ALAN TURNER

REMAINS OF *PACHYCROCUTA BREVIROSTRIS* (CARNIVORA, HYAENIDAE) FROM THE LOWER PLEISTOCENE SITE OF UNTERMASSFELD

1. Introduction

The remains of the Hyaenidae from Untermaßfeld were originally to have been described by the late Professor Björn Kurtén. At the time of his death, he had prepared a brief manuscript describing the half dozen mainly adult specimens recovered by the excavators up to the time of his last visit to the collections in Weimar in 1985. Since then more material has been recovered from the site, mostly of juvenile specimens. This paper deals with the entire sample recovered at the time of my visits to the collections in June 1990 and December 1991. Kurtén's original manuscript has been made available to me by the custodian of his papers, Dr. Lars Werdelin, and I have thus been able to incorporate his observations on the specimens seen by him and to employ some of the comparative data that he had assembled for his discussion.

All measurements are given in millimetres. In the tables of dental measurements, L and B are length and breadth of respective teeth. Lp is length of the protocone on PM_4, Lt is the length of the talonid on M_1, and Mc indicates the known presence or absence of a metaconid. C-Cd is the distance from the anterior surface of the lower canine to the posterior of the condyle, P2-M1 is the inclusive length of the cheek-tooth row, Depth A and P are the dorso-ventral depths of the mandible at the diastema and behind M_1, BP3 is the maximum bucco-lingual breadth of the mandible below PM_3. For the upper carnassial, Ba is the width at the protocone, Bbl is the width of its metastyle blade, Lp is the length of the paracone and Lm is the length of the metastyle. BL is the basal length of the skull. For the metapodia of Tab. 5, TL is total length, PML is the mediolateral width of the proximal articulation, PAP is its anteroposterior width, SW is the minimum mediolateral shaft width and DW is the mediolateral width of the epicondylar region.

2. Descriptions

Family: Hyaenidae Gray, 1869
Genus: *Pachycrocuta* Kretzoi, 1938
Pachycrocuta brevirostris (Aymard, 1846)

Synonomy (after Werdelin and Solounias 1991)
1846 *Hyaena brevirostris* – Aymard, 153
1870 *Hyaena sinensis* – Owen, 422-424
1884 *Hyaena felina* – Lydekker, 285
1889 *Hyaena robusta* – Weithofer, 46
1893 *Hyaena brevirostris* – Boule, 85-97
1908 *Hyaena bathygnatha* – Dubois, 1265
1925 *Hyaena sinensis* – Zdansky, 22-23
1928 *Hyaena sinensis* – Zdansky, 42-47
1930 *Hyaena sinensis* – Teilhard and Piveteau, 101-104
1932 *Crocuta sivalensis* – Pilgrim, 134-137
1934 *Hyaena sinensis* – Pei, 91-110
1934 *Hyaena zdanskyi* – Pei, 110-116
1934 *Hyaena licenti* – Pei, 120-121
1938 *Pachycrocuta brevirostris* – Kretzoi, 118
1952 *Crocuta* cf. *brevirostris* – Toerien, 295
1954 *Hyaena bellax* – Ewer, 579
1956 *Hyaena brevirostris* – Kurtén, 38-39
1970 *Pachycrocuta brevirostris* – Ficcarelli and Torre, 18
1970 *Pachycrocuta felina* – Ficcarelli and Torre, 18
1970 *Pachycrocuta bellax* – Ficcarelli and Torre, 18
1974 *Hyaena (Parahyaena) brevirostris* – Hendey, 149
1974 *Hyaena (Parahyaena) bellax* – Hendey, 149

1980 *Pachycrocuta brevirostris* – Howell and Petter, 605-607
1980 *Pachycrocuta bellax* – Howell and Petter, 607-610
1986 ?*Pachycrocuta bellax* – Turner, 207-208
1987 *Pachycrocuta brevirostris* – Turner, 326
1989 *Pachycrocuta licenti* – Huang, 197-204
1989 *Pachycrocuta sinensis* – Huang, 197-204
1990 *Pachycrocuta brevirostris* – Turner, 357

2.1. Annotated list of Material

All of the specimens from the site are held in the Forschungsstation für Quartärpaläontologie Weimar der Senckenbergischen Naturforschenden Gesellschaft.

Adult and juvenile jaws, skulls and teeth and non-isolated teeth
left adult mandible with all teeth except I_1 and I_3, IQW 1980/15 918 (Mei. 15 429); left adult mandible with all teeth, IQW 1990/23 457 (Mei. 22 976); left and right mandibles of young adult with P_2, P_3 and C_{inf} still erupting and left dC_{inf} still present, IQW 1986/21 369 (Mei. 20 888); right anterior fragment of adult mandible with broken root of C_{inf}, IQW 1989/23 343 (Mei. 22 862); left adult maxilla with P^2-M^1 present, IQW 1980/16 085 (Mei. 15 596); left maxilla and premaxilla of old adult with I^2, I^3, P^2-P^4 present, IQW 1983/19 556 (Mei. 19 076) [to which isolated upper canine IQW 1987/21 872 (Mei. 21 391) probably belongs]; right maxilla and premaxilla of old adult with I^2, I^3, C^{sup}, P^1-P^4 present, IQW 1983/19 555 (Mei. 19 075) [probably same individual as IQW 1983/19 556 (Mei. 19 076)]; snout of young adult with maxillae and palatine processes, premaxilla and most of the permanent dentition except the left I^2 and left C^{sup}, IQW 1990/23 650 (Mei. 23 179); snout of an old adult with maxillae and palatine processes, premaxilla and complete permanent dentition except for the left P^1, IQW 1990/23 625 (Mei. 23 154); left crushed juvenile mandible with deciduous teeth in wear, IQW 1988/22 460 (Mei. 21 979); left juvenile mandible with deciduous teeth in wear and M_1 visible in crypt, IQW 1988/22 486 (Mei. 22 106); right juvenile mandible with dM_2 just beginning to emerge and broken roots of other deciduous teeth, IQW 1982/17 891 (Mei. 17 411); right juvenile mandible with deciduous teeth just in wear, IQW 1988/22 730 (Mei. 22 249) (Mei. 22 249); right juvenile mandible fragments, IQW 1988/22 600 (Mei. 22 119), and various teeth [right M_1 enamel cap, IQW 1988/22 601 (Mei. 22 120); right P_4 enamel cap, IQW 1988/22 602 (Mei. 22 121); right dM_3, IQW 1988/22 603 (Mei. 22 122); right dC_{inf}, IQW 1988/22 604 (Mei. 22 123); fragments of right dM_4, IQW 1988/22 605 (Mei. 22 124) and IQW 1988/22 608 (Mei. 22 127); right C_{inf} enamel cap, IQW 1988/22 607 (Mei. 22 126)]; left and right mandibles of single juvenile individual with dM_2 still erupting and slight wear on other deciduous molars, IQW 1990/23 407 (Mei. 22 926), plus two permanent enamel germs, IQW 1990/23 409 (Mei. 22 928) and IQW 1990/23 408 (Mei. 22 927); left juvenile mandible with dM_2 just erupting and slight wear on other deciduous molars, IQW 1990/23 475 (Mei. 22 994); fragments of skull, mandible and teeth of a single juvenile individual [fragment of basioccipital, basisphenoid, sphenoid, maxillary with palatine process, frontal and orbital IQW 1986/21 766 (Mei. 21 285); right dI^3, IQW 1986/21 768 (Mei. 21 287); left P^3 enamel cap, IQW 1986/21 769 (Mei. 21 288); left dC^{sup} enamel cap, IQW 1986/21 770 (Mei. 21 289); left P^4 enamel cap fragments, IQW 1986/21 771-21 773 (Mei. 21 290-21 292); posterior mandible fragment with M_1 starting to erupt, IQW 1986/21 774]; fragments of skull and teeth of a single juvenile individual [right maxillary fragment with dM^2, alveolus of dM^3 and P^1 visible in crypt, IQW 1988/22 733 (Mei. 22 252); left premaxilla with dI^1 amd dI^2, IQW 1988/22 734 (Mei. 22 253); right P^3 enamel cap, IQW 1988/22 735 (Mei. 22 254); right P^4 paracone and metastyle fragments, IQW 1988/22 736 (Mei. 22 255), IQW 1988/22 742 (Mei. 22 261) and IQW 1988/22 743 (Mei. 22 262); right dM^4, IQW 1988/22 737 (Mei. 22 256); enamel caps of two I^{sup}s, IQW 1988/22 738 (Mei. 22 257) and IQW 1988/22 739 (Mei. 22 258); two indeterminate enamel caps, IQW 1988/22 740 (Mei. 22 259) and IQW 1988/22 741 (Mei. 22 260)]; broken upper deciduous teeth and some broken permanent enamel caps of a single individual (left and right dM^2, left and right dM^3, left and right dI^3, left dC^{sup}, left and right dI^1, left dI^2, right dM^4 fragment, left and right P^1 caps, left and right C^{sup} caps and six other enamel caps), IQW 1989/23 103 (Mei. 22 622); right broken enamel cap of P^4, tips of three other permanent premolar enamel caps and the enamel cap of a right P^1,

