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

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Abstract: A skull and associated mandible from the upper level of Kemiklitepe in Turkey 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 *Homootherium*.

Zusammenfassung: Ein Schädel und der dazu gehörende Unterkiefer aus der Oberschicht von Kemiklitepe in der Türkei gehören zu den vollständigsten bekannten Exemplaren von *Machairodus*.

Sie erweisen sich als bedeutend höher entwickelt als die Exemplare aus der unteren Schicht. Die kladistische Analyse dieser Gattung lässt keine gut bestimmte Kladen erkennen ; sie weist viel mehr auf ein allmähliches Erwerben der Schädel- und Zahnspezialisierungen hin, die *Homootherium* kennzeichnen.

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 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; uppercase 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 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.2A) 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.2B, 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 on 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 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 on 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 from 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 precisely given. 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.3A). 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 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.3B), increase in size from i1 to i3, and diverge upwards in front view. Their morphology is obscured by wear and imperfect preservation.

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

Maximum width over orbits = 115

Minimum post-orbital width = 66

Width of brain-case = 79

From I3 to posterior border of glenoid = 203

Length condylo-I3 = 277

From orbit to front of crown base of C = 107

Length of mandibular diastema = ca. 32

Depth of corpus below diastema = 38.2

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 young 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 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 Greece), 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 skull. 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 not deformed 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 *Homootherium*, 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 *Homootherium*, which form 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.

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Captions to Figures

Fig.1. The skull of *Machairodus giganteus* from Kemiklitepe UEK-124. A: lateral view; B: upper view. Scale = 10 cm.

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.3. Mandible UEK-124. A: lateral view; B: dorsal view. Scale = 5 cm.

Fig.4. The shortest tree.

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

List and states of the 22 characters

| metric characters | | 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 | | 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 | |

The matrix used in the cladistic analysis

| | 0 | 1 | 2 |
|-------|-------------|-------------|----|
| 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?????? | ?????111?? | ?0 |
| 10 | 2??111????? | 0?????111?2 | 10 |
| 11 | 212?0122?? | ?????0111? | 11 |
| 12 | ?1?????200 | 0?1????11?? | ?? |
| 13 | 11211?2211 | 011100?1?2 | 1? |
| 14 | ?1120?0110 | 1?1????11?2 | 21 |
| 15 | ???101????? | ??????????? | 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???? | ??????????? | ?? |
| 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??111?? | ?? |
| 30 | 23????210?? | ?????1021? | ?? |
| 31 | 2??32?0122 | 102201?212 | 11 |
| 32 | 233????112 | 201?211211 | 01 |
| 33 | ??2?2?????? | ??????12?? | 0? |