A skull of *Machairodus giganteus* (Felidae, Mammalia) from the Late Miocene of Turkey

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With 4 figures

Abstract: A skull and associated mandible from the upper level of Kemiklitepe is one of the most complete known specimens of *Machairodus*. It is distinctly more derived than specimens from the lower level. Cladistic analysis of this genus does not allow recognition of well-defined clades, but suggests instead gradual acquisition of the cranial and dental specializations that characterise *Homotherium*.

Zusammenfassung: Ein Schädel mit dazugehörendem Unterkiefer aus der oberen Schicht von Kemiklitepe gehört zu den vollständigsten bekannten Exemplaren von *Machairodus*. Er ist bedeutend höher entwickelt als die Exemplare aus der unteren Schicht. Die kladistische Analyse dieser Gattung lässt keine gut bestimmten Clades erkennen; sie weist vielmehr auf ein allmähliches Erwerben der Schädel- und Zahnspezialisierungen hin, wie sie *Homotherium* kennzeichnen.

Key-words: Mammalia, Felidae, *Machairodus*, Late Miocene, Turkey, phylogeny, cladistics.

Introduction

The site of Kemiklitepe (meaning "the hill of bones"), in Western Turkey, was discovered by Yalcinlar in 1946. The main field collection there was made in 1989-1990 by SEN and co-workers (SEN 1994). They recognised (BONIS et al. 1994) two main stratigraphic units, an upper level KTA-KTB

yielding a fauna of MN 12-equivalent age, and a lower level, KTD, perhaps of MN 11-equivalent age. The carnivores collected by SEN et al. were studied by BONIS (1994). The only carnivore described from the lower level (KTD) is a fragment of skull with incomplete mandible, that BONIS referred to *Machairodus aphanistus*, but the genus was not mentioned from the upper level (KTA-KTB).

However, before the campaign led by SEN, some specimens had been collected by various workers. Some of them are housed in the Musée Guimet, Lyon, but most are in the Museum of the University of Izmir. Among the latter is the skull described here, which had not been reported previously. It is numbered UEK-124 and was collected by Feral Arslan in 1991 in the upper part of the section (level KTA-KTB), and is therefore more recent than the one described by BONIS (1994).

In the following descriptions, measurements are in millimetres; upper case denotes upper teeth, lower case denotes lower teeth.

Systematic description

Family   Felidae GRAY, 1821
Genus   *Machairodus* KAUP, 1833

Machairodus giganteus (WAGNER, 1848)

The skull is relatively well preserved, especially its left side. The main missing parts are the inner orbit, palate, and most of the premaxillae and most of the bulla. Still, it is one of the most complete and best preserved *Machairodus* skulls known (Fig. 1).

The dorsal profile forms a gently convex curve from the nasal aperture to the missing top of the lambdoid crest. The temporal lines meet a short distance behind the orbits, and make up a high sagittal crest. The frontal is almost flat between the orbits. A hole in its central part, made prior to fossilisation, was the centre of a blow that also produced radial cracks in the whole frontal area. It was likely responsible for the death of the animal, but its origin remains unknown.

In lateral view, the dorsal profile rises steeply, so that the missing rear part of the sagittal crest is much elevated above the occlusal line. The root of the

