower teeth

Twenty eight more or less complete branches of mandibles belong to not less than 15 individuals. Two groups of mandibles were distinguished. Shallow and relatively slender mandibles with slightly convex ventral margin under P_3, evidently, belong to females: IQW 1980/16553 (Mei. 16074) (Taf. 105, 1-3), IQW 1980/15309 (Mei. 14821) and IQW 1980/15308 (Mei. 14820) (Taf. 106, 1-6). More massive and high mandibles, with a straight ventral margin, appear to belong to males: IQW 1980/16939 (Mei. 16460) (Taf. 103, 2-3), IQW 1982/17995 (Mei. 17515) (Taf.105, 4-6).

Twelve specimens belong to old individuals with very worn dentition; some of them have pathological changes in the teeth. On specimens IQW 1980/15919 (Mei. 15430), IQW 1982/17972 (Mei. 17492), and IQW 1983/19213 (Mei. 18733) alveoli of P_1 are missing, the specimen IQW 1984/20111 (Mei. 19631) lacks the alveoles of M_3. Strong bulges of bony tissue often occur around the alveolus of M_1. The specimen IQW 1980/16939 (Mei. 16460) has P_1 and P_2 joined into one threerooted tooth (Taf. 36, 2-3).

The mandible is on the whole long and relatively shallow in the horizontal ramus. The height of the mandible measured between the highest point of the coronoid process and the lowest point of the lower margin of the ramus, perpendicular to the toothrow, is 70.5 mm in specimen IQW 1980/15309 (Mei. 14821) and 68.9 mm in IQW 1982/17995 (Mei. 17515). Other mandible measurements are listed in Tab. 3.

Premolars in a mandible are separated by diastemas or set closely together. A diastema most often occurs between P_2 and P_3. Main axes of molars and premolars most commonly coincide or are parallel to each

	Lm	La C-M_3	La P_1-M_3	La P_1-M_2	La P_{1-4}	La M_{1-3}	D behind M_1	D behind P_1
1980/16939 (Mei. 16460)	136.0	–	–	–	–	–	24.5	20.0
1980/17151 (Mei. 16672)	–	97.0	83.0	77.5	44.5	39.7	21.0	–
1980/15919 (Mei. 15430)	–	99.5	–	–	–	40.0	25.0	19.0
1980/17152 (Mei. 16673)	–	94.0	78.0	74.5	40.0	39.0	–	–
1980/15308 (Mei. 14820)	135.5	95.5	80.5	77.2	43.5	38.6	22.4	17.6
1980/15309 (Mei. 14821)	135.0	96.0	80.5	76.6	43.4	38.5	23.1	–
1980/16553 (Mei. 16074)	128.0	91.0	77.8	–	39.7	39.3	22.7	18.1
1980/15357 (Mei. 14869)	–	100.0	82.0	75.9	43.3	40.0	24.0	19.1
1982/17995 (Mei. 17515)	–	–	84.4	79.0	43.4	42.8	24.5	20.5
1982/18013 (Mei. 17533)	–	–	81.0	71.8	42.0	41.0	23.6	19.7
1983/19913 (Mei. 18733)	137.0	92.0	–	–	–	38.5	22.1	17.9
1983/18939 (Mei. 18499)	130.0	91.0	78.5	74.0	41.2	38.5	–	19.0
1984/20111 (Mei. 19631)	–	100.0	83.3	79.0	44.4	42.5	–	–
1986/21596 (Mei. 21115)	–	–	–	79.1	42.6	–	24.3	20.7
1986/21084 (Mei. 20603)	–	–	–	78.8	45.2	–	22.8	19.5

Tab. 3 *Canis mosbachensis*, Untermaßfeld. Measurements of mandible (mm).

		C		P_1		P_2		P_3	
		L	W	L	W	L	W	L	W
1980/16939	(Mei. 16460)	9.0	6.6	–	–	10.1	–	11.6	5.2
1980/17151	(Mei. 16672)	9.4	6.0	6.0	4.1	10.2	4.4	11.7	4.5
1980/15919	(Mei. 15430)	–	–	–	–	–	–	12.3	5.0
1980/17152	(Mei. 16673)	9.5	6.6	–	–	10.3	5.2	11.3	5.0
1980/15308	(Mei. 14820)	10.5	6.8	5.5	4.0	10.5	4.7	12.0	4.9
1980/15309	(Mei. 14821)	10.0	7.0	5.4	3.5	–	–	12.1	5.0
1980/15753	(Mei. 15265)	–	–	–	–	–	–	–	–
1980/15920	(Mei. 15431)	–	–	–	–	–	–	–	–
1980/16553	(Mei. 16074)	9.8	6.7	–	–	10.8	5.0	11.9	5.0
1980/15357	(Mei. 14869)	–	–	6.2	4.0	–	–	–	–
1982/17995	(Mei. 17515)	–	–	5.4	4.1	10.8	5.0	11.9	5.1
1982/18013	(Mei. 17533)	–	–	5.9	4.5	11.5	5.4	12.1	5.4
1983/18939	(Mei. 18499)	–	–	–	–	–	–	11.1	5.0
1982/18592	(Mei. 18112)	–	–	–	–	10.2	4.5	11.2	4.8
1982/18591	(Mei. 18111)	–	–	–	–	–	–	–	–
1984/20111	(Mei. 19631)	–	–	–	–	11.2	5.0	13.1	5.9
1984/20112	(Mei. 19632)	–	–	–	–	–	–	–	–
1984/20000	(Mei. 19520)	10.3	7.4	5.5	4.5	11.5	5.2	13.4	5.8
1986/21596	(Mei. 21115)	11.0	7.6	6.0	4.1	11.0	5.2	–	–
1986/21085	(Mei. 20604)	–	–	–	–	11.6	4.9	12.5	5.1
1986/21084	(Mei. 20603)	10.2	6.9	6.3	3.9	11.2	5.0	12.2	5.0

Tab. 4a *Canis mosbachensis*, Untermaßfeld. Measurements of lower teeth (mm).

other. The relatively straight toothrow is only sometimes slightly curved at the juncture of P_4 and M_1. The masseteric fossa is deep and its anterior margin reaches the level of the M_2 posterior root. A large mental foramen is located below the first root of P_2, and a smaller foramen is below P_3. In lateral view the paraconid top of M_1 is generally situated a little higher from the top of the main cusp of P_4, but some specimens have these tops at the same level.

All specimens of the Untermaßfeld wolf have P_3 located in the mandible lower than P_2 and P_4, so that in lateral view the main cusp of P_3 is distinctly lower than main cusps of P_2 and P_4. *Canis etruscus* from Italy lacks this feature, unlike the Middle Pleistocene medium-sized canids from Mosbach, Betfia V, Petralona Cave, and Cullar de Baza 1 (H.-D. Kahlke 1961, Bild 1; Terzea and Jurcsák 1969, Fig. 1A; Kurtén and Poulianos 1977, 52; Alcalá and Morales 1989, Fig. 4).

Lower incisors are almost never preserved, and only separate, very worn teeth occur. Canines are relatively narrow at the base and are sometimes distinctly inclined to the horizontal ramus. P_1 is a single-rooted and single-cusped tooth. P_2 sometimes has a posterior cusplet, though most specimens lack it. P_3 has two posterior cusplets behind the main cusp. P_4 has two posterior cusplets and a well-developed posterolingual cingulum. The top of the first accessory cusp is highly elevated relative to the top of the second posterior cusplet. The latter is located closely to the cingulum. About half of the specimens have this cusplet well-separated from the cingulum. P_4 from other mandibles shows a tendency towards the joining of the cingulum cusplet and the second accessory cusp.

The lower carnassial is large, with a relatively long talonid. The metaconid on M_1 is well developed, but projects less medially than that of *Canis etruscus* and *C. arnensis*. The talonid of M_1 has a large hypoconid and lesser entoconid connected by a strong transverse crest. The talon basin for the protocone of

	P_4		M_1			M_2		M_3	
	L	W	L	W	Trl	L	W	L	W
1980/16939 (Mei. 16460)	13.2	6.5	23.8	9.2	16.4	10.9	8.1	–	–
1980/17151 (Mei. 16672)	12.7	5.7	23.3	8.0	15.5	10.8	7.8	–	–
1980/15919 (Mei. 15430)	14.2	6.4	25.1	9.5	16.7	–	–	–	–
1980/17152 (Mei. 16673)	–	–	23.5	8.9	16.5	10.8	7.7	–	–
1980/15308 (Mei. 14820)	13.4	6.2	24.0	9.3	16.2	10.5	7.7	4.2	4.1
1980/15309 (Mei. 14821)	13.5	6.2	23.9	9.1	16.0	–	–	–	–
1980/15753 (Mei. 15265)	14.7	6.7	25.9	9.8	18.8	–	–	–	–
1980/15920 (Mei. 15431)	–	–	23.4	8.8	15.9	10.0	7.7	–	–
1980/16553 (Mei. 16074)	13.5	6.1	24.0	9.0	16.5	10.2	7.2	–	–
1980/15357 (Mei. 14869)	13.6	6.0	23.7	9.0	16.3	10.0	7.3	–	–
1982/17995 (Mei. 17515)	13.7	6.4	25.8	9.6	18.1	10.4	7.8	5.7	5.1
1982/18013 (Mei. 17533)	14.2	6.3	–	–	–	11.8	–	5.5	5.0
1983/18939 (Mei. 18499)	13.0	6.2	–	8.6	16.6	–	–	–	–
1982/18592 (Mei. 18112)	12.5	6.3	–	8.9	16.5	–	–	–	–
1982/18591 (Mei. 18111)	–	–	25.0	9.3	17.3	–	–	–	–
1984/20111 (Mei. 19631)	14.5	7.0	–	–	–	–	–	5.2	4.8
1984/20112 (Mei. 19632)	13.5	6.2	24.2	9.5	16.5	10.9	7.0	3.9	3.2
1984/20000 (Mei. 19520)	14.9	7.2	–	10.2	–	–	–	–	–
1986/21596 (Mei. 21115)	14.0	6.6	25.5	9.3	18.1	10.8	7.1	–	–
1986/21085 (Mei. 20604)	14.3	6.3	25.0	9.0	17.5	11.2	7.8	–	–
1986/21084 (Mei. 20603)	–	–	25.0	–	17.9	11.0	8.0	–	–

Tab. 4b *Canis mosbachensis*, Untermaßfeld. Measurements of lower teeth (mm).