IQW 1987/22211 (Mei. 21730); left anterior dM^2 fragment, left P^1 enamel cap and one incisor fragment, IQW 1990/23480 (Mei. 22999); right dM^4 and left dM_2, two lower dI_{inf} and two enamel caps, IQW 1990/23478 (Mei. 22997); three dI_{inf}, six enamel caps and six assorted mandible fragments, IQW 1989/23153 (Mei. 22672); left broken dM_3 and dM_4 plus two permanent molar enamel caps, probably from one individual, IQW 1989/23104 (Mei. 22623); broken left dM_3 and right deciduous teeth fragments (dC_{inf}, dM_2, dM_4), IQW 1990/23479 (Mei. 22998); four deciduous molar fragments and rear fragment of right dM_4, IQW 1990/23408 (Mei. 22927); portion of occipital bone with condyles, juvenile, IQW 1990/23476 (Mei. 22995).

Isolated upper permanent teeth
left isolated adult worn I^1, IQW 1990/23422 (Mei. 22941); right isolated worn adult I^2, IQW 1983/19557 (Mei. 19077); right isolated worn adult I^3, IQW 1983/19558 (Mei. 19078); left isolated immature enamel cap of C^{sup}, IQW 1988/22744 (Mei. 22263); left isolated enamel shell of P^3, IQW 1980/16865 (Mei. 16386); left isolated anterior fragment of unworn P^4, IQW 1980/16877 (Mei. 16398).

Isolated lower permanent teeth
left isolated adult I_2, IQW 1987/22113 (Mei. 21632); left isolated adult I_3, IQW 1987/22202 (Mei. 21721).

Isolated upper milk teeth
right isolated dC^{sup}, IQW 1980/16557 (Mei. 16078); left isolated dC^{sup}, IQW 1986/21767 (Mei. 21286); right isolated dM^2, IQW 1987/22210 (Mei. 21729); right isolated dM^2, IQW 1983/19550 (Mei. 19070); left isolated dM^2, IQW 1987/222167 (Mei. 21736); left isolated dM^3, IQW 1983/19549 (Mei. 19069); left anterior half of isolated dM^3, IQW 1987/22216 (Mei. 21735); right isolated dM^3, IQW 1986/21093 (Mei. 20612); right isolated parastyle and root of dM^3, IQW 1987/22209 (Mei. 21728); right anterior fragment eroded and polished of dM^3, IQW 1981/17739 (Mei. 17260).

Isolated lower milk teeth
left posterior fragment isolated dM_2, IQW 1988/22486 (Mei. 22005); left isolated dM_2, IQW 1990/23477 (Mei. 22996); right isolated dM_3, IQW 1987/22274 (Mei. 21793).

Postcranial material
broken atlas vertebra, IQW 1987/22125 (Mei. 21644); left metacarpal II, IQW 1986/21299 (Mei. 20818); right metatarsal V, somewhat eroded and damaged, IQW 1983/19545 (Mei. 19065); a metapodial shaft and distal articulation, missing the proximal articulation, IQW 1980/17175 (Mei. 16696); left humerus diaphysis of juvenile, unfused at both ends, with puncture marks on distal surfaces, IQW 1989/23120 (Mei. 22639); left distal humerus fragment, IQW 1980/15907 (Mei. 15418); right humerus shaft fragment, IQW 1981/17652 (Mei. 17174).

Coprolites
Some 80 coprolites or fragments of coprolite.

2.2. Descriptions

The hyaena material from Untermaßfeld is entirely typical of the widely distributed species *Pachycrocuta brevirostris*. The adult specimens of teeth and jaws are massive, far exceeding the dimensions of other hyaenas of the period. Cranial, mandibular and dental measurements of individual adult specimens are given in Tab. 1 and 2, together with appropriate comparative measurements on specimens from other localities as indicated. Measurements for juvenile specimens are given in Tab. 3 and 4. Measurements of the metapodials are given in Tab. 5. All measurements on the Untermaßfeld specimens are my own; sources of measurements for other specimens are given in the appropriate tables.

		Specimen		C L	C B	P₂ L	P₂ B	P₃ L	P₃ B	P₄ L	P₄ B	P₄ Lp	M₁ L	M₁ B	M₁ Lt	M₁ Mc	C-Cd	P₂-M₁	Depth A	Depth P	BP3
Untermaßfeld	(author)	IQW 1980/15 918 Mei. 15 429)	(L)	22.3	17.8	18.4	13.6	22.5	18.0	26.7	17.4	12.8	30.8	14.5	6.2	–	220	91.7	52.4	53.8	22.4
		IQW 1986/21 369 (Mei. 20 888)	(L)	erupting		19.0	13.0	24.0	–	26.4	15.7	13.6	29.2	15.0	5.4	–	c198	c92	–	48.7	24.4
		IQW 1986/21 369 (Mei. 20 888)	(R)	erupting		19.0	–	23.7	–	26.7	16.0	13.1	29.4	15.2	5.6	–	–	–	50.9	–	25.2
		IQW 1990/23 457 (Mei. 22 976)	(L)	22.5	17.0	19.3	13.6	22.6	17.6	27.1	16.8	12.6	30.1	14.7	5.9	–	–	94.0	53.0	–	26.5
		IQW 1988/22 601 (Mei. 22 120)	(R)	–	–	–	–	–	–	28.0	–	13.5	32.9	15.9	6.1	–					
Sainzelles	(Boule 1893,	Type		24.0	–	19.0	14.5	26.0	19.0	28.0	17.0	–	30.0	15.0	4.5	–	223	100	58.0	64.0	
	Kurtén 1972)	NHMB Sai 1		–	–	–	–	25.3	18.8	26.0	–	–	–	–	–		–	–	–	–	–
Gombaszőg	(Kurtén,	UNM V59/1083		–	–	17.8	12.2	–	–	25.6	16.7	14.4	27.9	14.2	4.4		–	90	–	–	–
	unpublished)	UNM V59/1024		–	–	18.2	13.5	23.6	17.9	–	–	–	–	–	–			88	–	–	–
		UNM V72.87		22	–	19.1	13.5	24.4	17.9	25.8	17.0	13.9	30.8	16.3	5.0		–	94	–	–	–
		UNM V60/1775		22.4	–	18.2	14.5	24.3	18.1	26.0	18.1	14.0	29.7	15.6	3.8		–	90	–	–	–
		No no.		–	–	–	–	–	–	25.8	17.1	13.5	29.6	15.5	4.4		–	–	–	–	–
		UNM V59/1020	(P₃)	–	–	–	–	26.0	–								–	–	–		–
		UNM V59/1038	(P₄)							25.9	17.9	13.7	–	–	–						
Venta Micena	(Martinez	VM 2271		–	–	17.7	12.5	25.2	15.6	25.2	16.2	–	27.8	13.7	–		–	–	–	–	–
	Navarro 1991)	VM 3548		–	–	18.4	13.5	24.1	16.3	25.6	16.3	–	28.8	14.6	–		–	–	–	–	–
		VM 2272		–	–	–	–	–	–	24.0	15.3	–	27.8	14.2	–		–	–	–	–	–
		VM 2275		–	–	–	–	–	–	–	–	–	30.4	15.8	–		–	–	–	–	–
		VM 2274		–	–	–	–	–	–	–	–	–	29.5	15.0	–		–	–	–	–	–
		VM 85 2I11		–	–	–	–	–	–	–	–	–	30.5	16.4	–		–	–	–	–	–
		VM 85 2J11		–	–	–	–	–	–	–	–	–	28.8	14.9	–		–	–	–	–	–
		VM 2276		–	–	–	–	–	–	–	–	–	29.5	15.2	–		–	–	–	–	–
		VM 85 C3		–	–	–	–	–	–	–	–	–	29.1	14.5	–		–	–	–	–	–
Val d'Arno	(author)	IGF 834	(L)	21.5	17.3	18.5	13.2	22.9	17.0	25.8	16.7	13.2	29.5	13.7	5.3	–	–	92.0	55.6	58.7	27.4
		IGF 838	(R)	21.4	17	19.0	12.8	23.4	16.6	26.0	16.3	12.4	28.6	14.3	5.6	–	–	96.6	53.0	–	25.4
		M4478 BMNH	(L)		alv 18.1	13.3	23.6	17.5	–	–	–	–	–	–	–	–	–	–	–	–	26.1
		M4478 BMNH	(L)	–	–	–	–	–	–	24.3	16.7	–	alv 28	13.9	4.5	?	–	–	–	56.4	–
Ceyssaguet	(author)	No no., Marseille	(R)	21.7	11.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vallonnet	(Lumley et al.	No no.		–	–	–	–	–	–	–	–	–	29.6	14.8		–	–	–	–	–	–
	1988)	No no.		–	–	–	–	–	–	–	–	–	30.5	16.6		–	–	–	–	–	–