Fig. 1. Skull of *Machairodus giganteus* from Kemiklitepe UEK-124. A: lateral view; B: upper view. Scale = 10 cm.
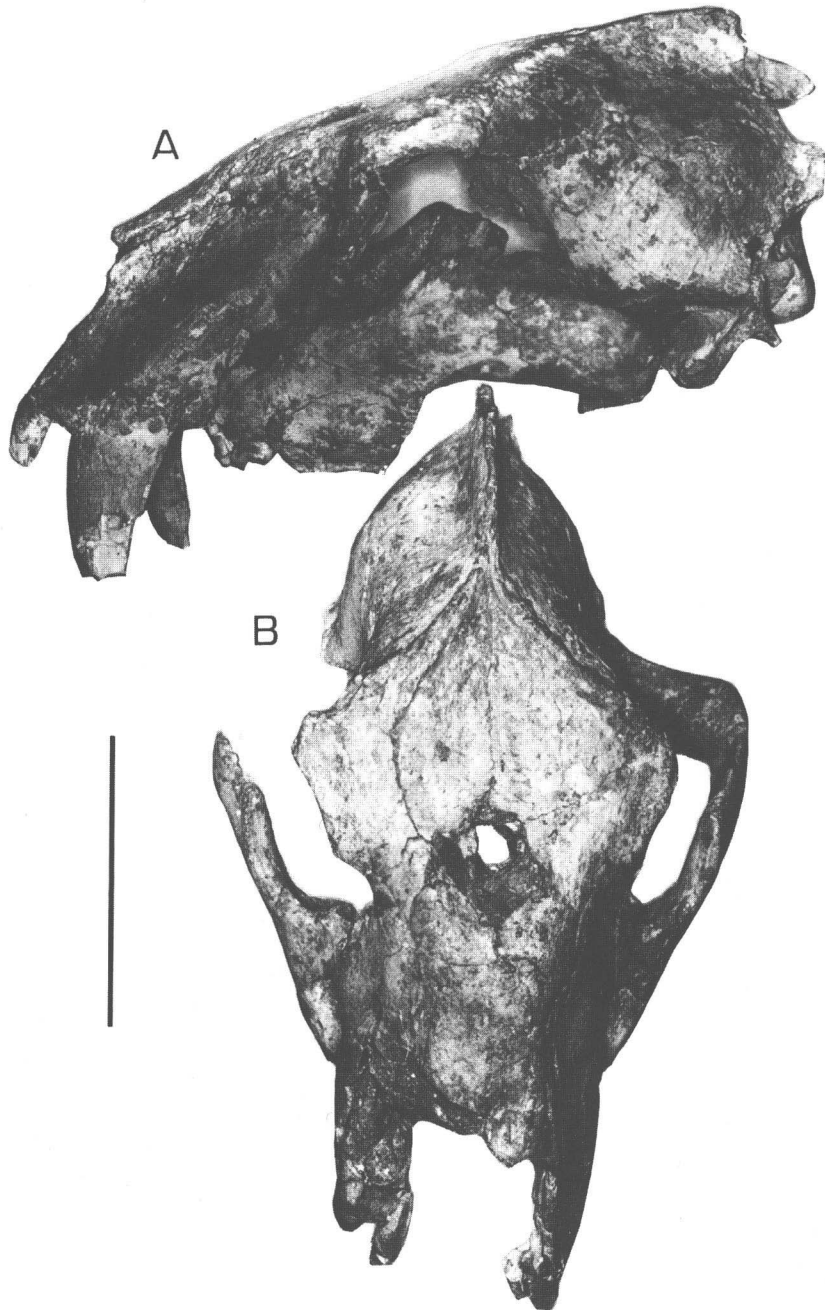
Fig. 1 (Legend see p. 96)

canine bulges out on the maxilla. It forms, together with the crown of the tooth, a regular curve whose extension would pass through the middle of the orbit. The posterior border of the root of the zygoma rises vertically behind the teeth, under the post-orbital process of the jugal. Thus, the orbit, being mostly above the teeth, is rather anterior. Behind it, the zygomatic arch, short and strongly built, is oriented antero-posteriorly, parallel to the tooth-row, forming a gentle arch. In lateral view, the glenoid cavity is at the same level as the lower border of the zygomatic arch, thus much higher than the tooth-row. The post glenoid process is of moderate size. The posterior face of the zygomatic arch is vertical. Behind the external auditory meatus, the mastoid process (Fig. 2 A) assumes the shape of a rectangle directed obliquely downwards and forwards; thus, it is convergent downwards with the posterior face of the zygomatic arch. The paroccipital process, short and spine-shaped, pressed against the posterior face of the bulla, is directed postero-laterally, and is thus perpendicular to the mastoid rectangle. It is strongly protruding backwards, and a deep notch separates it from the condyle. The masseter insertion on the zygomatic arch is poorly defined. It does not reach the maxilla. The zygomatic arches are less broad than in *Panthera*, indicating more reduced temporal muscles. The occipital area, high and narrow, is limited laterally by the occipital crest and is heavily sculptured.