M^1 is large and deep. A prominent metastylid usually occurs behind the metaconid, though specimens without the metastylid are also present. A small hypoconulid shelf is usually present on M_1, but its development can range from near absence to prominence. M_2 is usually long compared with M_1, though specimens with relatively short M_2 occur; it has a large protoconid and prominent, large metaconid. The well-developed anterobuccal cingulum borders the protoconid of M_2. Most of the specimens from Untermaßfeld have a simple structure of M_2, but there are some with more complicated M_2 morphology. For example, the associated mandibles IQW 1980/15308 (Mei. 14820) and IQW 1980/15309 (Mei. 14821) (Taf. 106, 1-6) have a distinct paraconid and two small cusplets behind the metaconid. M_3 of all the samples is small, rounded in cross section, bearing two cusps.
Measurements of mandibles are listed in Tab. 4.

Comparison of mandibles and lower teeth
According to the dimensions of the lower teeth, the Untermaßfeld wolf resembles *Canis etruscus* from Valdarno and Olivola, as well as *C. mosbachensis* from Central Europe (Mauer, Mosbach, Voigtstedt, Hundsheim, Stránská Skála, and other localities), and is on the average a little larger than the late Early and Middle Pleistocene medium-sized canids from southern regions of Europe (Fig. 3).
Canis mosbachensis is sometimes considered as a subspecies of *C. lupus*, although the investigation shows that mandibles of small wolves *C. etruscus* and *C. mosbachensis*, as well as of the Untermaßfeld wolf, differ from those of the recent wolf. Apart from smaller dimensions, the mandible of the Untermaßfeld wolf differs from that of *C. lupus* by a straight toothrow, which is not sharply curved outside in the junction of P_4 and M_1. This latter feature appears to belong only to gray wolves, whereas fossil

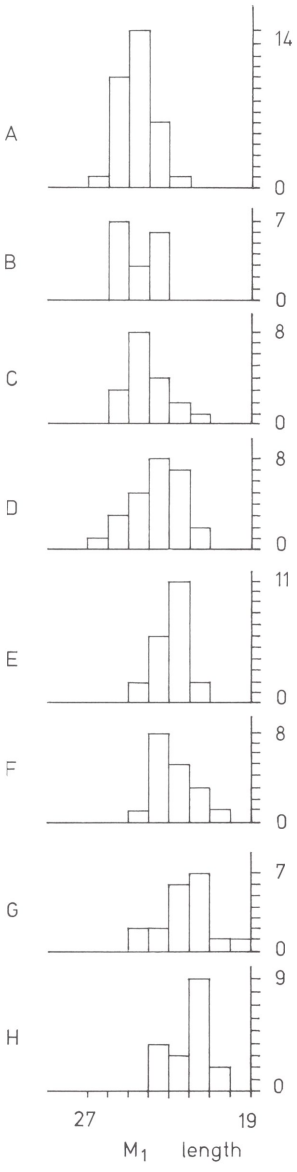

Fig. 3 Histograms of length of M_1 (mm) for *Canis etruscus, Canis mosbachensis* and *Canis arnensis*. – A *C. etruscus* (N=21) from Peccioli, Olivola, Matassino, Ostine, Le Ville, Inferno (after Rook 1993). – B *C. mosbachensis* (N=16) from Untermaßfeld. – C *C. mosbachensis* (N=18) from Gombasek, Hundsheim, Mauer, Mosbach, Voigtstedt, Westbury (after Soergel 1925; Kretzoi 1938; Thenius 1954, 1965; Adam 1959; Bishop 1982). – D *C. mosbachensis* (N=26) from L'Escale, upper level (after Bonifay 1971). – E *C. mosbachensis* (N=21) from L'Escale, lower level (after Bonifay 1971). – F *C. mosbachensis* (N=18) from Stránská Skála (after Musil 1972). – G *C. mosbachensis* (N=19) from Petralona Cave, Crenian level (after Kurtén and Poulianos 1981). – H *C. arnensis* (N=18) from Gerakarou, Sainzelles, Tasso, Upper Valdarno (after Rook 1993).

canids, including the large *Canis (Xenocyon)*, together with recent *C. latrans* Say and *C. pallipes* Sykes have relatively straight lower toothrows.

Canis lupus has the premolars in the mandible set lower than the molars, so that the basis of the crown, as well as the paraconid top of M_1, is located distinctly higher than the crown basis and the top of P_4. Mio-Pliocene small dogs from the »*Canis*« sp. group, as well as *Vulpes,* have premolars located high in a mandible, so that the top of main cusp of P_4 is at the same level as, or higher than, the top of the paraconid of M_1. The same relationship of P_4 and M_1 is characteristic for *C. etruscus*, whereas the Untermaßfeld wolf, as well as *C. mosbachensis*, with relatively high-set premolars, have the top of P_4 located slightly lower than the top of the paraconid of M_1.

Most fossil canids, including the Untermaßfeld wolf, have a well-developed posterolingual cingulum at P_3 and P_4. *Canis latrans* and *C. pallipes* also have this character, whereas *C. lupus* almost lacks it. The second posterior cusplet is formed on the cingulum. The degree of its development varies among canids. Among the Pliocene small dogs »*Canis*« *odessanus* this cusplet occurs as a minute cusplet on the cingulum. The Early-Middle Pleistocene small wolf has the second posterior cusplet far greater than Pliocene canids. It should be noted that *C. etruscus* from Valdarno and Olivola have this cusplet well separated from the cingulum, whereas among the Untermaßfeld wolf population, as well as among other *C. mosbachensis*, there is a tendency for joining of the cusplet with the cingulum, as evidently happened among *C. lupus*. Difference in the molar morphology from *C. lupus*, as well as from coyote-like dogs, is also rather distinct. The Untermaßfeld wolf, like other Early-Middle Pleistocene small wolves and in contrast to *C. lupus*, has a talonid basin on M_1 which is deeper and more closed from the lingual side. The metaconid is larger, and a weak hypoconulid shelf often occurs. This shelf is almost undeveloped among *C. lupus* and it varies among fossil small wolves, but it is large among recent coyotes and coyote-like *C. arnensis*. The Untermaßfeld wolf, like other fossil forms and in contrast to *C. lupus*, has a well-developed anterobuccal cingulum on M_2. As was cited in in the description, the Untermaßfeld wolf shows a trend to the complication of cusps on the talonids of M_1 and M_2. *Canis etruscus* together with *C. lupus* and *C. pallipes,* had a simpler morphology of the talonid of the lower molars.

The occurrence of accessory cusps – metastylid, entocristid, and entoconulid – on the talonid of lower molars is considered as a derived character of the genus *Canis* (Berta 1988). According to this feature, the M_1 of the Untermaßfeld wolf shows more derived condition than the carnassial of *Canis etruscus*.

2.2.3. Postcranial skeleton

Vertebrae. Wolves usually have seven cervical vertebrae. In the Untermaßfeld collection they are represented by 13 fragments.

Atlas IQW 1980/15327 (Mei. 14839) (Taf. 107, 1). It has a typical *Canis* morphology. The intervertebral foramen is elongated anterolaterally and is located close to the cranial border. A large fossa atlantis is situated at a distance of 11.0 mm, whereas a foramen transversarium is at 8.4 mm from the caudal margin of atlas.

Measurements of atlas IQW 1980/15327 (Mei. 14839) are: Greatest length - 38.3 mm. Greatest diameter transverse - 73.8 mm. Anterior diameter transverse - 40.0 mm.

Axis IQW 1984/20170 (Mei. 19690) (Taf. 107, 2). Its measurements are: Dorsal length - 51.0 mm. Greatest diameter of articular facies - 17.0 mm. Transverse diameter of articular facies - 10.5 mm.

Third cervical vertebra IQW 1984/20166 (Mei. 19686) and fourth cervical vertebra IQW 1984/20162 (Mei 19682) (Taf. 107, 3-4). Greatest dorsal length of third vertebra - 36.0 mm, of the fourth - 35.0 mm.

Thoracic vertebrae IQW 1984/20165 (Mei. 19685) (Taf. 107, 5, 7) and IQW 1984/20163 (Mei. 19683) (Taf. 107, 6, 8). There are 9 fragments, which are poorly preserved, so that the determination of the number of a vertebra in thoracic series is impossible. The greatest dorsal length of the thoracic vertebrae ranges from 15.5 to 16.5 mm. *Canis lupus* usually has 13 vertebrae in the thoracic series, with 11 of them equal in length, whereas the 12th and 13th vertebrae are somewhat larger. The calculation shows that the length of the whole series of the Untermaßfeld wolf is approximately 21-23 cm, whereas among *C. lupus* this length varies from 28 to 35 cm (N = 12).