Tab. 1a *Pachycrocuta brevirostris*, Untermaßfeld. Measurements of the lower jaws and teeth (adults) (mm). (For explanation of the abbreviations see introduction).

		Specimen		C L	C B	P2 L	P2 B	P3 L	P3 B	P4 L	P4 B	P4 Lp	M1 L	M1 B	M1 Lt	M1 Mc	C-Cd	P2-M1	Depth A	Depth P	BP3
Süßenborn	(author)	IQW 1965/5 439 (Süßenborn 5 439)	(R)	–	–	–	–	–	–	28.6	17.6	13.4	–	–	–	–	–	–	–	–	–
Sidestrand	(author)	M6164 BMNH	(L)	21.2	17.6	roots	roots		–	–	–	–	–	–	–	–	–	–	–	–	–
		M17922 BMNH	(L)	–	–	18.0	13.7	–	18.0	27.4	alv 18	alv 15	–	–	–	–	–	94.0	54.3	60.0	–
Bacton	(author)	288 962 Norwich	(R)	alv 22	17.7	19.1	14.0	24.5	17.3	25.0	17.0	13.0	–	–	–	–	–	–	55.9	26.8	–
Stránská skála	(Kurtén 1972)	E 5383	(L)	–	–	18.3	13.8	23.7	19.4	27.1	19.0	13.5	30.0	15.7	–			91.0	–	63.0	28.9
		No No.		–	–	19.1	14.1	–	–	–	–	–	–	–	–		–	–	–	–	–
		E 5383	(L)	–	–	–	–	24	18.5	–	–	–	–	–	–		–	–			
		E 5383	(R)	–	–	–	–	24.7	19.2	–	–	–	–	–	–		–	–	–	–	–
		E 5383	(L)	–	–	–	–	23.9	18.6	–	–	–	–	–	–		–	–	–	–	–
		1901	(R)	–	–	–	–	25.3	18.6	–	–	–	–	–	–			–	–	–	–
		2540	(L)	–	–	–	–	24.5	–	–	–	–	–	–	–		–	–	–	–	–
		No no.	(L)	–	–	–	–	29.9	18.2	–	–	–	–	–	–		–	–	–	–	–
		E 5383	(L)	–	–	–	–	–	–	27.5	18.9	14.1	–	–	–		–	–	–	–	–
		E 5383	(L)	–	–	–	–	–	–	29.1	19.7	14.2	–	–	–		–	–	–	–	–
		E 5383	(R)	–	–	–	–	–	–	–	17.8	–	–	–	–		–	–	–	–	–
		Sch 212	(R)	–	–	–	–	–	–	25.2	16.8	–	–	–	–		–	–	–	–	–
		Sch 214	(L)	–	–	–	–	–	–	29.2	20.0	14.8	–	–	–		–	–	–	–	–
		1902	(R)	–	–	–	–	–	–	–	–	–	29.8	15.0	3.6	–	–	–	–	–	–
		1907	(R)	–	–	–	–	–	–	–	–	–	29.0	15.1	3.5	–	–	–	–	–	–
		No no.	(L)	–	–	–	–	–	–	–	–	–	30.5	16.2	4.0	–	–	–	–	–	–
Manastirec	(Kurtén 1989)	296	(L)	–	–	–	–	25.3	19.0	26.0	17.0	–	–	–	–	–	–	–	–	–	–
		297	(L)	–	–	19.2	13.6	27.5	18.6	27.5	18.8	–	28.6	16	–	–	–	94.0	–	–	–
		298	(R)	–	–	–	–	25.9	17.7	28.0	17.6	–	30.3	15.4	–	–	–	–	–	–	–

Tab. 1b *Pachycrocuta brevirostris*, Untermaßfeld. Measurements of the lower jaws and teeth (adults) (mm). (For explanation of the abbreviations see introduction).

				C		P¹	P²		P³		P⁴					M¹			
				L	B	B	L	B	L	B	L	B	Bbl	Lp	Lm	B	BL	RB	MB
Untermaßfeld	(author)	IQW 1980/16085 (Mei. 15596)	(L)	alv.		alv.	20.0	13.6	25.8	18.6	40.8	25.0	13.1	13.9	16.0	14.4	–	–	–
		IQW 1983/19556 (Mei. 19076)	(L)	alv.		alv.	22.1	14.2	28.2	20.2	–	23.5	broken			–	–	–	–
		IQW 1983/19555 (Mei. 19075)	(R)	21.9	15.8	alv.	21.3	13.5	28.0	–	44.8	–	12.9	–	–	–	–	–	–
		IQW 1987/21872 (Mei. 21391)	(L)	–	15.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		IQW 1980/16865 (Mei. 16386)	(L)	–	–	–	–	–	25.4	18.0	–	–	–	–	–	–	–	–	–
		IQW 1990/23650 (Mei. 23179)	(L)	alv.		8.0	21.4	14.8	25.7	19.5	44.6	23.9	12.9	15.4	18.1	17.4	–	86	128
		IQW 1990/23650 (Mei. 23179)	(R)	23.0	–	8.4	21.9	14.6	27.2	20.0	44.8	23.3	13.3	15.6	18.1	17.4	–	–	–
		IQW 1990/23625 (Mei. 23154)	(L)	21.8	15.6	alv.	22.7	16.3	26.6	19.4	45.1	23.9	13.3	14.1	17.6	15.0	–	89	127
		IQW 1990/23625 (Mei. 23154)	(R)	broken		8.2	21.8	15.5	27.8	20.0	43.9	24.3	13.0	14.2	16.3	15.5	–	–	–
Würzburg–Schalksberg	(Schütt 1974)	Spec. 1	(L)	–	–	–	–	–	–	–	42.2	–	13.5	14.5	16.8	14+	–	–	–
		Spec. 2	(L)	–	–	8.3	21.0	14.3	27.0	–	–	–	–	13.6	–	–	–	–	–
Sainzelles	(Boule 1893)	Type		24.0	–	8.0	22.0	16.0	27.0	21.0	44.5	25.0	–	–	17.0	–	322	–	–
	(author)	Luminy, no no.	(L)	–	–	–	23.2	15.2	27.9	21.2	44.5	27.1	15.3	14.4	17.0	–	–	–	–
Gombaszőg	(Kurtén unpublished)	UNM V59/1079 (C^{sup})		20.1	16.3	–	–	–	–	–						–	–	–	–
		UNM V59/1066 (P^4)									43.8	26.3	14.9	15.5	17.5			–	–
Venta Micena	(Martinez Navarro 1991)	VM 2279		–	–	–	21.5	13.5	26.4	17.5	42.5	24.6	–	–	–	–	–	–	–
		VM 2280		–	–	–	–	–	26.7	17.5	–	23.7	–	–	–	–	–	–	–
		VM 2281		–	–	–	18.7	13.0	26.4	17.6	36.5	23.8	–	–	–	–	–	–	–
		VM ss		–	–	–	–	–	–	–	45.1	25.5	–	–	–	–	–	–	–
Val d'Arno	(author)	IGF 12470		22.4	15.2	8.0	21.1	11.4	27.6	18.9	41.5	22	13.6	12.5	15.2	–	–	–	–
		IGF 839		–	–	8.0	–	–	26.2	–	–	–	–	–	–	19.0	–	–	–
		IGF 838		21.0	15.3	8.8	20.7	14.4	25.2	19.3	40.2	24.4	13.2	13.6	15.5	–	–	–	–
Stránská skála	(Kurtén 1972)	Sch 213	(R)	–	–	–	–	–	–	–	42.6	–	13.6	14.3	16.0	–	–	–	–
Cueva Victoria	(Pons Moyà and Moyà Solà 1979)	No no.	(L)	–	–	–	–	–	–	–	41.2	24.7	–	13.5	15.7	–	–	–	–