The basicranial area, well preserved on the left side, is the most interesting part of the skull (Fig. 2 B, C). The posterior border of the pterygoid flange is at the level of the glenoid fossa, thus more posterior than in modern Felids, and it is also more vertical. The oval foramen is directed anteriorly and much less ventrally than in modern Felids, as noted by BONIS (1994). On both sides of the area between it and the foramen rotundum are small cliff-like elevations which doubtless represent remnants of the alisphenoid canal, completely lost in modern Felids, but still present in the specimen from the lower level of Kemiklitepe (BONIS, 1994). The roof of the canal seems to have been missing in life, rather than broken after death. The petro-tympanic suture is no longer traceable, perhaps because of the old age of the animal. The antero-ventral part of the bulla is flattened behind the middle lacerate foramen so that the inflated part of the bulla is restricted to the area behind the external auditory meatus. Most of the bulla is broken away. An internal

Fig. 2. Skull UEK-124. A: lateral view of auditory region; 2: ventral view of skull base, stereo pair; C: ventro lateral view of skull base, stereo pair; the arrows point to the remnants of the alisphenoid canal. Scale = 5 cm.
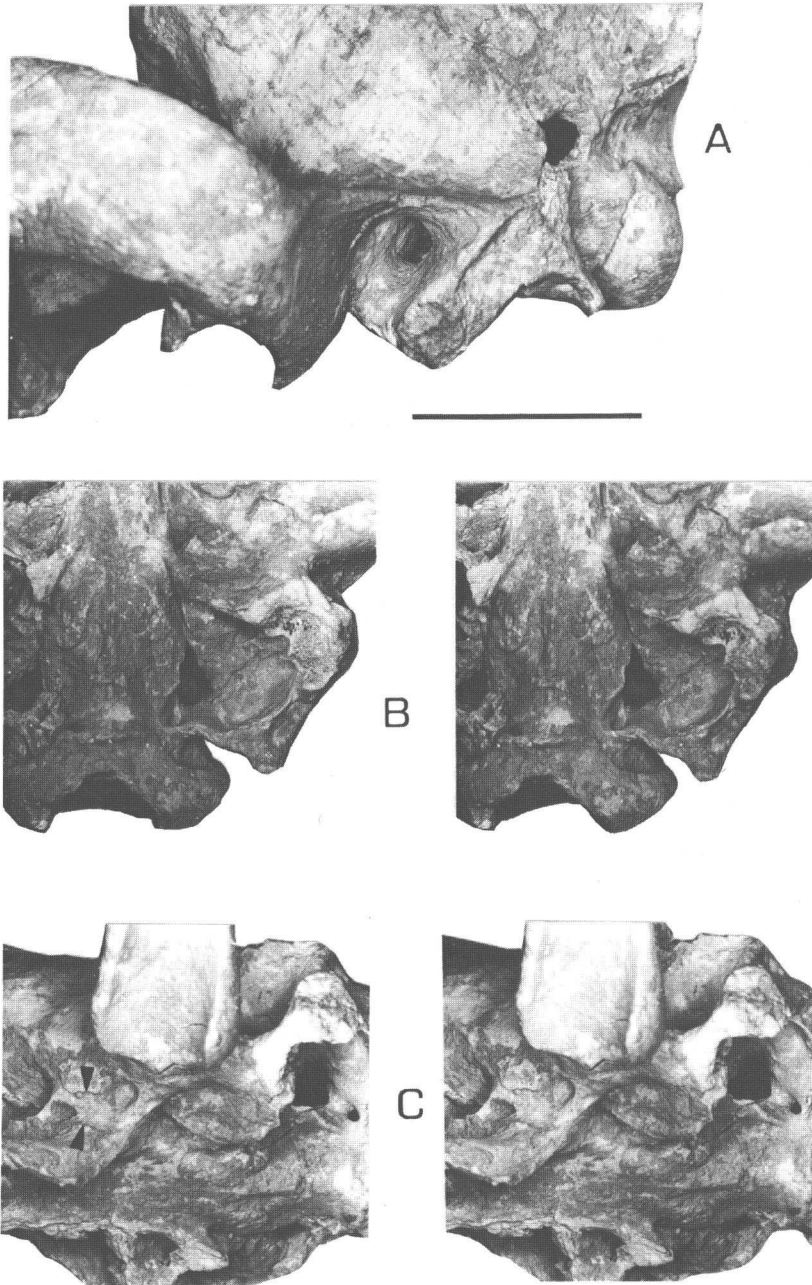
Fig. 2 (Legend see p. 98)