Lumbar vertebrae from first to seventh (Taf. 107, 9-15). The Untermaßfeld collection yields 16 vertebrae from 3 individuals. Dorsal length of seven associated lumbar vertebrae (Taf. 107) are: 27.4 mm, 27.0 mm, 25.5 mm, 24.5 mm, 23.5 mm, 21.5 mm, 21.0 mm. The whole length of the lumbar series is near 17-18 cm, among *C. lupus* this length is 24-29 cm (N = 12).

Sacrum IQW 1984/20132 (Mei. 19652) (Taf. 107, 16-17). Only one sacrum occurs, its greatest length measured parallel to the medium line is 37.0 mm, among *C. lupus* this length ranges from 46.0 to 80.0 mm (N = 12).

There are seven caudal vertebrae in the Untermaßfeld collection, IQW 1984/20129 (Mei. 19649) and IQW 1980/15541 (Mei. 15053) (Taf. 107, 18-20).

Scapula IQW 1980/15786 (Mei. 15298) (Taf. 41, 6-8) and 4 distal fragments from 3 individuals occur in the collection. Relatively small, slender scapulae IQW 1984/20095 (Mei. 19615) and IQW 1984/20126 (Mei. 19646) are, evidently, from females. The tuber scapulae is larger and better developed among males. The glenoid cavity of the scapula has an oval shape; its morphology does not differ from that of *Canis lupus*. Measurements of scapula are listed in Tab. 5.

	IQW 1984/20095 (Mei. 19615)	IQW 1984/20126 (Mei. 19646)	IQW 1984/20148 (Mei. 19668)	IQW 1980/15786 (Mei. 15298)
Greatest diameter of articulating end	25.3	23.0	21.2	16.0
Least width of neck across articulating end	25.0	23.6	21.2	15.5
Greatest width of glenoid cavity	–	26.4	23.5	–
Greatest transverse diameter of glenoid cavity	30.0	26.8	25.0	18.3

Tab. 5 *Canis mosbachensis*, Untermaßfeld. Measurements of scapula (mm).

Humerus IQW 1980/15303 (Mei. 14815) (Taf. 108, 1-2). A single complete humerus and 14 proximal and distal fragments from 4 individuals occur in the Untermaßfeld collection. All humeri are approximately equal, and therefore I did not distinguish males and females among them. The bone is slender and grace-

	GL	WP	AP	WS	WD	WT
IQW 1980/15303 (Mei. 14815)	169.6	26.5	39.5	11.5	30.7	21.4
IQW 1980/15505 (Mei. 15017)	–	26.0	37.5	12.2	–	–
IQW 1980/15325 (Mei. 14837)	–	–	–	11.4	30.2	21.5
IQW 1980/16603 (Mei. 16124)	–	–	–	–	31.8	23.2
IQW 1980/15715 (Mei. 15227)	–	–	–	–	30.5	21.0
IQW 1984/20127 (Mei. 19647)	–	–	–	11.0	29.0	19.2
IQW 1984/20122 (Mei. 19642)	–	–	–	–	30.7	22.4
IQW 1986/21523 (Mei. 21042)	–	–	–	11.0	29.7	19.9
IQW 1986/21524 (Mei. 21043)	–	–	–	11.0	30.1	19.8
WT – Greatest width of trochlea						

Tab. 6 *Canis mosbachensis*, Untermaßfeld. Measurements of humerus (mm).

	GL	WP	AP	WS	WD	AD
IQW 1980/16959 (Mei. 16480)	–	15.9	10.9	–	–	–
IQW 1980/15304 (Mei. 14816)	163.0	17.0	11.2	12.3	22.5	12.1
IQW 1980/15302 (Mei. 14814)	163.2	17.3	11.2	11.7	21.0	11.0
IQW 1980/15692 (Mei. 15204)	–	–	–	–	25.3	13.2
IQW 1982/18129 (Mei. 17649)	–	–	–	–	22.8	12.2
IQW 1984/19981 (Mei. 19501)	169.0	18.1	13.2	12.1	23.3	13.4
IQW 1984/20257 (Mei. 19777)	167.0	17.4	11.5	14.2	23.0	13.4
IQW 1986/21067 (Mei. 20586)	–	–	–	–	23.3	13.2
IQW 1980/16134 (Mei. 15645)	–	16.9	11.2	–	–	–
IQW 1984/20124 (Mei. 19644)	–	17.5	11.2	–	–	–

Tab. 7 *Canis mosbachensis*, Untermaßfeld. Measurements of radius (mm).

ful, and does not differ morphologically from *Canis* of L'Escale, but the Untermaßfeld humerus is a little larger (Tab. 15). It differs from the humerus of *Canis (Xenocyon) lycaonoides* IQW 1985/20693 (Mei. 20212) by smaller dimensions and the form of olecranon fossa, which is deeper among small wolves, so that the supratrochlear foramen is deeper. Measurements of humeri are listed in Tab. 6.

Four complete radii and 13 proximal and distal fragments from 6 individuals occur. A left complete radius IQW 1980/15302 (Mei. 14814) (Taf. 108, 3) is associated with the right radius IQW 1980/15304 (Mei. 14816) and with the humerus IQW 1980/15303 (Mei. 14815). In associated limb bones of Untermaßfeld wolf the radius is shorter than the humerus, and the radius/humerus ratio is 96.4%. The small wolf from L'Escale, on the other hand, does not have the distal part of fore limb bones shortened, and this ratio in associated bones exceeds 100% (102.3-103.2%). Measurements of radii are listed in Tab. 7.

The ulna is represented by 12 proximal and distal fragments, which belong to seven individuals. The most complete specimen IQW 1980/16611 (Mei. 16132) is pictured on Taf. 108, 4. Bones are well separated into two groups. More slender bones (5 fragments) evidently belong to females, more large and massive ones to males. The length of ulna (about 190-195 mm) was calculated by three, complementary fragments. This length corresponds to ulna dimensions of the wolf from L'Escale. Bonifay (1971) found a difference in size of the olecranon process among *Canis lupus* and L'Escale wolf, though this feature varies within the Untermaßfeld population. Measurements of ulnae are listed in Tab. 8.

Carpal bones, metacarpals, and phalanges. An almost complete right fore foot, IQW 1980/15310 (Mei.

	LC	LA	WP	AP	AC
IQW 1980/16611 (Mei. 16132)	36.4	26.2	11.2	18.5	19.0
IQW 1980/15813 (Mei. 15324)	36.5	25.2	11.3	19.4	19.1
IQW 1980/15323 (Mei. 14835)	37.6	26.5	11.0	19.8	17.2
IQW 1980/15750 (Mei. 15262)	39.7	29.2	–	23.4	18.0
IQW 1980/16490 (Mei. 16011)	–	25.2	–	20.5	–
IQW 1980/17351 (Mei. 16873)	–	28.0	–	–	18.0
IQW 1984/20118 (Mei. 19638)	36.5	26.0	11.2	18.9	18.4
IQW 1984/20117 (Mei. 19637)	34.5	23.2	11.0	17.5	16.1

LC – Greatest length from tuber olecrani to coronoid process
LA – Greatest length from tuber olecrani to anconeal process
AC – Anteroposterior diameter of ulna above coronoid process

Tab. 8 *Canis mosbachensis*, Untermaßfeld. Measurements of ulna (mm).

	NM	GL	WP	AP	WS	WD
IQW 1980/15314 (Mei. 14826)	Mc 1	23.0	5.2	6.0	4.3	5.6
IQW 1980/15310 (Mei. 14822a)	Mc 1	23.1	4.6	5.5	3.6	5.5
IQW 1982/17850 (Mei. 17370)	Mc 2	59.5	8.0	9.8	6.8	8.7
IQW 1980/15537 (Mei. 15049)	Mc 2	–	8.2	10.0	–	–
IQW 1980/15312 (Mei. 14834)	Mc 2	63.5	7.3	–	6.1	8.2
IQW 1984/20022 (Mei. 19542)	Mc 2	64.7	7.8	10.8	6.1	8.5
IQW 1986/21601 (Mei. 21120)	Mc 3	72.5	7.9	10.3	6.2	8.0
IQW 1986/21602 (Mei. 21121)	Mc 4	73.1.	7.1	10.5	6.2	8.3
IQW 1980/15533 (Mei. 15045)	Mc 4	71.5	7.9	11.4	6.3	8.5
IQW 1982/17967 (Mei. 17487)	Mc 5	55.7	10.2	9.7	7.2	9.7
IQW 1980/15310 (Mei. 14822d)	Mc 5	61.0	11.1	9.9	6.7	9.5

NM – Metacarpal number in metacarpal series

Tab. 9 *Canis mosbachensis*, Untermaßfeld. Measurements of metacarpal series (mm).

14822), is represented on Taf. 110, 1-26. Additionally, the collection yields remains of six fore feet from 4 individuals. A total of 60 fragments occurs.

The greatest length of manus IQW 1980/15310 (Mei. 14822) measured from the proximal surface of scapho-lunar bone to the distal end of the third middle phalanx is about 130-135 mm. The transverse diameter of the proximal end of the metacarpal series (from Mc I to Mc V) is 30 mm. Length of metacarpal III is 72.5 mm, which is on the average a little more than that of the L'Escale wolf, and corresponds to dimensions of this metacarpal among *Canis mosbachensis* from Stránská Skála and Hundsheim (Tab. 15).

There are some carpal measurements (mm). Greatest length of pisiform: range 16.2-16.7, av. 16.4, N = 5. Proximal transverse diameter of pisiform: range 9.3-10.2, av. 9.8, N = 5. Distal transverse diameter of pisiform: range 8.2-8.7, av. 8.5, N = 5. Greatest transverse diameter of scapho-lunar: range 20.7-22.8, av. = 21.7, N = 5. Measurements of metacarpals are listed in Tab. 9.