Tab. 2 *Pachycrocuta brevirostris*, Untermaßfeld. Measurements of skulls and teeth (adults) (mm). (For explanation of the abbreviations see introduction).

			D₂		D₃		D₄		
			L	B	L	B	L	B	Lt
IQW 1988/22587	(Mei. 22105)	(L)	16.8	9.4	19.5	9.2	23.0	8.4	5.8
IQW 1988/22730	(Mei. 22249)	(R)	16.8	9.1	19.4	9.2	23.0	8.4	5.8
IQW 1988/22603	(Mei. 22122)	(R)	–	–	19.2	9.4	–	–	–
IQW 1987/22274	(Mei. 21793)	(R)	–	–	18.7	9.4	–	–	–
IQW 1990/23407	(Mei. 22926)	(L)	16.7	–	19.7	9.4	–	–	–
IQW 1990/23407	(Mei. 22926)	(R)	16.6	–	19.7	9.3	22.4	8.1	5.8
IQW 1990/23475	(Mei. 22994)	(L)	15.9	–	19.3	8.9	22.8	8.4	6.1
IQW 1990/23477	(Mei. 22996)	(L)	16.7	8.8	–	–	–	–	–

Tab. 3 *Pachycrocuta brevirostris*, Untermaßfeld. Deciduous lower teeth (mm). (For explanation of the abbreviations see introduction).

			D^2		D^3				
			L	B	L	Ba	Bbl	Lp	Lm
IQW 1986/21766	(Mei. 21285)	(L)	16.9	10.1	28.4	9.8	6.3	12.5	10.2
IQW 1888/22733	(Mei. 22252)	(R)	18.0	10.3	–	–	–	–	–
IQW 1986/21093	(Mei. 20612)	(R)	–	–	27	–	6.8	11.2	10.4
IQW 1987/22210	(Mei. 21729)	(R)	16.7	9.6	–	–	–	–	–
IQW 1987/22216	(Mei. 21735)	(L)	–	–	–	9.6	–	11.2	–
IQW 1989/23103	(Mei. 22622)	(R)	–	–	28.7	9.5	6.4	12.0	10.7

Tab. 4 *Pachycrocuta brevirostris*, Untermaßfeld. Deciduous upper teeth (mm). (For explanation of the abbreviations see introduction).

			TL	PML	PAP	SW	DW
Metacarpal II (L)	IQW 1986/21299	(Mei. 20818)	97.1	17.1	–	12.7	20.7
Metatarsal V (R)	IQW 1983/19545	(Mei. 19065)	83 0	–	20.7	10.5	13.8
Metapodial indet.	IQW 1980/17175	(Mei. 16696)	–	–	–	11.9	16.0

Tab. 5 *Pachycrocuta brevirostris*, Untermaßfeld. Metapodial measurements (mm). (For explanation of the abbreviations see introduction).

Permanent Dentition

(Taf. 121-125; Taf. 126, 5-7; Fig. 1-5)

The lower incisors are not remarkable. They show the usual increase in size from I_1 to I_3. Two cusps on the lingual surface behind the main crown form a 'V'-shaped ridge which is almost symmetrical on I_1 and becomes less so on I_2 and I_3 (Taf. 125).

The lower canine is large and stout, with a marked cingulum that rises to form a triangle on the lingual surface of the tooth before continuing in a ridge to the tip. The crown is high, measuring 33 mm in the case of 1980/15918 (Mei. 15429) although around 5 mm is clearly missing from the tip through wear (Taf. 124; Fig. 4).

P_2 has a large protoconid with a marked keeling. The anterior cusp is generally small, but the posterior cusp is variable in size and may be quite prominent in some specimens, such as 1980/15918 (Mei. 15429), and smaller in others, such as 1986/21369 (Mei. 20888) (Taf. 125) and 1990/23457 (Mei. 22976).

P_3 also has a high protoconid, strong keeling and a generally large posterior cusp, and exhibits a rather weak cingulum. P_4 is a robust tooth with a large posterior cusp and a well-developed anterior cusp in addition to the protoconid. Keeling is marked, but the cingulum is notable only on the anteroexternal surface (Taf. 125).

M_1 is a high tooth with a long talonid (Taf. 124-126, 5-7; Fig. 4). The cingulum is generally weak, although it becomes prominent on the anteroexternal part. The paraconid is large and the protoconid short. The cusps on the talonid are rather variable in number and orientation, and it is difficult to identify a metaconid on any of the specimens with certainty. One and sometimes two cusps appear on the talonid, which is long, and are usually in line with the main axis of the tooth. The larger cusp is seemingly a hypoconid. The talonid seems to show wear from early adulthood owing to occlusion with the M^1, which adds to the difficulties of discerning cusps (Taf. 124, 2; Fig. 4b).

The mandible itself is massive and deep all the way along, with a single, large mental foramen under P_2. The masseteric fossa is well-defined.

The upper incisors are quite well represented (Taf. 121-122; Fig. 1). I^3 is large and has a strongly recurved crown. I^1 is smaller than I^2 which is in turn smaller than I^3, and both I^1 and I^2 have strong anterior cusps and two smaller, virtually symmetrical posterior cusps. Wear tends to produce an even planation across the tips of all four central incisors.

The upper canine is massive. Isolated worn specimens can be distinguished from similar-sized canines of larger cats by the absence of the bulging of the root seen in felid upper canines. The triangle at the base of the antero-internal ridge of the crown is a marked feature of the tooth. The unworn crown of C^{sup} in specimen IQW 1990/23 650 (Mei. 23 179) (Taf. 121) measures 38 mm in height on its buccal surface.

The P^1 is not remarkable. However, in fully adult individuals there is scarcely room for the tooth, which seems to be somewhat 'squeezed out' of the tooth row in a lingual direction by the encroaching canine and second premolar. The P^2 itself is squat and quite large, although the crown is not especially high. It tends to have a well-developed posterior cusp. P^3 can be very robust, although it too is not particularly hypsodont, and the posterior cusp may be large. P^4 is again a massive tooth, with a well-developed, keeled and pointed parastyle and a high paracone (Taf. 121). The protocone is quite large and angled somewhat forwards, and is set well below the parastyle and sharply demarcated from it by a v-shaped valley. The slope of this valley leading up to the tip is flattened, in contrast with the rounded lingual surface of the protocone. The metastyle is long, although relatively less than in *Crocuta* as Kurtén (1956, 1972) has stressed. There is no marked internal cingulum. All three of the main upper cheek teeth display basal triangles where the strong anterointernal keel meets the cingulum, paralleling the condition in the upper and lower canines.