ridge along the mastoid might represent a remnant of a septum dividing the bulla, as in the specimen from the lower level (BONIS 1994), but the internal part of the bulla is not preserved in our specimen. The glenoid foramen opens in the same position as in modern Felids. The basioccipital is very broad, especially in its middle part; the anterior tuberosities are large and rough, but not prominent, and the bone is depressed behind them, on both sides of a sagittal crest. The condylar foramen is well distinct from the posterior lacerate foramen, as in the specimen from the lower level.

The right upper canine is well preserved. It is of moderate size, so that even with the jaws closed, its tip did not reach the level of the lower border of the mandible. Both its anterior and posterior edges are regularly curved. The posterior keel is blunted by use, and the anterior edge is smoothed in its lower part, probably by wear against the lower canine. About two centimetres below the alveolar level, the anterior keel turns inward and fades out. The cross-section of the canine is symmetrical, with a rounded anterior edge and a sharper posterior one. There is no indication whatever of an anterior or lateral flattened or depressed area.

There is no P2, and a short diastema separates the canine trom P3, which is badly broken anteriorly. The posterior part is well preserved, although the lingual expansion is worn. The posterior cingulum is reduced, and not expanded labially. P4 is so heavily worn that its length cannot be given precisely. Nothing is visible of the blade morphology, but a strong root protrudes lingually, indicating that a small but distinct protocone was present, although its is now completely abraded.

An alveolus shows that a M1 was present, but its size cannot be estimated.

The lower jaw is only partly preserved. It includes the symphyseal area, except its basal part, with all front teeth, a part of the right corpus with the premolars, and the posterior part of the left one, with the coronoid apophysis. Both carnassials are missing.

The corpus mandibularis is of regular depth, being only slightly deeper anteriorly (Fig. 3 A). In lateral view, the lower border is gently concave at the level of p3, indicating that the antero-inferior area was angular rather than rounded, but there is no indication of a mental apophysis. The posterior mental foramen opens below the anterior root of p3.

The coronoid apophysis is high and narrow, not much more reduced than in *Panthera*.

All teeth are imperfectly preserved, and most of them are much worn. None of them bears any trace of crenulation. All incisors are set more anteriorly than the canines, so that most of i3, including its root, is visible laterally. They form a wide arch in upper view (Fig. 3 B), increase in size from i1 to i3, and diverge upwards in front view. Their morphology is obscured by wear and imperfect preservation.
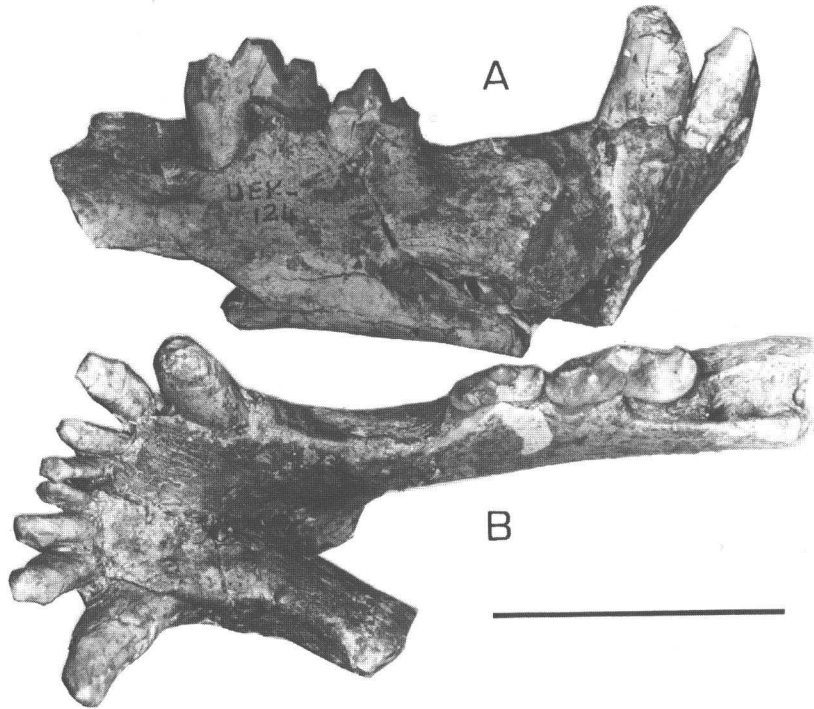
Fig. 3. Mandible UEK-124. A: lateral view; B: dorsal view. Scale = 5 cm.