The pelvis is represented by 8 badly preserved fragments from four individuals. All of them are approximately equal excluding the lesser specimen IQW 1984/20133 (Mei. 19653) pictured on Taf. 109, 1.

Measurements of pelvis IQW 1984/20133 (Mei. 19653) are: Greatest width of iliac bone: 38 mm. Minimum width of iliac bone: 18.8 mm. Greatest diameter of articular cavity: 18.4 mm. Among other specimens the diameter of articular cavity varies from 19.9 to 21.2 mm.

	GL	WP	WH	WS	TS	WD	TD
IQW 1980/16313 (Mei. 15824)	178.0	37.0	18.0	15.0	12.5	31.0	32.3
IQW 1980/15320 (Mei.14832)	–	37.2	17.2	–	–	–	–
IQW 1980/15317 (Mei.14829)	–	–	–	–	–	30.0	33.7
IQW 1980/15717 (Mei.15229)	–	–	–	–	–	30.7	33.8
IQW 1984/20119 (Mei.19639)	166.0	34.7	16.5	12.3	–	–	–
IQW 1984/20128 (Mei.19648)	–	39.5	18.3	–	–	–	–
IQW 1986/21529 (Mei.21048)	–	38.5	18.9	–	–	–	–
IQW 1984/20099 (Mei.19619)	–	39.3	18.5	–	–	–	–
WH – Greatest width of femur head							

Tab. 10 *Canis mosbachensis*, Untermaßfeld. Measurements of femur (mm).

	GL	WP	AP	WS	WD	AD
IQW 1980/16312 (Mei. 15823)	182.3	33.5	34.3	12.7	22.4	17.0
IQW 1980/15305 (Mei. 14817)	186.2	33.0	37.1	12.5	21.3	16.3
IQW 1983/19171 (Mei. 18691)	–	–	–	12.1	23.2	16.4
IQW 1984/20114 (Mei. 19634)	181.0	33.1	37.0	12.3	22.5	15.7
IQW 1985/20640 (Mei. 20189)	–	–	–	12.6	22.0	16.8
IQW 1986/21528 (Mei. 21047)	191.0	–	–	11.4	21.0	16.4
IQW 1986/21535 (Mei. 21054)	–	–	–	11.8	21.3	16.3

Tab. 11 *Canis mosbachensis*, Untermaßfeld. Measurements of tibia (mm).

Femur IQW 1980/16313 (Mei. 15824) (Taf. 109, 2-3) and 15 proximal and distal fragments from three individuals occur in Untermaßfeld. Right and left female femora IQW 1984/20119 (Mei. 19639) and IQW 1984/20120 (Mei. 19640) have more slender diaphyse and a small femur head. Dimensions and proportions of Untermaßfeld femora are comparable to those of the L'Escale wolf (Tab. 15). The femur pictured on Taf. 109 is associated with the tibia IQW 1980/16312 (Mei. 15823). Their femur/tibia ratio is 97.6%, whereas that of the wolf from L'Escale reaches 98.2% and among *Canis lupus* it is on the average closer to 100%. Measurements of femora are listed in Tab. 10.

A tibia IQW 1984/20114 (Mei. 19634) (Taf. 42,4) together with three complete tibiae and 15 proximal and distal fragments of 7 individuals occur in the Untermaßfeld collection. All bones are approximately equal in size. Their length is comparable to the tibial length of the small wolf from L'Escale and *Canis mosbachensis* from Stránská Skála. Tibia IQW 1980/15305 (Mei. 14817), according to the position in the excavation plan, is, evidently, associated with the radius IQW 1980/15302 (Mei. 14814) and humerus IQW 1980/15303 (Mei. 14815). The radius/tibia ratio in associated bones is 87.6%, in unassociated ones its mean value is 89.4%. Corresponding values for samples from L'Escale are 88.5-91.9% and 89.2%. In the Stránská Skála locality this ratio in unassociated bones is 87%. Measurements of tibiae are listed in Tab. 11.

Tarsal bones, metatarsals, and phalanges. A complete right hind foot is represented on Taf. 110, 27-48. The collection yields an associated left foot, as well as right and left feet from another individual together with fragments of two other hind feet from two individuals, a total of 83 bones.

The greatest length of the hind foot pictured on Taf. 110, measured from the proximal end of metatarsal series to the distal end of the third middle phalanx, is near 142-144 mm. Transverse diameter of the proximal end of the metatarsal series from Mt I to Mt IV is 23.2 mm. Measurements of metatarsals are listed in Tab. 12.

	NM	GL	WP	AP	WS	WD
IQW 1986/21544 (Mei. 21063)	Mt 2	73.8	–	13.2	6.0	8.3
IQW 1986/21545 (Mei.21064)	Mt 2	73.8	8.0	13.2	6.3	8.5
IQW 1986/21539 (Mei.21058)	Mt 3	81.0	8.8	14.4	7.3	8.3
IQW 1986/21538 (Mei.21057)	Mt 3	81.1	8.7	–	6.8	8.3
IQW 1980/15716 (Mei.15228)	Mt 3	73.9	8.7	13.5	7.2	8.6
IQW 1986/21541 (Mei.21060)	Mt 4	82.2	8.6	12.6	6.0	–
IQW 1986/21543 (Mei.21062)	Mt 4	82.2	8.9	12.0	6.0	7.8
IQW 1986/21542 (Mei.21061)	Mt 5	74.8	7.9	11.2	4.3	–
IQW 1986/21540 (Mei.21059)	Mt 5	75.3	8.2	10.4	5.5	8.2
NM – Metatarsal number in metatarsal series						

Tab. 12 *Canis mosbachensis,* Untermaßfeld. Measurements of metatarsal series (mm).

	GL	GW	LT	WT
IQW 1986/21333 (Mei. 20852)	28.0	21.1	17.4	14.8
IQW 1986/21532 (Mei. 21051)	27.2	20.5	16.2	13.2
IQW 1985/21013 (Mei. 20532)	25.5	18.0	17.4	13.6
IQW 1985/21536 (Mei. 21055)	27.0	20.8	17.0	13.5
LT – Greatest length of trochlea WT – Greatest width of trochlea				

Tab. 13 *Canis mosbachensis,* Untermaßfeld. Measurements of astragalus (mm).

	GL	GW	GA	WP	AP
IQW 1986/21546 (Mei. 21065)	44.6	16.9	19.2	11.7	13.2
IQW 1986/21537 (Mei. 21056)	43.8	17.9	18.6	11.2	13.1
IQW 1986/21534 (Mei. 21053)	47.5	18.3	19.2	12.9	14.4
IQW 1985/21012 (Mei. 20531)	41.6	16.2	17.6	11.3	13.7
IQW 1987/22291 (Mei. 21810)	–	–	18.3	11.0	13.5
GA – Greatest anteroposterior diameter of calcaneus					

Tab. 14 *Canis mosbachensis,* Untermaßfeld. Measurements of calcaneus (mm).

Five astragali are represented at Untermaßfeld. The specimen IQW 1986/21536 (Mei. 21055) (Taf. 110, 29) is associated with the right pes pictured on Taf. 110. Astragali belong to four individuals, one of which, the specimen IQW 1985/21013 (Mei. 20532), is, evidently, a female. Dimensions of astragali correspond to those of *Canis mosbachensis* from Hundsheim. The ratio of greatest width GW to greatest length GL of astragali from Untermaßfeld varies from 70.5 to 77.0%; the same values of this ratio were marked among the astragali of different recent species of the genus *Canis* (Gromova 1960). Measurements of astragali are listed in Tab. 13.

The Untermaßfeld collection includes five calcanei from four individuals. Calcaneus IQW 1986/21537 (Mei. 21056) (Taf. 110, 27) is associated with the right pes pictured on Taf. 110. Dimensions of the Untermaßfeld calcaneus correspond to those of *Canis mosbachensis* from Stránská Skála and Hundsheim and are somewhat larger than calcaneus of the wolf from L'Escale. Width of the tuber calcis of the calcaneus of the Untermaßfeld wolf is less than its anteroposterior diameter. According to Gromova

(1960), such proportions of tuber calcis are more characteristic of *Vulpes* and *Canis aureus* L., whereas among *C. lupus* the width of this tuber is almost the same or somewhat more than its anteroposterior diameter. Measurements of calcanei are listed in Tab. 14.

Comparison of postcranial skeleton

The postcranial skeleton of Untermaßfeld wolf agrees in dimensions and proportions of certain bones with the Middle Pleistocene European small wolves. On average, according to size, it is close to *Canis mosbachensis* from Stránská Skála and Hundsheim and is somewhat larger than the wolf from L'Escale.

It differs from the L'Escale wolf, as well as from recent gray wolf and coyote, in having the radius shorter than humerus (radius/humerus ratio is 96.4%). Proportions of segments of fore limbs of Untermaßfeld wolf are close to those of the Pliocene *Canis lepophagus*, which had a radius/humerus ratio of 93.4% (Kurtén 1974). Mio-Pliocene small dogs from the »*Canis*« sp. group had still shorter radii. Thus, the Untermaßfeld wolf, in contrast to the wolf from L'Escale, has more primitive proportions in segments of fore limbs.

Distal segments of hind limbs of the Untermaßfeld wolf, like those of wolves from Stránská Skála and L'Escale, were somewhat longer, with the radius/tibia ratio within 87.1-91.9%, av. = 88.9, N = 6. This ratio among recent wolves and coyotes is close to 100%, whereas among Mio-Pliocene small dogs it hardly exceeded 80% (Rook 1992; Tedford and Qiu 1996). According to radius/tibia ratios, Pleistocene wolves from Untermaßfeld, Stránská Skála, and L'Escale held an intermediate position between Pliocene and recent forms.