M^1 is preserved only in three specimens. It is not especially large, but it tends to show wear as soon as the permanent teeth come into occlusion, matching the condition on the talonid of M_1 and indicating that its function is retained. The tricuspid pattern may just be observed, especially in specimen 1990/23 650 (Mei. 23 179) (Taf. 121).

Deciduous dentition
(Taf. 126, 1-4)

The deciduous incisors and canines are not remarkable. The first lower deciduous molar, dM_2, is quite high crowned, with a sharp, well-keeled main cusp and strong anterior and posterior cusps. The keeling on the anterior cusp curves round and runs down towards the lingual cingulum.

The dM_3 is also very high crowned and keeled. When fresh, with its large main cusp flanked by strong and sharp anterior and posterior cusps, it somewhat resembles the permanent P_4 of the dirk-toothed cat *Megantereon cultridens*.

The lower milk carnassial, dM_4, has a long talonid with a trenchant cusp and a second, much smaller cusp on the cingulum.

In the upper jaw, dM^2 has a very high main cusp, a small anterior cusp that turns inwards, and a modest posterior cusp with a large apron area on the lingual surface that tends to develop a wear facet. The

Fig. 1 *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Left maxilla and premaxilla IQW 1983/19556 (Mei. 19076), with canine IQW 1987/21872 (Mei. 21391): a occlusal view; b buccal view; c lingual view. – Scale = ca. 1:1.

Fig. 2 *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Right maxilla IQW 1983/19555 (Mei. 19075): a occusal view; b buccal view; c lingual view. – Scale = ca. 1:1.

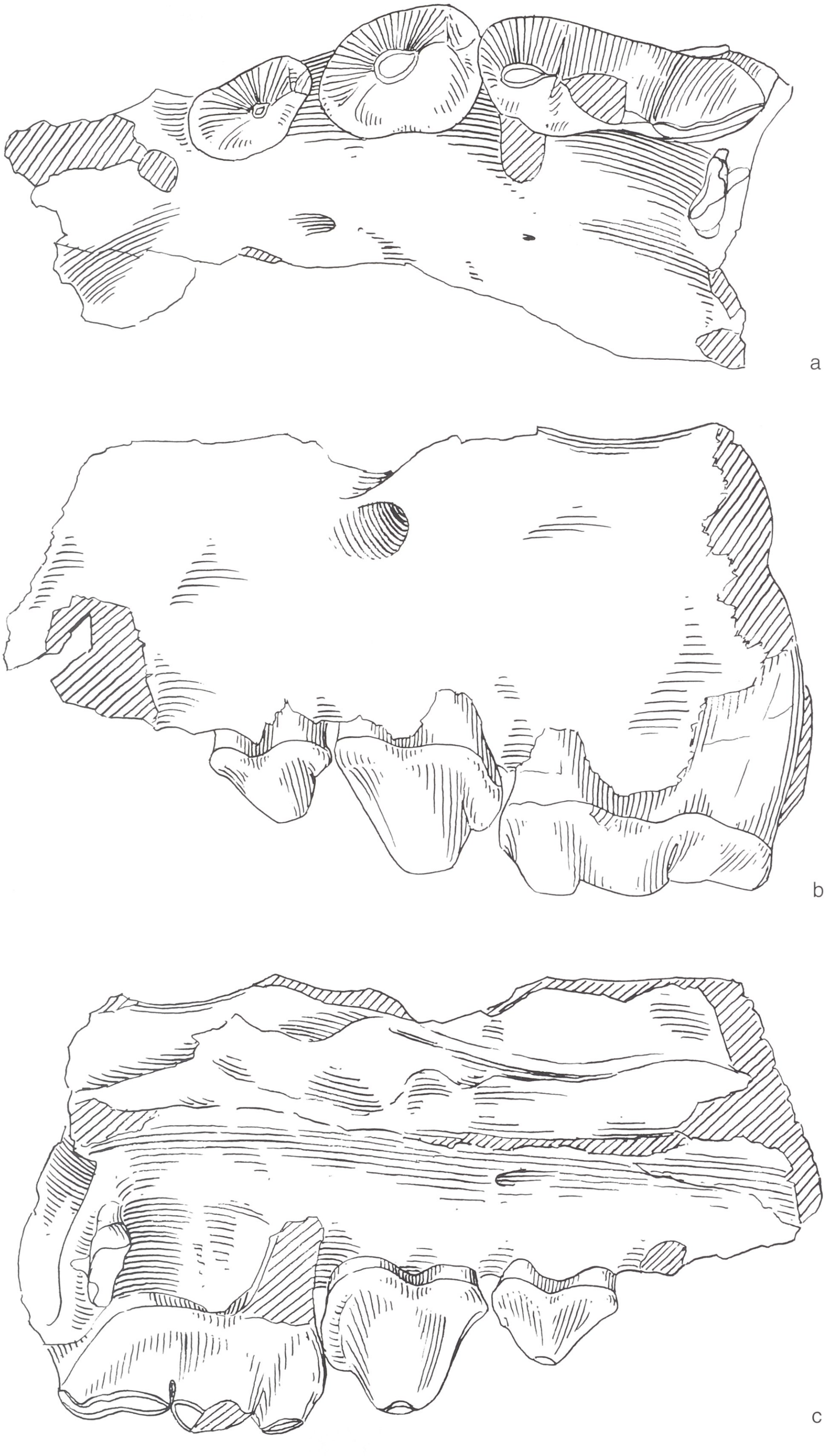

Fig. 3 *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Left maxilla IQW 1980/16 085 (Mei. 15 596): a occlusal view; b buccal view; c lingual view. – Scale = ca. 1:1.