The canines are also set wide apart (the distance between them and the midline is much greater than their thickness) and they diverge upwards. There is no evidence of crenulation, but there is a clear, although small, wear facet for I3, and probably a small one for the upper canine. In any case, antagonism between the canines was greatly reduced, and of weak functional significance. The diastema is of normal length (35 mm). There is no p2, as usual in this group. The p3 is broken and imperfectly preserved, but is unworn. It is low, with a weak anterior tubercle, and is closely pressed against p4. The latter has a strong anterior tubercle, whose long antero-posterior axis is slightly angled in respect to the tooth-row.

Measurements

	I3	C	P4	i1	i2	i3	c	p3	p4
Length	11.8	29.9	39+	4.3	6.2	7.8	15.0	18.5	27.2
Width	9.5	13.3	-	6.8	8.7	9.2	11.1	7.5	11.2+

Width over P4s = ca. 102
Minimum post-orbital width = 66
From I3 to posterior border
of glenoid = 203
From orbit to front of crown base
of C = 107
Depth of corpus below
diastema = 38.2

Maximum width over orbits = 115
Width of brain-case = 79
Length condylo-I3 = 277
Length of mandibular diastema
= ca. 32
Maximum depth at coronoid
process = 82

Cladistic analysis

In order to determine the phyletic relationships of the *Machairodus* from Kemiklitepe, we have performed a parsimonious cladistic analysis on 33 OTUs, most of them representing single specimens, or in a few cases small samples from very close localities. The cladogram is rooted by adding two outgroups with hypothetical ancestral states.

We used 22 characters, either discrete or metric. For the latter ones, we calculated the mean M and standard deviation S, and coded the character states as follows: $x > M + S : 0$; $M + S < x < M : 1$; $M < x < M - S : 2$; $x < M - S: 3$. We used ratios for most measurements, to avoid scale factor, but we have not attempted any allometric analysis. Given the relatively limited size range, and poor correlations, it would not be very significant. All characters are treated as additive.

Several other characters are in fact metric but cannot be precisely measured, and are treated as discrete. We have not used all of the characters often mentioned in the literature. Some of them are autapomorphic, or at least look autapomorphic because they can seldom be observed. We have not used canine wear, because lack of wear can just be due to early ontogenic age. We have not used enamel crenulations either, because they are often obscured by wear. Skull proportions would probably yield interesting results, but there are so few uncrushed skulls that reliable metric data are almost lacking.

The list of references, definition of character states and matrix are given in the appendix.

The parsimonious cladistic analysis yielded a single shortest tree (87 steps, $ci = 51$, $ri = 76$; Fig. 4). The many missing data in the matrix, and the