Greatest lenght	Untermaßfeld			L' Escale After Bonifay (1971)			Stránská Skála after Musil (1972)			Hundsheim after Thenius (1954)		
	N	range	av.	N	range	av.	N	range	av.	N	range	av.
Humerus	1	169.0		4	145.0-160.0	152.9	1	170.7				
Radius	4	163.0-169.0	165.5	6	148.0-168.0	156.3						
Ulna	–			5	175.0-206.0	185.3	1	194.7				
Femur	2	166.0-178.0	172.0	5	160.6-179.0	171.7	2	195.4-196.2	195.8			
Tibia	4	181.0-191.0	185.1	7	160.0-191.0	175.2						
Astragalus	4	25.5- 28.5	26.9	2	26.0- 38.7	32.3						
Calcaneus	4	41.6- 47.5	44.3	2	24.4- 39.2	31.3	2	43.3- 45.1	44.2		45.8	
Metacarpale III	1	72.5		2	63.8- 64.8	64.3	4	71.7- 73.0	72.4	2	70.6-73.5	72.0
Metatarsale III	3	73.9- 81.1		2	71.4- 72.5	71.9						

Tab. 15 Small wolf from various European localities. Comparative measurements of limb bones (mm).

2.3. *Canis (Xenocyon) lycaonoides* (Kretzoi, 1938)

2.3.1. Upper teeth

Specimens of incomplete M^1 with a broken paracone occur: IQW 1984/20196 (Mei. 19716) (Taf. 111, 1) and M^2 IQW 1986/21080 (Mei. 20599) (Taf. 112, 3).

M^1 is large, slightly compressed in a middle part of the crown. Its length across the protocone basin is 12.7 mm. The metacone is large and low-crowned. The protocone basin is shallow and surrounded by a crista joined with the strong protocone. The metaconule and protoconule are not developed. Anterolingually the tooth is bordered by a weak basal cingulum. The hypocone is represented by a small ridge on the cingulum, and is located posterolingually in relation to the protocone. The hypocone basin is almost undeveloped. M^2 is large and subtriangular in cross section. The buccal cingulum is not well developed. The paracone and metacone are low-crowned. The metacone length is only slightly less than the length of paracone. The protocone is very close to the lingual margin of tooth. The length of M^2 is 9.8 mm, the length in the middle part of the crown is 9.0 mm, the width of M^2 is 13.2 mm.

Comparison of upper teeth

Dimensions of M^2 are similar to those of the largest specimens of *Canis mosbachensis* from Untermaßfeld. According to the structure of M^1, the large canids differ from *C. mosbachensis* in the lack of metaconule and protoconule cusps and by a shallower and broader protocone basin and reduced hypocone basin. In the structure of M^2 they differ by more subequal size of the protocone and metacone, a less developed cingulum, and by reduction of the basin behind the protocone. The morphology of M^1 and M^2 of the large Untermaßfeld canid agrees with that of upper molars of *C. (Xenocyon) lycaonoides* from Stránská Skála, Zasukhino and Tologoj (Musil 1972; Sotnikova 1988).

2.3.2. Mandible and lower teeth

The collection includes a left mandible with I_3-M_3 IQW 1985/20555 (Mei. 20074) (Taf.111, 2-4); an incomplete left mandible with P_2, P_4-M_3 and isolated incisors IQW 1985/21000 (Mei. 20519) (Taf. 112, 1-2) and fragment of left mandible with P_3-P_4, IQW 1984/19954 (Mei. 19474).

The material belongs to three individuals, two of which are very large, whereas the specimen IQW 1985/21000 (Mei. 20519) is smaller and was of younger age at death.

Mandibles are large and massive. The length of mandible IQW 1985/20555 (Mei. 20074) from incisors to mandibular condyle is 203 mm. The height of this jaw, measured between the highest point of the coronoid process and the lowest point of ventral margin of mandible, is 96.2 mm. Its depth below the first root of M_1 is 32.6 mm, behind M_1 – 33.0 mm in comparison with 31.2 and 29.4 mm in mandible IQW 1985/21000 (Mei. 20519). The height of the coronoid process from the dorsal surface of the condyle to coronoid apex is less than that from mandibular condyle to ventral margin of the angular process. The masseter fossa is deep, and its anterior margin reaches the level of the last root of M_2. A large mental foramen is located below the anterior root of P_2, and a smaller foramen is positioned below the anterior root of P_3. The tooth row is straight, and long axes of P_4 and M_1 coincide or are parallel to each other. The ventral margin of mandible is relatively straight. The top of the main cusp of P_4 reaches the level of the top of the paraconid of M_1. The symphysis is high and short, and its posterior margin reaches the level of P_1.

Canines and incisors differ from those of small wolves only by larger dimensions. P_1 is single-rooted and single-cusped. P_2 has a posterior accessory cusp in the specimen IQW 1985/20555 (Mei. 20074) and is without this cusp in the specimen IQW 1985/21000 (Mei. 20519). P_3 has a posterior accessory cusp and a well-developed posterolingual cingulum. P_4 has two posterior accessory cusps and a strong posterolingual cingulum. The second posterior accessory cusp is represented by a minute cusp well separated from the cingulum. M_1 is long and relatively narrow. Specimen IQW 1985/20555 (Mei. 20074) has a prominent metaconid and talonid with a centrally-positioned, large and dominant hypoconid, and a vestigial entoconid. The strong transverse crest joins the hypoconid and vestigial entoconid. In the specimen IQW 1985/21000 (Mei. 20519) the entoconid on M_1 is better developed and represents a minute cusp; the centrally-positioned hypoconid is dominant.

M_2 is long in specimen IQW 1985/20555 (Mei. 20074) and relatively short in the other mandible. It is subtriangular in cross section. A weak anterobuccal cingulum occurs on the M_2. The protoconid is large and located slightly ahead of the metaconid. The metaconid is small on the large mandible and relatively large on the lesser jaw. A well-developed hypoconid is positioned behind the protoconid. M_3 occurs in both mandibles. Measurements of mandibles and teeth are listed in Tab. 16.

Comparison of mandible and lower teeth

The morphology of the talonid of M_1 with a dominant centrally-positioned hypoconid and the occurrence of M_3 permits us to refer the large Untermaßfeld canid to *Canis (Xenocyon) lycaonoides*. Dimensions of mandible IQW 1985/20555 (Mei. 20074) correspond to those of the largest representatives of this species, whereas the mandible IQW 1985/21000 (Mei. 20519) is closer in size to the lower size-range of *C. (Xenocyon) lycaonoides* (Tab. 17).

The Untermaßfeld large canid differs from the common morphotype of *C. (Xenocyon) lycaonoides* by

		IQW 1985/20555 (Mei. 20074)	IQW 1985/21000 (Mei. 20519)	IQW 1984/19954 (Mei. 19474)
I_3-M_3	La	135.7	–	–
C_1–M_3	La	129.3	–	–
P_1–M_3	La	103.0	93.0	–
P_1–P_4	La	53.5	49.6	–
M_1–M_2	La	49.5	44.5	–
I_1	L	5.2	4.5	–
	W	3.0	3.1	–
I_2	L	–	5.2	–
	W	–	3.1	–
I^3	L	7.3	6.4	–
	W	5.8	6.2	–
P_1	L	6.5	6.4	–
	W	5.0	4.0	–
P_2	L	13.2	12.3	–
	W	6.0	5.7	–
P_3	L	14.9	13.2	15.0
	W	7.0	–	6.5
P_4	L	17.4	16.9	17.6
	W	8.2	8.2	8.1
M_1	L	30.2	27.7	–
	TrL	22.3	21.5	–
	W	11.5	11.0	–
M_2	L	13.2	10.5	–
	W	8.6	8.0	–
M_3	La	5.0	6.2	–
	W	–	5.5	–

Tab. 16 *Canis (Xenocyon) lycaonoides,* Untermaßfeld. Measurements of mandible (mm).

the occurrence of vestigial or minute entoconids and an unreduced metaconid on the lower carnassials, as well as by the occurrence in specimen IQW 1985/20555 (Mei. 20074) of P_2 with posterior accessory cusp and relatively short M_2 in specimen IQW 1985/21000 (Mei. 20519).

Most Middle Pleistocene specimens of *C. (Xenocyon) lycaonoides* from Gombasek, Mosbach, Würzburg-Schalksberg and Westbury-sub-Mendip have an unicuspid, trenchant talonid and a reduced metaconid on M_1 (Kretzoi 1938; Schütt 1974; Bishop 1982). The same morphology of M_1 was marked among *C. (Xenocyon) lycaonoides* from Koněprusy (cast AMNH 23086), three of four specimens of Stránská Skála, as well as among Asian specimens from the Olyor fauna of North Siberia and Transbaikalia, (Musil 1972; Sotnikova 1978, 1988). However, the occurrence of the second cusp on the talonid of M_1 as a minute cusp, was seen on the left M_1 in mandible GIN 3848/355-67 from Lakhuti-2 and on one specimen from Stránská Skála.vestigial

More consistent occurrence of a minute or vestigial entoconid on M_1 and greater variations in common characters of *C. (Xenocyon) lycaonoides* can be seen in late Early Pleistocene samples. Asian forms have a minute entoconid on M_1 in the specimen F:AM 97046 from China (Ma Fang, Shou Yang district, Shansi), as well as in two of the three carnassials found in Nalaikha (Mongolia, PIN 3747). The Untermaßfeld specimens agree with the sample PIN 3747-256 in having a minute entoconid, an unreduced metaconid and a relatively short M_2. In Europe, large canids with reduced entoconid of M_1 are known from Cueva Victoria and Venta Micena (Pons Moyà and Moyà Solá 1978; Pons Moyà 1987; Martinez