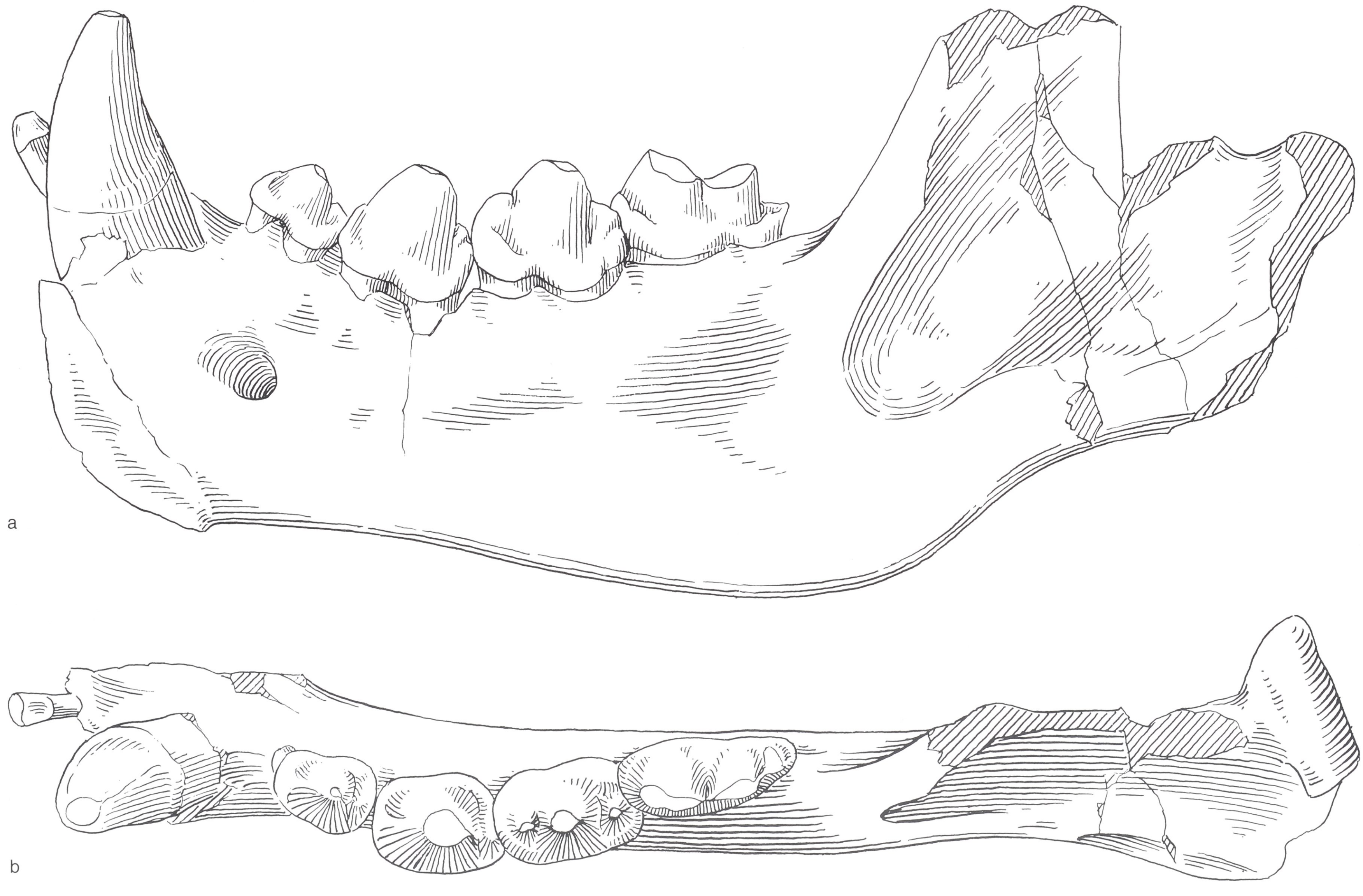

Fig. 4a-b *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Left mandible IQW 1980/15 918 (Mei. 15 429): a buccal view; b occlusal view. – Scale = ca. 1:1.

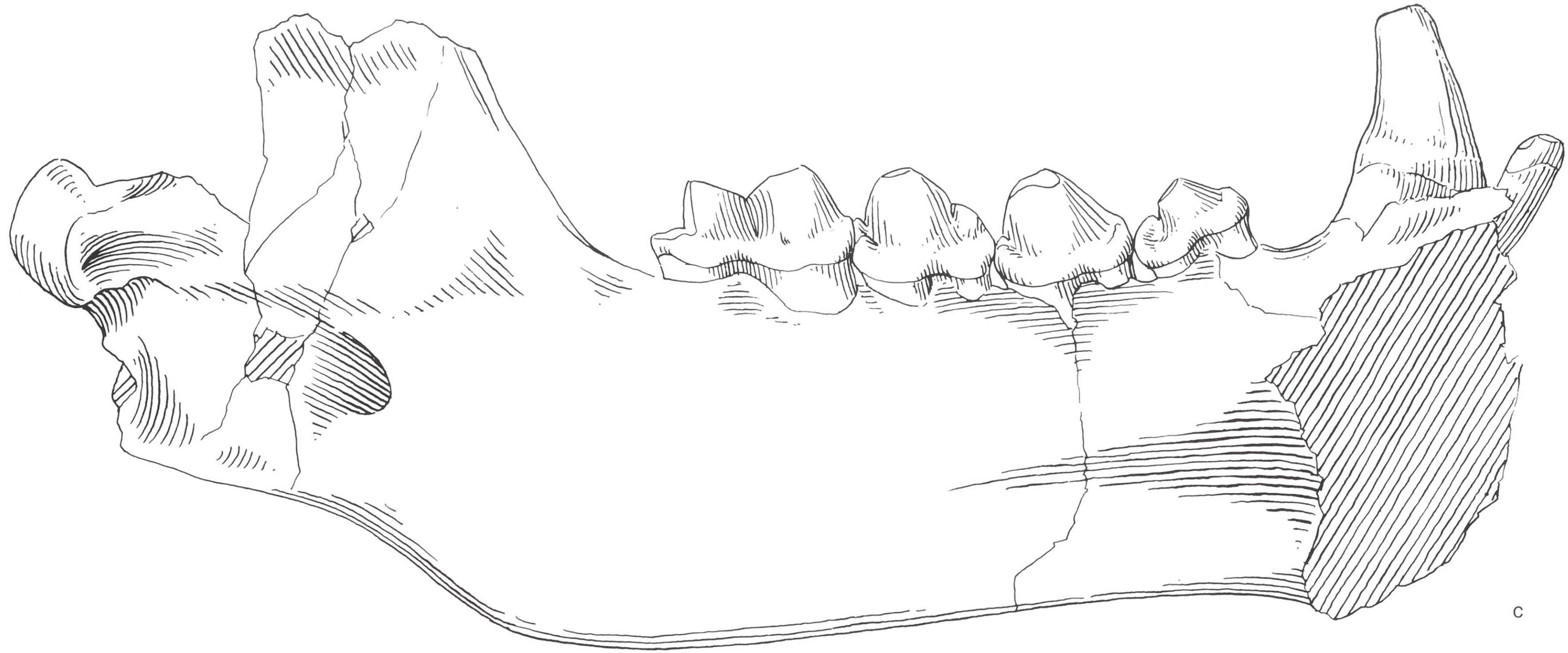

Fig. 4c *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Left mandible IQW 1980/15918 (Mei. 15429): c lingual view. – Scale = ca. 1:1.

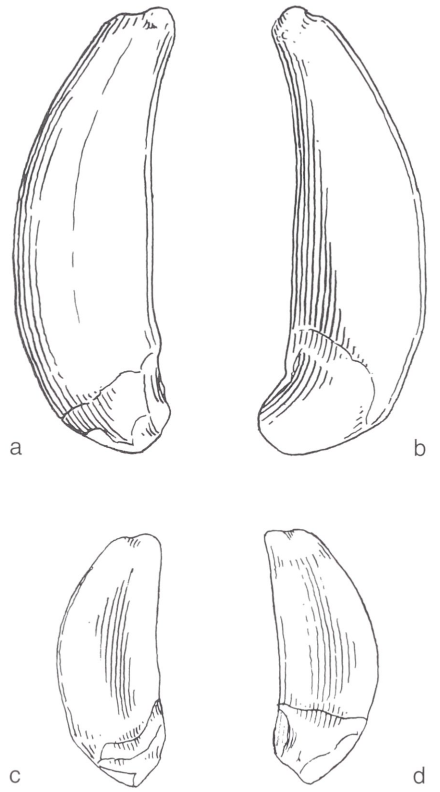

Fig. 5 *Pachycrocuta brevirostris* (Aymard), Untermaßfeld. Right I^3 IQW 1983/19558 (Mei. 19078): a lingual view; b buccal view. Right I^2 IQW 1983/19557 (Mei. 19077): c lingual view; d buccal view. Scale = ca. 1:1.

upper milk carnassial, dM^3, is a long tooth with a well-developed parastyle and paracone and a less robust metastyle. There is no real protocone, although a third root develops below the small cusped area. The dM^4 is low-crowned and three rooted, with the lingual root quite long.

Postcranial material
(Taf. 127)
The atlas vertebra IQW 1987/22125 (Mei. 21644) is missing the wings. The width of the anterior articulation, and therefore the approximate bi-condylar width of the skull from which it came, is 60mm. The second left metacarpal is large and robust, although the posterior portion of the proximal articulation is broken, as is the fifth right metatarsal. The unidentified metapodial fragment IQW 1980/17175 (Mei. 16696) is also robust, and is clearly hyaenid in view of the morphology of the distal articulation. Measurements of these metapodial specimens are shown in Tab. 5. The three humerus specimens provide no useful measurements or any notable anatomical detail, although one of them bears interesting traces of damage discussed in the next section.