Outgroups
Charmoille
Eppelsheim
Bled Douarah
Los Valles
Can Llob Santiga
Akçaköy
Kemiklitepe D
Montredon
Grebeniki
MN12-MN13, Spain
Pavlodar
Yushe,Shansi
Samos
Kemiklitepe A-B
Mahmutgazi
Küçükyozgat
Baode, Shansi
M.palanderi Loc.30
Loc.113
M. tingi Loc.30
Taraklia
Kalmakpai
Fan Tsun
Vathylakkos
Halmyporotamos
Aïn Brimba
Langebaanweg
Hadar
Senèze
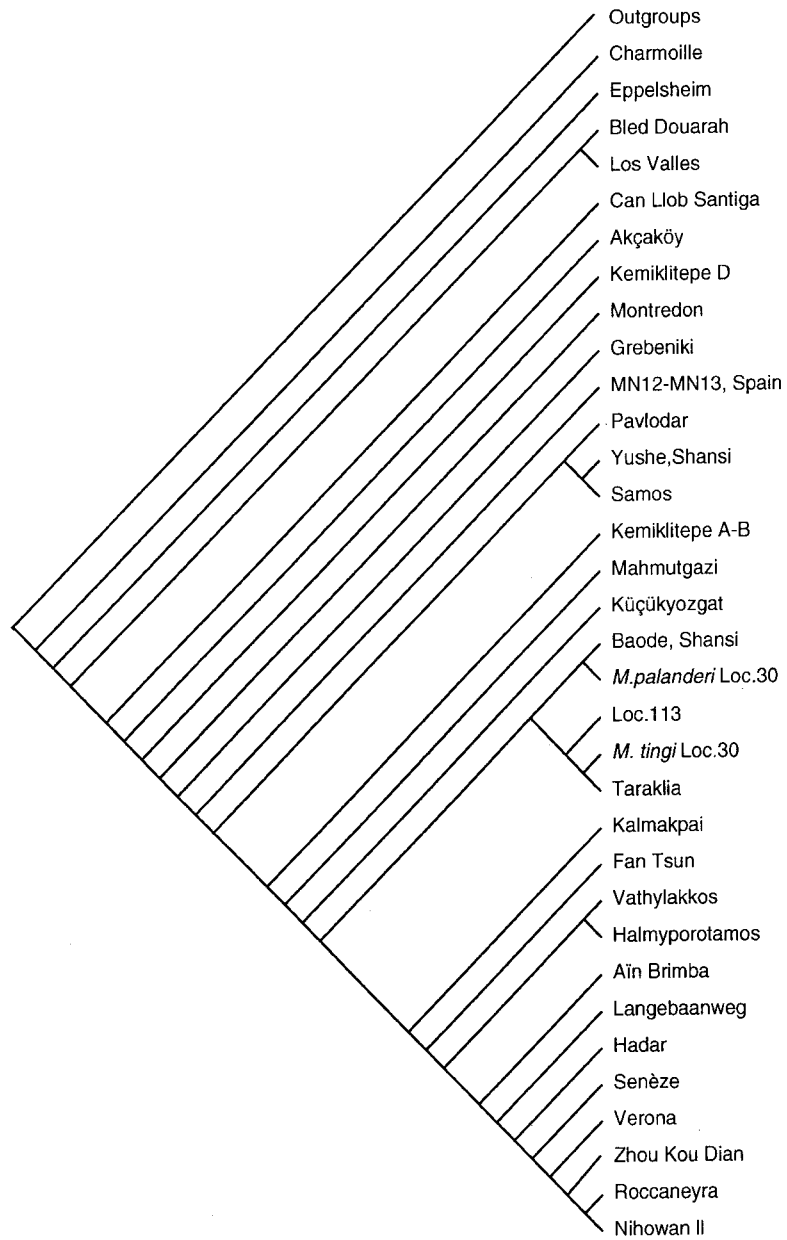Verona
Zhou Kou Dian
Roccaneyra
Nihowan II

Fig. 4. Cladistic analysis: the shortest tree.

great intraspecific variability of machairodonts, already noticed by several authors, especially BEAUMONT (1975) certainly account for the lack of well defined groups. Rather different cladograms can be obtained by increasing only marginally the length of the tree, and the one shown in Fig. 4 should be regarded as a mere tentative proposal.

The lower branches of the tree can be united in a paraphyletic group that could be called *Machairodus aphanistus*. *M. alberdiae* from Los Valles is close to the poorly known *M. robinsoni* from Bled Douarah in Tunisia, as noted by GINSBURG et al. (1981), but both can be included in the group of *M. aphanistus*. As suggested by BONIS (1994), *M. pseudaeluroides* from Akçaköy can be included here, although its strongly compressed upper canine is an unexpected derived feature here. All these forms are of Vallesian or Vallesian-equivalent age. Interestingly, the specimen from Kemiklitepe D (BONIS 1994) branches immediately higher, lending support both to its specific identification and to the early Late Miocene age of this level, but its position might well be partly due to the lack of upper teeth, upon which most of this part of the cladogram is based.