Locality	Length					Depth behind		
	P_1-M_2	P_3	P_4	M_1	M_2	P_2	P_4	M_2
Untermaßfeld	98.0	14.9	17.4	30.2	13.2	29.7	33.1	37.0
Untermaßfeld	87.0	13.2	16.9	27.7	10.5	–	28.2	32.0
Westbury (after Bishop 1982)	92.0	13.7	–	28.5	13.3	26.4	29.0	34.0
Westbury (after Bishop 1982)	–	–	–	29.6	–	–	34.5	–
Mosbach (after Schütt 1974)	–	–	17.0	29.0	–	–	33.5	–
Würzburg (after Schütt 1974)	–	14.3	17.5	29.0	–	29.0	–	–
Koněprusy (cast AMNH 23096)	–	–	16.0	30.1	13.3	28.0	–	37.0
Zasukhino	–	–	17.8	30.2	13.1	–	–	–
Lakhuti	90.0	14.0	17.0	27.9	12.2	25.0	30.7	–
Chukochtya	97.0	–	–	29.5	14.3	29.5	31.8	37.5
Chukochtya	88.5	–	–	26.2	13.1	27.0	28.7	34.6
Adycha	93.5	14.0	17.1	28.6	13.8	26.0	31.4	35.7
Nalaikha	91.7	–	–	28.4	12.9	28.0	33.3	38.1
Nalaikha	91.5	14.6	17.2	27.8	11.4	27.1	32.0	–
Nalaikha	95.5	14.1	16.6	28.3	12.4	26.0	31.5	33.2
Nalaikha	90.5	–	16.0	29.0	12.4	26.9	31.1	37.1
Locality 18 (after T. de Chardin 1940)	88.0	–	–	26.5	11.0	–	27.0	–

Tab. 17 *Canis (Xenocyon) lycaonoides.* Comparative measurements of lower teeth and mandibles (mm).

Navarro 1992). The Untermaßfeld specimens agree with the Cueva Victoria sample in the occurrence of the minute entoconid and a short M_2, and with the Venta Micena specimens in having the minute entoconid (VM-2227) and posterior accessory cusp on P_2 (VM-2255).

2.3.3. Postcranial skeleton

An incomplete humerus, with its proximal end broken, IQW 1985/20693 (Mei. 20212) (Taf. 113, 1-2). Size is large compared with that of *C. (Xenocyon) lycaonoides* from Stránská Skála. The form of the trochlea and supratrochlear foramen does not differ from those of *C. mosbachensis*. At the same time, the olecranon fossa is small and shallow, and is not so elevated as that of the small wolf from Untermaßfeld. Measurements are listed in Tab. 18.

	Untermaßfeld IQW 1985/20693 (Mei. 20212)	Stránská Skála 1	2
Shaft width in the middle	17.2	17.8	–
Greatest width of distal end	49.0	45.1	46.0
Greatest width of trochlea	38.3	33.5	34.0

Tab. 18 *Canis (Xenocyon) lycaonoides.* Comparative measurements of the humerus (mm).

3. Determination of the systematic and evolutionary position of the small wolf from Untermaßfeld

Examination of the abundant Untermaßfeld material suggests that in cranial and dental characters the small wolf from this locality is similar to the group of medium-sized fossil canids represented in Europe by *Canis etruscus* and *C. mosbachensis*. Among them the Untermaßfeld *Canis* shows a very close agreement with the late Early-Middle Pleistocene small wolf *C. mosbachensis*.

Canis mosbachensis was identified by Soergel (1925) among small wolves from Mauer and Mosbach. Thenius (1954) referred this canid to *C. lupus mosbachensis* because of its similarity to the small recent southern wolf *C. pallipes*, which is often considered as a subspecies of *C. lupus*. Bonifay (1971) described the small wolf from the Middle Pleistocene in France (L'Escale) as *C. etruscus*, and synonymized *C. mosbachensis* under *C. etruscus*. However, Torre (1974) distinguished the Late Villafranchian *C. etruscus* from the L'Escale small wolf and showed some similarity of the latter to the group of gray wolves *(C. lupus)*.

The long nomenclatural history of *C. mosbachensis* was summarised by Musil (1972), who referred it to a separate species. In spite of that, most researchers have followed the nomenclature of Thenius and assigned this wolf to subspecies of *C. lupus* (Schütt 1973, 1974; Kurtén and Poulianos 1977, 1981; Bishop 1982; Tsoukala 1992), or, following Bonifay, referred it to *C. etruscus* (Alcalá and Morales 1989).

A new point of view was proposed lately by Italian researchers, who suggested that the latest Villafranchian-Galerian medium-sized canids from the Mediterranean were not connected with the *C. etruscus – C. mosbachensis* lineage, but continued the phylogenetic line of the *C. arnensis* coyote-like dog. Medium-sized canids from Cueva Victoria, Venta Micena, Pirro Nord, Apollonia, and Oubeidiyeh were referred to *C.* cf. *arnensis,* whereas the similar forms of Galerian time span from Le Vallonnet, Colle Curti, Huéscar-1, Cullar de Baza 1, L'Escale, and Petralona, were assigned to *C.* aff. *arnensis* advanced form (Rook and Torre 1996).

The principal characters for identifying these canids as a coyote-like dog were the averagely smaller dimensions relative to small wolves and some differences in dental ratios. The fragmentary character of the material from the majority of localities mentioned above does not permit discussion of their specific affinities, but comparison with the rich material from L'Escale shows the dimensions of this canid and dental ratios, as well as most of other features, to overlap with the range of variation seen in the Untermaßfeld population. Therefore, I refer the L'Escale form to the group of fossil small wolves.

Comparative analysis of the abundant Untermaßfeld material shows the occurrence of numerous characters that separate the small wolf from *C. lupus* and *C. arnensis*, and for the majority of them it is similar to the fossil small wolves *C. etruscus* and *C. mosbachensis*.

Characters that unite the Untermaßfeld wolf with the *C. etruscus – C. mosbachensis* group are: size moderate for the genus *Canis*, narrow and elongated muzzle, slightly curved toothrow in the junction of P^4 and M^1, moderate elevation of frontals above rostrum, relatively narrow braincase, relatively small incisors, P^4 with a well-developed lingual cingulum and prominent protocone located slightly anteriorly, M^1 with a complete buccal cingulum and large hypocone basin, as well as relatively large size of M^1 and M^2. In the lower jaw these characters are: a shallow mandible, a relatively straight toothrow and highly set premolars, narrow and posteriorly elongated premolars, P_2 often without the posterior accessory cusp, P_4 with a well-developed posterolingual cingulum, M_1 with a strong metaconid and moderate hypoconulid shelf, and M_2 with a well-developed anterobuccal cingulum. Additionally, *C. mosbachensis* is characterised by relatively short distal segments of fore limbs.

Most of the features mentioned above were marked among the group of small Pliocene dogs, and within the genus *Canis* they can be considered as primitive characters. They are represented to a greater or lesser extent among the less specialised recent forms, namely *C. latrans*, *C. rufus* and *C. pallipes*.

Characters which distinguish the Untermaßfeld small wolf from *C. etruscus* and unite it with *C. mosbachensis* are manifested in the narrower frontal shield, premolars set relatively lower, in the occurrence of a slightly curved mandible, which sometimes takes place in the junction of P_4 and M_1, in the more complete structure of P_2 and P_3 with posterior accessory cusps, in the occurrence of the second accessory cusp on P_4 most commonly not separated from the cingulum and, finally, in the more complete

structure of the talonid of M_1 and M_2. Based on these characters, the wolf from Untermaßfeld to is referred *C. mosbachensis*, which is considered as a separate and more advanced species in the lineage of Early-Middle Pleistocene small wolves of Europe.

Canis mosbachensis from Untermaßfeld agrees with the Middle Pleistocene wolf from L'Escale according to a lot of cranial, dental, and skeletal characters, but it differs by the ratio LP^4:LM^{1-2} and shows a more primitive stage in the radius/humerus ratio. According to these data, we can suggest that the Untermaßfeld wolf represents the early stage of development of *C. mosbachensis* and consider it as the late Early Pleistocene representative of the lineage of small wolves in Europe.

4. Determination of systematic and evolutionary position of the large canid from Untermaßfeld

Kretzoi (1938) was the first to describe a large canid with trenchant talonid of M_1 as a new genus and species *Xenocyon lycaonoides* based on the study of fossil remains from Gombasek. Later, similar forms were recorded from several Middle Pleistocene localities of the Central Europe and were described under different names (Kretzoi 1941, 1942; Thenius 1954). The nomenclature of these canids was revised by Musil (1972), although the priority of the specific name *lycaonoides* was pointed out by Schütt (1973). The most complete specific synonymy and diagnosis were suggested by Schütt (1974) on the basis of material from Würzburg-Schalksberg.

A principal character by which *Xenocyon lycaonoides* was established was the presence of a single, dominant, central-positioned cusp (hypoconid) on the talonid of M_1. A vestigial entoconid on M_1 of *X. lycaonoides* was indicated for the first time by Musil (1972) in one of four specimens of M_1 from Stránská Skála. This character was added to the specific diagnosis of *X. lycaonoides* after the investigation of mandibles from Zasukhino, Nalaikha and Lakhuti-2, on which the entoconid on lower carnassials varied from a minute cusp to its complete absence (Sotnikova 1988, 1989).

A minute entoconid on M_1 in the mandible IPS VM-2257 of *Xenocyon* from Venta Micena permitted Pons Moyà (1987) to suggest that *Xenocyon* and the large canid *Canis falconeri* with bicuspid talonid of M_1 are related taxa.