3. Discussion

3.1. Age Structure and Numbers of Individuals

The bulk of the sample is made up of the teeth and jaws of juvenile hyaenas, and these could be placed in a number of groups according to the development and wear on the deciduous dentition. The lower deciduous canine tends to wear at the tip into a flat surface. The dM_2 erupts last, by which time there is some wear on dM_4 but only slight wear on dM_3. The mandible is evidently growing strongly throughout the sequence because dM_2 has to emerge at a considerable angle to the main axis of the tooth row in order to find room, and yet by the time that it comes into wear it has taken up its correct orientation (Taf. 126, 3-4).

The youngest stage (1) contained one individual, the right mandible IQW 1982/17891 (Mei. 17411) in which the dM_2 is only just emerging and still below the level of the alveolus.

The second stage (2), with dM_2 starting to erupt, contains two individuals, right mandible IQW 1990/23475 (Mei. 22994) and left and right mandibles IQW 1990/23407 (Mei. 22926). Four other individuals [IQW 1989/23104 (Mei. 22623), IQW 1990/23478 (Mei. 22997), IQW 1990/23479 (Mei. 22998) and IQW 1989/23103 (Mei. 22622)] fell within either stages (1) or (2), but there is probably little difference in the ages of the animals in the two groups anyway.

The third stage, with all of the milk molars in wear but with only very slight wear on dM_2, contains two individuals, the left mandible IQW 1988/22486 (Mei. 22106) and the right mandible IQW 1988/22730 (Mei. 22249).

The fourth stage, where all of the milk molars are starting to show moderate wear, contains at least three individuals based on left mandible IQW 1988/22460 (Mei. 21979), right mandible IQW 1988/22600 (Mei. 22119) and two isolated left dM_2, IQW 1990/23477 (Mei. 22996) and IQW 1988/22486 (Mei. 22005).

The fifth and last juvenile stage, with considerable wear on all of the teeth, contains one individual, the isolated right dM_3 IQW 1987/22274 (Mei. 21793). The juvenile sample therefore contains at least thirteen individual animals.

Among the adult hyaenas, the youngest, as indicated by the stages of eruption and wear on the teeth, is clearly the animal represented by the left and right mandibles IQW 1986/21369 (Mei. 20888) (Taf. 125). Two further individuals are represented by the left mandibles IQW 1980/15918 (Mei. 15429) and IQW 1990/23457 (Mei. 22976). The left maxilla IQW 1980/16085 (Mei. 15596) (Fig. 3) could belong to the same individual as mandible IQW 1980/15918 (Mei. 15429) (Fig. 4), but the left and right maxillae IQW 1983/19556 (Mei. 19076) and IQW 1983/19555 (Mei. 19075) are from an older individual than any of the mandibles and clearly represent a fourth adult animal (Fig. 1-2). The isolated left C^{sup}, IQW 1987/21872 (Mei. 21391), probably belongs to IQW 1983/19556 (Mei. 19076) (Mei. 19076) (Fig. 1). The snout IQW 1990/23650 (Mei. 23179) is from an animal of similar age to that represented by the paired mandibles IQW 1986/21369 (Mei. 20888), but it is too large to fit them and represents a fifth adult. The second snout, IQW 1990/23625 (Mei. 23154), comes from an animal of similar age to that from which mandible 1990/23457 (Mei. 22976) derives, and the degree of fit suggests that they may very well belong to a single individual. In all, based on the dental and gnathic specimens, the Untermaßfeld sample therefore contains remains from a minimum of eighteen hyaenas.

3.2. Size

Pachycrocuta brevirostris has been described as a gigantic hyaena that rivalled a lion, *Panthera leo*, in size (Boule 1893, 89; Kurtén 1968, 65). It might be useful to put this statement into some perspective. Most known specimens are of fragmentary jaws, dentitions and isolated teeth, and while they are evidently large in comparison with other hyaenid species it is difficult to guage the relative size of the live animal from these. However, Boule (1893) provides various measurements for the virtually complete type skull and mandible from Sainzelles in the Auvergne (Tab. 1-2). The basal length of 322mm may be compared with my own basal length measurements for a sample of 19 southern African male lion skulls (in mm).

Mean ± S. E.	S. D.	Range
294 ± 6.4	28.0	242-328

These figures suggest that the Sainzelles skull is indeed large. Of course the specimen is the only complete skull, but comparison of its various dimensions with those of other less complete specimens from Untermaßfeld and elsewhere (Tab. 1-2) suggest that it is not simply a single giant. It is therefore clear that both Boule and Kurtén were correct in their assessment of *Pachycrocuta brevirostris* as a giant among hyaenas.

3.3. Palaeoecology

Most samples of *Pachycrocuta brevirostris* contain small numbers of individuals, most of which are adult animals. Given the relatively large number of young hyaenas present in the Untermaßfeld assemblage, it is worth considering the potential ecological information to be gained from a study of the age structure of the sample.

Comparative studies of modern spotted hyaenas (*Crocuta crocuta*) and brown hyaenas (*Parahyaena brunnea*) suggest that the deciduous teeth appear at or shortly after birth and that the full permanent dentition is in place by the age of 15 months (Kruuk 1972; Mills 1990). On this basis, all of the 13 juvenile specimens from Untermaßfeld were less than one year old at death, assuming broad comparability in the rate of dental development. Both brown and spotted hyaenas may be born throughout the year, although there is evidence for seasonality in the published figures (Mills 1990, Figs 4, 3 and 4, 8; Kruuk 1972, Fig. 6). Indeed, Skinner (1976) argued for a strong seasonal cycle in the case of the brown hyaena in the Transvaal Province of South Africa between August and November, that is in the late winter and spring of the southern hemisphere. It is likely that in temperate Europe there would be an increased impetus towards seasonal breeding, although it is difficult to decide such a matter with certainty. If the Untermaßfeld hyaenas *did* breed on a seasonal basis, with births peaking in the spring, then the range of ages in the juvenile sample do tend to show some clumping that might in turn point to a seasonal element in the deposition. The first three stages of juvenile tooth development, before significant wear takes place on the dM_2, are probably quite closely spaced in time. Even the fourth stage contains milk teeth with only a moderate amount of wear, and the first four stages contain 12 of the 13 juvenile animals. These 12 animals point to deposition perhaps during the earlier summer months. The youngest of the adult specimens, IQW 1986/21369 (Mei. 20888), has its permanent canines and second and third premolars still erupting, pointing to an age of between 12 and 15 months at death (Mills 1990), which could also indicate deposition during the earlier part of the summer during the individual's second year of life. It is difficult to say more on this topic with the data available.

So far as the food consumption habits of the Untermaßfeld hyaenas were concerned, we have two main lines of evidence. The first is provided by the bones of the other larger mammals present at the site, many of which are extensively damaged in a manner fully consistent with damage caused to bones by modern spotted hyaenas (Sutcliffe 1970; Kruuk 1972; Mills 1990; R.-D. Kahlke 1987 and pers comm.; direct observations of the author). Other things being equal, the ability to destroy bone depends on the size of the hyaena, the strength of the jaw musculature and the structure of the teeth, and *Pachycrocuta brevirostris* was eminently suited to such activities. Moreover, its sheer size would have meant that it could successfully compete for carcases. But while this evidence implies that the carcases were eaten by the hyaenas, in itself it provides an incomplete picture of either the circumstances or the intensity of consumption.

The second line of evidence is afforded by the eighty or so coprolites found in the deposits. These vary in size, the largest being some 80 mm in greatest diameter, and while many look as though they have been excreted, others have the packed-together appearance of faeces in a living or recently dead hyaena gut. All are typical of the faeces of hyaenas on a bone-rich diet, and are produced by these animals as a result of their ability not only to smash and eat bones but also to digest the organic fraction of bone and to excrete the inorganic residue (Kruuk 1972; Mills 1990). No other carnivores are capable of that level of bone consumption, and therefore cannot produce similar faecal masses. Some of the Untermaßfeld coprolites with broken surfaces contain visible fragments of bone (Taf. 127, 3-4).