Leaving aside the poorly described specimen from Grebeniki, the following branches reflect the progressive acquisition of the derived traits that characterise *M. giganteus*. These include larger size (reflected in a larger p4), a shorter P3, which later also becomes narrower (except in Greek specimen), reduction of the protocone of P4, which becomes relatively longer through addition of a preparastyle, further reduction of M1, reduction of the lower canine in respect to the incisors or m1, and a stronger anterior cuspid on p4. Cranial features are almost unknown in *M. aphanistus*, but reduction of the alisphenoid canal and strengthening of the zygomatic arches probably occurred here.

In higher branches, advanced dental features include shortening of p3, followed by shortening of P3, increase of shearing specialisations of the carnassials, with the loss of m1 talonid, reduction of P4 protocone, and secondary reduction of the anterior cuspid of p4 in the highest branches. At the same time, changes in skull architecture occurred too, but are difficult to figure precisely, as there are too few well preserved skulls. The zygomatic arch becomes more curved, the mastoid process longer and the glenoid cavity lowered in respect to the auditory foramen, and the orbit is farther from the canine. Significant new results could probably be provided by 3-D analysis, but would require direct access to several undeformed skulls.

Unambiguous taxonomic results are few. The specimen UEK-124 clearly falls among the specimens usually referred to *M. giganteus*, but it is hard to provide a diagnosis of this species. The same is true of the genus *Homotherium*, and this explains why the generic attribution of several specimens has been disputed (Fan Tsun, Aïn Brimba). The skull from Fan Tsun, said to

be of Pleistocene age, branches rather low on the tree, which would be of better agreement with an earlier age, as surmised by PETTER & HOWELL (1987). The skulls from Halmyropotamos and ravin X look misplaced, but have a narrow P4, like *Homotherium*, which forms the last group. It consists of the six highest branches, which have been referred to as many species. Better estimates of intra-specific variability are needed before this can be accepted.

Acknowledgements

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Appendix

The 33 OTUs used in the cladistic analysis, roughly listed by age. The numbers refer to those of the matrix.

1	Bled Douarah	Late Miocene	*M. robinsoni*	KURTÉN, 1976
2	Los Valles	Late Miocene	*M. alberdiae*	GINSBURG et al., 1981
3	Can Llobat, Santiga	Late Miocene	*M. cf. aphanistus*	BEAUMONT & CRUSAFONT 1982
4	Charmoille	Late Miocene	*M. aphanistus*	BEAUMONT, 1975
5	Eppelsheim	Late Miocene	*M. aphanistus*	BEAUMONT, 1975, 1987
6	Akçaköy	Late Miocene	*M. pseudaeluroides*	SCHMIDT-KITTLER, 1976
7	Montredon	Late Miocene	*M. cf. aphanistus*	BEAUMONT, 1988
8	Kemiklitepe D	Late Miocene	*M. aphanistus*	BONIS, 1994
9	Mahmutgazi	Late Miocene	*M. aphanistus*	SCHMIDT-KITTLER, 1976
10	Küçükyozgat	Late Miocene	*M. romeri*	SENYÜREK, 1957
11	Vathylakkos	Late Miocene	*M. giganteus*	KOUFOS, 2000
12	Grebeniki	Late Miocene	*Pogonodon copei*	PAVLOW, 1914
13	Kemiklitepe A-B	Late Miocene	*M. giganteus*	this paper
14	Taraklia	Late Miocene	*M. aphanistus taracliensis*	RIABININ, 1936
15	Samos	Late Miocene	*M. giganteus*	BEAUMONT, 1975
16	Pavlodar	Late Miocene	*M. irtyshensis*	ORLOV, 1936
17	Halmyropotamos	Late Miocene	*M. aphanistus*	MELENTIS, 1967
18	MN 12 / 13, Spain	Late Miocene	*M. giganteus*	MORALES & SORIA, 1979
19	Loc. 113	Late Miocene	*M. palanderi*	ZDANSKY, 1924
20	Kalmakpai	Late Miocene	*M. kurteni*	SOTNIKOVA, 1992
21	Loc.30	Late Miocene	*M. tingi*	ZDANSKY, 1924
22	Loc.30	Late Miocene	*M. palanderi*	ZDANSKY, 1924
23	Yushe, Shansi	Late Miocene	*M. tingi*	CHANG, 1957
24	Baode, Shansi	Late Miocene	*M. palanderi*	CHANG, 1957
25	Langebaanweg	Early Pliocene	*Machairodus sp.*	HENDEY, 1974
26	Aïn Brimba	Pliocene	*M. africanus*	PETTER & HOWELL, 1987
27	Hadar	Late Pliocene	*H. hadarense*	PETTER & HOWELL, 1988
28	Roccaneyra	Late Pliocene	*H. nestianus*	BONIS, 1976
29	Fan Tsun	Early Pleistocene ?	*Machairodus sp.*	PETTER & HOWELL, 1987
30	Nihowan II	Early Pleistocene	*M. nihowanensis*	TEILHARD & PIVETEAU, 1930
31	Senèze	Early Pleistocene	*H. crenatidens*	BALLÉSIO, 1963
32	Zhou Kou Dian	Mid. Pleistocene	*M. ultimus*	TEILHARD, 1939
33	Verona	Mid. Pleistocene	*H. moravicum*	BONIS, 1984