This point of view was accepted and thoroughly discussed by Rook (1994) in the review of large Plio-Pleistocene canids of the Old World, where *Xenocyon* was interpreted as a subgenus of the genus *Canis*. In this study the Plio-Early Pleistocene *Canis falconeri* from Europe, *C. antonii* from Asia and *C. africanus* from Africa were referred to the supraspecific group *Canis (Xenocyon)* ex gr. *falconeri*, although Middle Pleistocene large canids were attributed to *C. (Xenocyon) lycaonoides*. Both forms with bicuspid talonid of M_1 and canids from Venta Micena, Cueva Victoria and Campbellpore with a large dominant hypoconid and very reduced or absent entoconid on the lower carnassial, were included in the group of Plio-Early Pleistocene canids *Canis (Xenocyon)* ex gr. *falconeri*.

Investigation of the material from Untermaßfeld, as well as the analysis of more than 10 specimens of large Canidae with a dominant hypoconid on talonid of M_1 from Russia (Siberia), Tadjikistan and Mongolia, and comparison with already known specimens from this group actually reveal a number of similarities with the large Plio-Pleistocene canids, which have the bicuspid talonid of M_1. The similarities are as follows: large size, high and robust mandible with a relatively low coronoid process and complete toothrow not bowed outward in the centre, highly located premolar row with the top of P_4 positioned on one level with a paraconid top of M_1, P_2 often without the posterior cusplet, P_4 with two posterior accessory cusps, a well-developed posterolingual cingulum and second posterior cusplet well separated from cingulum, a relatively reduced metaconid of M_1 and M_2, lower crowned M^1 and M^2 with a relatively weakly developed buccal cingulum and reduced metaconule and protoconule on M^1.

Similarity in size and characters supports the point of view of Pons Moyà (1987) and Rook (1994) on close phylogenetic relationships of Plio-Pleistocene large canids with the bicuspid and unicuspid talonid of M_1.

Bicuspid talonid samples with a normally developed entoconid have a more lateral position of hypoconid on talonid of M_1, whereas samples with reduced or absent entoconid have the more central location of hypoconid. Analysis of carnassials (N=20) with a central-positioned hypoconid, allows us to trace

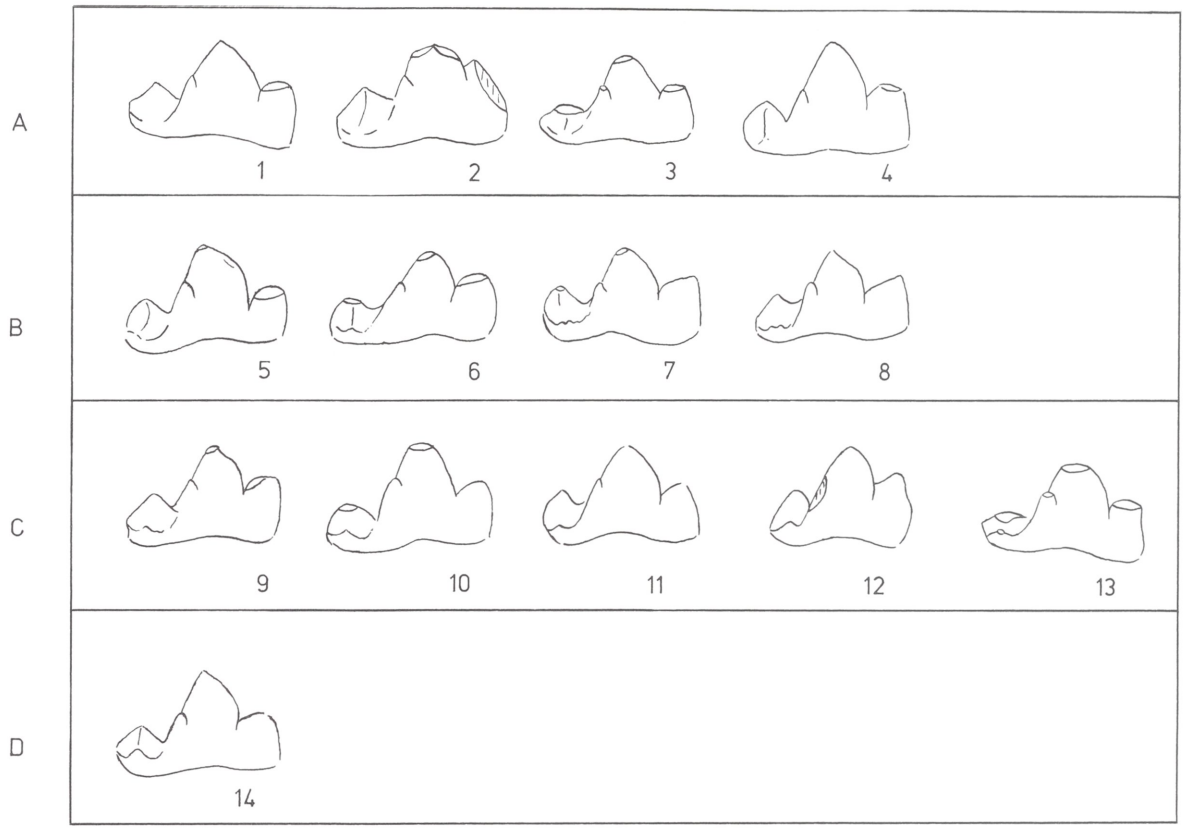

Fig. 4 Various stages of development of the entoconid of M_1 in *Canis (Xenocyon)*; A entoconid absent; B lingual cingulum or vestigal entoconid present; C minute entoconid present; D normal entoconid present. – 1 Koněprusy(AMNH 23096 cast). – 2 Zasukhino (GIN 4370/90-3-11). – 3 Chukochya (GIN 835-312/25). – 4 Chukochya (CIN 835-562/35). – 5 Adycha (GIN Ad-6). – 6 Nalaikha (PIN 3747-131). – 7 Lakhuti-2 (GIN 3848/335-67, right). – 8 Untermaßfeld [IQW 1985/20555 (Mei. 20074)]. – 9 Lakhuti-2 (GIN 3848/355-67, left). – 10 Ma Fang (F:AM 97046). – 11 Venta Micena (IPS VM 2257). – 12 Untermaßfeld [IQW 1985/21000 (Mei. 20519)]. – 13 Nalaikha (PIN 3747-256). – 14 Upper Valdarno (IGF 865 GIN cast).

different stages of reduction of entoconid from a minute cusp through the vestigial cusp to the low-lingual cingulum or its absence, whereas the bicuspid talonid structure is more stable (Fig. 4). Therefore, I consider the distinguishing of two groups among Plio-Pleistocene large canids according to the position of hypoconid on M_1 (lateral or central) to be more justified. In this case the group *C. (Xenocyon) falconeri* will include Pliocene-early Early Pleistocene canids with a bicuspid talonid of M_1, whereas *C. (Xenocyon) lycaonoides* will include late Early-Middle Pleistocene forms with a reduced or absent entoconid on M_1. The latter group will include the Untermaßfeld large canid, as well as similar forms from Venta Micena, Cueva Victoria, Campbellpore and other localities.

Apart from differences in the structure of the M_1 talonid, *C. (Xenocyon) lycaonoides* demonstrates a number of characters indicating the presence of dental adaptation for hypercarnivory seen as a derived stage (Berta 1988). Derived characters that distinguish *C. (Xenocyon) lycaonoides* from the group of *C. (Xenocyon) falconeri* are: metaconid of M_1 and M_2 is on the whole more reduced, M_2 and talonid of M_1 are narrower, hypoconid of M_1 is large and centrally-positioned, a minute entoconid shows the trend to be lost, M^1 has a reduced hypocone and hypocone basin, M^1 and M^2 have the trend to become narrower.

Among *C. (Xenocyon) lycaonoides*, canids with the unicuspid talonid of M_1 are well documented from Middle Pleistocene deposits ranging within the Brunhes palaeomagnetic epoch, whereas forms with

varied entoconid M_1 were recorded from the late Early Pleistocene/beginning of Middle Pleistocene localities that range within the Matuyama paleomagnetic epoch (Venta Micena, Cueva Victoria, Nalaikha, and Lakhuti-2). Middle Pleistocene *C. (Xenocyon) lycaonoides* show more stable characters. Among older representatives of *C. (Xenocyon) lycaonoides* from Venta Micena, Cueva Victoria, and Nalaikha, variations in the degree of development of the metaconid on M_1 and M_2, as well as in the number of cusps on premolars and in dimensions of M_2, were marked. The Untermaßfeld *C. (Xenocyon) lycaonoides* shows the same balance of characters and degree of development of entoconid on M_1 as earlier forms do, which permits to consider it as the late Early Pleistocene representative of the lineage of large canids with the hypercarnivory trend in dental adaptations.

5. Stratigraphic and geographic distribution of small wolf and *Canis (Xenocyon)* assemblage and biostratigraphical position of the canid-fauna from Untermaßfeld

The small wolf and large canid *Canis (Xenocyon)* were common members of the Early Quaternary faunal community in Eurasia. In Asia the earliest findings of the small wolf *Canis* ex gr. *chihliensis-palmidens* and *C. (Xenocyon) antonii* are known from the Late Pliocene (Nihewanian) of China (Teilhard de Chardin and Piveteau 1930; Rook 1994). In Europe this Canidae association appeared at the beginning of the Early Pleistocene and was represented in mammal localities of the Tasso faunal unit by *Canis etruscus* and *C. (Xenocyon) falconeri* (Rook 1993).