Of course, the ability to consume bone does not always mean that the option is exercised. As Kruuk (1972) showed, extensive bone consumption is a behaviour that tends to be employed by hyaenas that are scavenging, or are facing stiff competition for carcases from other predators. In the absence of such pressures they tend to eat the more fleshy portions of carcases and simply leave the rest. One possibility is that the damage to the Untermaßfeld ungulate bone, and the presence of bone-rich coprolites, represents opportunistic scavenging. Support for that may be sought in the fact that the accumulation contains semi-complete body parts that are thought to have been washed together by a slow-moving body of water bringing bodies down from perhaps several kilometres away (R.-D. Kahlke, pers. comm.). Such carcases must have had enough soft tissue to hold them together, and would have provided a sufficiently attractive source of food for a hyaena. But if that is so, then the evidence for scavenging by *Pachycrocuta brevirostris* at Untermaßfeld depends largely on the specific circumstances of the assemblage formation, and cannot be generalised to infer a single mode of feeding for the species in all circumstances. Larger carnivores are opportunistic feeders, and in the absence of very specific adaptations that restrict choice (such as in the case of the cheetah, *Acinonyx jubatus*, which can really only obtain food by a high-speed chase) they will hunt or scavenge as circumstances dictate.

Some other inferences about the food procuring habits of *Pachycrocuta brevirostris* may however be drawn from a consideration of the other large carnivores present. Those recorded from the site are *Megantereon cultridens, Homotherium crenatidens*, *Panthera gombaszoegensis*, *Acinonyx pardinensis*, *Xenocyon lycaonoides* and *Canis lupus mosbachensis*. The variety of large predators alone is likely to have ensured that maximum advantage be taken of any opportunities for feeding, as may be seen today in the game areas of Africa (Kruuk 1972; Schaller 1972; Mills 1990). But both *H. crenatidens* and *A. jubatus* are likely to have hunted rather than scavenged, since neither was dentally equipped to deal with previously exploited carcases, especially true for the sabre-tooth. Both of these cats are also likely to have left carcases with abundant soft tissues, suggesting that scavenging would have been a major option. In sum, it seems likely that *Pachycrocuta brevirostris* was well equipped to scavenge, would have had every opportunity to do so and certainly took advantage of circumstances at sites such as Untermaßfeld.

One other interesting point may be mentioned. The juvenile humerus diaphysis IQW 1989/23 120 (Mei. 22 639) bears puncture marks at the distal end, just above the olecranon fossa (Taf. 127, 1-2). One on the lateral side is 5.5 mm in diameter, while one almost diametrically opposite it on the medial side is 7.0 mm in diameter and penetrates more deeply into the bone. A second puncture on the medial side lies distally to the 7.0 mm hole, but is less clear-cut than either of the other two. The most sensible interpretation is that they have been made by the upper and lower canines and the upper third incisor of a large carnivore, although it is difficult to identify the species responsible with any certainty.

Summary

The Untermaßfeld sample contains a minimum of five adult and thirteen juvenile individuals of the hyaena *Pachycrocuta brevirostris*, mostly represented by cranial and dental remains. Comparisons with measurements for specimens from other European sites confirms that this was indeed a gigantic hyaena that rivalled a modern lion in size. The age structure of the juvenile animals, based on tooth eruption and wear stages, may suggest that deposition was concentrated during the summer months.

Damage to the bones of large ungulates at the site, together with the relative frequency of coprolites indicative of a bone-rich diet, implies that *P. brevirostris* scavenged in the vicinity. The structure of the large carnivore community of the period is likely to have provided considerable scope for a scavenger able to expropriate or guard carcases and to consume bone.

Zusammenfassung

Das Untermaßfelder Fundmaterial enthält Fossilreste von mindestens 5 adulten und 13 juvenilen Individuen der Hyänenart *Pachycrocuta brevirostris*. Sie sind zum überwiegenden Teil durch Cranial- und Zahnreste repräsentiert. Die zusätzlich herangezogenen Vergleichsmaße von Exemplaren aus anderen europäischen Fundstellen bezeugen, daß es sich hierbei um eine riesige Hyänenart handelt, die dem heute lebenden Löwen an Größe gleichkommt. Die anhand eruptierter Zähne sowie der Abrasionsstadien ermittelte Altersstruktur der juvenilen Individuen deutet darauf hin, daß die fossilen Knochenreste während der Sommermonate akkumuliert wurden.

Die nachgewiesenen Fraßspuren an Knochen großer Huftiere und die für eine knochenreiche Ernährung sprechende relative Häufigkeit von Koprolithen lassen darauf schließen, daß *P. brevirostris* in unmittelbarer Nähe der Fundstelle gefressen hat. Das zu dieser Zeit bestehenden Artengefüge der Carnivoren begünstigte offenbar Aasfresser dieser Größenkategorie.

Acknowledgement

I thank Professor Dr. Dr. H.-D. Kahlke for his invitation to study the Untermaßfeld hyaenas, and himself, Dr habil. R.-D. Kahlke and other members of staff at the Institut for every assistance and kind hospitality. The work was funded by grants from the Royal Society and the former DDR Academy of Sciences, and was undertaken within a larger programme of research supported by The Leverhulme Trust.

References

Boule, M. 1893: Description de l'*Hyaena brevirostris* du Pliocene de Sainzelles pres le Puy (Haute-Loire). Ann. Sci. Nat., ser 8, 15, 85-97, Paris.

Kahlke, R.-D. 1987: Die unterpleistozänen *Hippopotamus*-Reste von Untermaßfeld bei Meiningen (Bezirk Suhl, DDR). Dissertation, Ernst-Moritz-Arndt-Universität Greifswald), 167 pp. + 21 ann. + 102 tab. + 27 fig. + 18 pl., Greifswald.

Kruuk, H. 1972: The Spotted Hyaena. 335 pp., Univ. Chicago Press; Chicago.

Kurtén, B. 1956: The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. Am. Mus. Nov. 1764, 1-48, New York.

1968: Pleistocene Mammals of Europe. 317 pp., Weidenfeld and Nicolson; London.

1972: Fossil Hyaenidae from the excavations at Stránská Skála. Anthropos 20, 113-120, Brno.

1989: Giant hyaena, *Hyaena brevirostris* Aymard (Mammalia, Carnivora), from the Middle Pleistocene of Manastirec, Yugoslavia. Ann. Zool. Fenn. 26, 145-147, Helsinki.

Lumley, H. de, Kahlke, H.-D., Moigne, A.-M. and Moulle, P. E. 1988: Les faunes de grands mammifères de la grotte du Vallonnet, Roquebrune-Cap-Martin, Alpes-Maritimes. L'Anthropol. 92, 2, 465-496, Paris.

Martinez Navarro, B. 1991: Revision sistematica y estudio cuantitativo de la fauna de macromamiferos del yacimiento de Venta Micena (Orce, Granada). Ph. D. Thesis, Universidat Autònoma de Barcelona, 265 pp., Barcelona.

Mills, G. 1990: Kalahari Hyaenas. 290 pp., Unwin Hyman; London.

Pons-Moyà, J. and Moyà-Solà, S. 1979: La fauna de carnivoros del Pleistoceno medio (Mindel) de la Cueva Victoria (Cartagena, España). Acta Geol. Hisp. 13, 54-58, Barcelona.

Schaller, G. B. 1972: The Serengeti Lion. 360 pp., Univ. Chicago Press; Chicago.

Schütt, G. 1974: Die Carnivoren von Würzburg-Schalksberg. N. Jb. Geol. Paläont., Abh. 147, 61-90, Stuttgart.

Skinner, J. D. 1976: Ecology of the brown hyaena *Hyaena brunnea* in the Transvaal with a distribution map for southern Africa. S. Afr. J. Sci. 72, 262-269, Johannesburg.

Sutcliffe, A. J. 1970: Spotted hyaena: crusher, gnawer, digester and collector of bones. Nature 227, 1110-1113, London.

Turner, A. 1990: The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. Geobios 23, 349-368, Lyon.

Werdelin, L. and Solounias, N. 1991: The Hyaenidae: taxonomy, systematics and evolution. Fossils and Strata 30, 1-104, Stockholm.