Appendix (Cont.)

List and states of the 22 characters

metric characters

#	character	0	1	2	3	mean	s
0	W C> / L C>	very thick	thick	thin	very thin	0.432	0.056
1	L P3 / L P4	P3 very long	P3 long	P3 short	P3 very short	0.479	0.152
2	W P4 / L P4	P4 very thick	P4 thick	P4 thin	P4 very thin	0.372	0.07
3	L p3 / L p4	p3 very long	p3 long	p3 short	p3 very short	0.673	0.137
4	L p4	p4 very long	p4 long	p4 short	p4 very short	24.8	3.3
5	LC< / Lm1	C< very short	C< short	C< long	C< very long	0.568	0.074

non-metric characters

#	character	0	1	2
6	axis of C root / orbit	anterior	tangential	through orbit
7	ant. border orbit / P4	rear of P4	more anterior	very anterior
8	zygomatic arch	weak	strong	very strong
9	curvature zygomatic arch	weak	strong	very strong
10	glenoid fossa / alveolar line	much higher	higher	same level
11	glenoid fossa	oblique	transversal	
12	mastoid process	short	medium	long
13	alisphenoid canal	present	vestigial	absent
14	condylar / post. lacerius foramina	separate	merging	fused
15	posterior part of P3	broad	narrow	
16	preparastyle on P4	absent	present	
17	protocone of P4	present	reduced	absent
18	size of M1	small	very small	
19	distance from /c to sagittal plane	< diameter C	± diameter C	> diameter C
20	anterior cuspid of p4	weak	moderate	large
21	talonid of m1	present	absent	

Appendix (Cont.)

The matrix used in the cladistic analysis

	0	1 0	2 0
Outg1	0001?3??00	0?000?0000	00
Outg2	0001?3??00	0?000?0000	00
1	0??13?????	??????????	?0
2	0??032????	?????0??0	??
3	0???2?????	?????0100?	0?
4	0??11?????	??????????	00
5	???113????	?????000?0	10
6	300?2?12??	?????0000?	00
7	1?1123????	?????010?0	00
8	210122??0?	??100?000?	?0
9	?1111?????	?????11??	?0
10	2??111????	0????111?2	10
11	212?0122??	?????0111?	11
12	?1?????200	0?1???11??	??
13	1121?2211	011100?1?2	1?
14	?1120?0110	1?1???11?2	21
15	???101????	?????????2	20
16	???101????	??????????	1?
17	212????1??	111??012??	??
18	???110????	?????011??	1?
19	?11210011?	011??11202	11
20	2112112100	112?011112	11
21	2??20?????	?????112?2	2?
22	312???21??	?????1121?	??
23	?1110?2???	?????????2	??
24	311???2110	011??1?21?	??
25	122???????	?????1111?	?1
26	222???1???	1?2???????	??
27	133?1?1111	102?11?21?	??
28	1333301012	2122110212	01
29	111???2111	2?1??11??	??
30	23???210??	?????1021?	??
31	2??32?0122	10220?212	11
32	233????112	201?211211	01
33	???2?2????	??????12??	0?