Finds of Plio-Early Pleistocene representatives of this group of canids are very rare in Eurasia, whereas in the Middle Pleistocene they were widespread. In Europe this assemblage is represented by *Canis mosbachensis* and *C. (Xenocyon) lycaonoides* and is well documented from the Central European localities of Koněprusy, Vértesszölös-2, Würzburg-Schalksberg, Mosbach-2, Gombasek, Stránská Skála, and Žirany 1, 3. The age of these local faunas is correlated with Holsteinian, Elsterian, and Cromerian of Central European stratigraphic schemes (H.-D. Kahlke 1975; Wolsan 1993). Mammal assemblages of the same time span, which contain this Canidae association, are known in England (Westbury-sub-Mendip) and Greece (Petralona Cave) (Bishop 1982; Tsoukala 1992).

In Asia, North Siberia, in the basins of Chukoch'ya and Adycha Rivers Middle Pleistocene remains of small wolf and *C. (Xenocyon) lycaonoides* are associated with deposits of the upper Olyor Formation, and in Transbaikalia (Zasukhino) and Tadjikistan (Lakhuti-2) these associations are known from Early to Middle Pleistocene transitional faunas (Sotnikova 1978, 1988, 1989). In China (Locality 18) *C.* cf. *chihliensis* and *C. (Xenocyon) dubis (= lycaonoides)* were recorded from close in age deposits (Teilhard de Chardin 1940).

Thus, at the end of the Early and in the Middle Pleistocene the distribution area of these canids stretched from England to Greece in Europe and from high latitudes in Siberia to southern Tadjikistan and China in Asia.

There are substantially less data on the late Early Pleistocene distribution of this association. In Central Europe up to now *C. (Xenocyon) lycaonoides* was recorded only from Middle Pleistocene deposits, whereas in southern Europe it was reported from two local faunas in Venta Micena and Cueva Victoria, which are interpreted as transitional between the typical Late Villafranchian and Middle Pleistocene faunas (Agustí et al. 1987).

In Asia the Nalaikha fauna from Mongolia, which, according to palaeomagnetic data, is placed in the Matuyama Chron below the Jaramillo reversal, is close to this stratigraphic level (Zhegallo, pers. comm.). The Ma Fang fauna from Shou Yang district (Shansi, China), where *Megantereon* and *Pachycrocuta brevirostris* occur together with *C. (Xenocyon) lycaonoides* evidently, corresponds to the same time interval.

Therefore, this Canidae association occurred in Eurasia from the end of the Pliocene to the mid-Middle Pleistocene. Its occurrence in deposits younger than 0.3 Ma is unknown.

In the Pleistocene these canids developed in two directions. Large forms exhibited a trend to hypercarnivory, whereas the hypocarnivorous trend is traced among small wolves. This specialisation is well seen in molars of these canids. Plio-early Early Pleistocene forms have a primitive type of M_1 morphology

with normally developed entoconid and no increase in the quantity of cusps. Among *C. mosbachensis* the talonid of M_1 has a tendency to be more complicated compared with the talonid of *C. etruscus*. Among late Early Pleistocene *C. (Xenocyon) lycaonoides* the reduced entoconid is preserved, whereas it is absent among Middle Pleistocene forms. The Untermaßfeld Canidae association reveals a complex of features on M_1 characteristic of canids of the end of the Early Pleistocene.

Summary

Fossil Canidae from Untermaßfeld near Meiningen, Southern Thuringia, Germany, are described as *Canis mosbachensis* Soergel and *Canis (Xenocyon) lycaonoides* (Kretzoi).

Remains of *C. mosbachensis* (more than 300 specimens) belonging to 15 adult and old individuals are represented by incomplete skulls, mandibles and parts of the postcranial skeleton. Examination of the skull shows that it differs greatly both from the coyote-like dog *C. arnensis* and from recent gray wolf *C. lupus*, and agrees more with the recent small wolf *C. pallipes*. Among fossil Canidae the Untermaßfeld small canid shows close affinities with the group of Early-Middle Pleistocene small wolves represented in Europe by *C. etruscus* and *C. mosbachensis.* The Untermaßfeld wolf differs from *C. etruscus* in a number of features that can be considered as derived characters. Specifically, the lower molars of the wolf from Untermaßfeld, as well as the molars of other *C. mosbachensis*, demonstrate the tendency of cusps on the trigonid and talonid of M_1 and M_2 to be more complicated. Like Middle Pleistocene small wolves from Stránská Skála and L'Escale, the Untermaßfeld canid tends to have distal segments of fore limbs shorter than these of hind ones. It is distinguished from the L'Escale wolf by more primitive proportions of segments of the fore limbs, with the radius/humerus ratio lesser than 100%.

Based on the character analysis, the Untermaßfeld wolf is referred to *C. mosbachensis* and is interpreted here as a member of the small wolf lineage. According to proportions of limb bones, it can be considered as a somewhat more primitive form than the Middle Pleistocene small wolf from L'Escale.

The large canid from Untermaßfeld is represented by mandibles, upper molars and one humerus. Large size, a complete molar toothrow and the presence of dominant hypoconid on the talonid of M_1 allow us to refer this canid to *C. (Xenocyon) lycaonoides*. The principal character distinguishing the Untermaßfeld large form from the common *C. (Xenocyon) lycaonoides* is the presence of a minute or vestigial entoconid on the lower carnassials. Based on the investigation of *C. (Xenocyon)* carnassials from different regions and stratigraphic levels, the development of the hypercarnivorous trend in M_1 among these canids was traced.

The analysis of stratigraphic distribution of large canids shows that a normally developed entoconid occurred among Plio-early Early Pleistocene forms, whereas the reduced entoconid was characteristic of late Early Pleistocene forms and also occurred among canids whose stratigraphic distribution was limited to the Matuyama Chron. Middle Pleistocene forms, as a rule, demonstrate the complete absence of entoconid on M_1. Based on these data, *C. (Xenocyon) lycaonoides* from Untermaßfeld is interpreted as a late Early Pleistocene representative of the lineage of large Plio-Pleistocene canids.

Zusammenfassung

Aus der Fundstelle Untermaßfeld bei Meiningen (Südthüringen, Deutschland) werden *Canis mosbachensis* Soergel und *Canis (Xenocyon) lycaonoides* (Kretzoi) beschrieben.

Die Funde von *C. mosbachensis* (mehr als 300 Stücke) gehören zu 15 adulten bis spätadulten Individuen. Sie werden durch unvollständige Schädel, Mandibeln und Teile des postcranialen Skelettes repräsentiert. Die Untersuchungen der Schädel zeigen Abweichungen sowohl gegenüber den kojotenartigen Caniden *Canis arnensis* als auch gegenüber dem rezenten Grauwolf *Canis lupus.* Übereinstimmungen bestehen eher mit dem rezenten kleinen Wolf *C. pallipes*. Unter den fossilen Caniden weisen die Untermaßfelder Formen enge Beziehungen zu den frühmittelpleistozänen kleinen Wölfen auf, die in Europa durch *C. etruscus* und *C. mosbachensis* repräsentiert sind. Der Untermaßfelder Wolf unterscheidet sich von *C. etruscus* in einer Reihe abgeleiteter Merkmale. Insbesondere lassen sowohl die unteren Molaren des Wolfes von Untermaßfeld als auch die anderer Funde von *C. mosbachensis* einen Trend zur Komplizie-

rung der Spitzen von Trigonid und Talonid des M_1 und M_2 erkennen. Ebenso wie die mittelpleistozänen kleinen Wölfe der Stránská Skála und von L'Escale zeigt der Wolf von Untermaßfeld die Tendenz zur Verkürzung der distalen Segmente der Vordergliedmaßen im Vergleich zu den Segmenten der Hintergliedmaßen. Vom Material aus L'Escale läßt sich der Wolf durch primitivere Proportionen der Segmente der Vordergliedmaßen, mit einem Radius/Humerus-Quotienten kleiner 100, abtrennen.
Basierend auf dieser Merkmalsanalyse wird der Untermaßfelder Wolf *C. mosbachensis* zugeordnet und als Vertreter der Stammeslinie der kleinen Wölfe angesehen. Aufgrund der Proportionen der Extremitätenknochen kann er im Vergleich zum mittelpleistozänen Wolf von L'Escale als etwas primitivere Form angesehen werden.
Der großwüchsige Canide aus Untermaßfeld ist durch Mandibeln, obere Molaren und einen Humerus repräsentiert. Die großen Dimensionen, eine komplette Molarenreihe und das Vorhandensein eines dominanten Hypoconids auf dem Talonid des M_1 erlauben die Zuordnung dieses Caniden zu *C. (Xenocyon) lycaonoides*. Das Hauptmerkmal, das diese Form von anderen Funden des *C. (Xenocyon) lycaonoides* unterscheidet, ist das Vorhandensein eines kleinen bis winzigen Entoconids auf den unteren Reißzähnen. Anhand der Reißzähne von *C. (Xenocyon) lycaonides* sowohl regional als auch stratigraphisch unterschiedlicher Herkunft ist die Entfaltung des hypercarnivoren Trends der M_1 zu verfolgen.
Die Analyse der stratigraphischen Verbreitung der großen Caniden zeigt, daß ein normal entwickeltes Entoconid unter den Formen des Plio- und frühen Unterpleistozäns auftrat, während ein reduziertes Entoconid für Caniden des Spätunterpleistozäns sowie der Matuyama-Epoche charakteristisch ist. Bei mittelpleistozänen Formen fehlt das Entoconid am M_1 in der Regel. Auf Grund dieser Merkmale wird *C. (Xenocyon) lycaonoides* von Untermaßfeld als spätunterpleistozäner Repräsentant der Stammeslinie plio-pleistozäner großer Caniden interpretiert.

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