

# A new species of *Machairodus* from the late Miocene Kalmakpai locality in eastern Kazakhstan (USSR)

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A new species, *Machairodus kurteni* is described from the late Miocene locality Kalmakpai in eastern Kazakhstan (USSR). Other Vallesian and Turolian species of *Machairodus* in the USSR are discussed. Evolutionary changes appear to have taken place in the genus *Machairodus* during the Turolian. In the morphology of the dentition, *M. kurteni* is intermediate between *Machairodus* and *Homotherium*.

## 1. Introduction

The fossil locality of Kalmakpai (Fig. 1) was discovered by a geologist, B. A. Borisov in 1960. It is located in the Zaisan depression, 160 km SE of the town Zaisan in Kazakhstan, USSR. The Karabulak suite on the right bank of the Kalmakpai River is lithologically subdivided into two parts: the upper, reddish-brown part, 30 m thick, and the lower, yellowish grey one, 29.4 m thick. The mammalian fauna of Kalmakpai has been found in the upper part (Borisov 1964).

Abundant fossil material has been obtained from the locality during excavations carried out by the Palaeontological Institute (PIN) of the USSR Academy of Sciences in 1961–1967. The Kalmakpai fauna has been tentatively dated to the Pliocene (Ruscinian) on the basis of the geological position of the Karabulak Fm. in the Neogene sequence in the Zaisan depression. The Kalmakpai locality is currently known to contain

the following mammal taxa: *Vormela* sp., *Martes* sp., *Plesiogulo crassa* Teilhard, *Adcrocuta eximia* (Roth & Wagner), *Hyaenictitherium hyaenoides orlovi* Semenov, *Machairodus kurteni* Sotnikova, *Hipparion hippidioides* Sefve, *H. elegans* Gromova, *Chilotherium* sp., *Sinootherium zaisanensis* Bayshashov, *Cervavitus* sp., *Procapreolus* sp., *Samotherium* sp., *Paleotragus* (*Yuorlovia*) *asiaticus* Godina, *Tragocerus* sp., and *Gazella dorcadoides* Schl. (Dmitrieva 1977, Zhegallo 1966, 1978, Godina 1979, Bayshashov 1986, Semenov 1989).

An analysis of the Kalmakpai fauna indicates that the complex is largely dominated by Turolian forms. Most of the mammalian genera reported from Kalmakpai have a wide stratigraphic range limited by the end of the Turolian. These include *Chilotherium*, *Sinootherium*, *Tragocerus*, *Adcrocuta* and *Hyaenictitherium*. The evolutionary level of the genera *Hyaenictitherium* and *Machairodus* places the Kalmakpai fauna in the late Turolian.

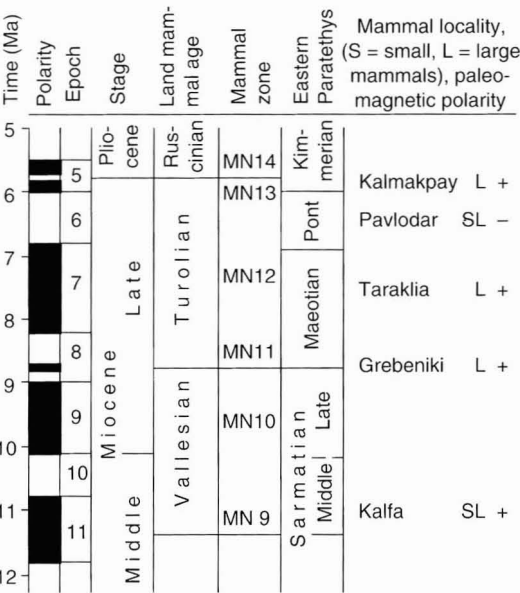


Fig. 1. The stratigraphic and paleomagnetic position of miocene mammal localities in the USSR (Pevzner & Vangengeim 1990).

In the Kalmakpai section the bone-bearing beds are confined to a zone of normal magnetization (Jakhimovich, pers. comm.) and correlates with the lower part of the palaeomagnetic epoch 5. Consequently, the Kalmakpai fauna may be allocated to the zone MN 13.

The Kalmakpai Carnivora have not been studied in detail except *Hyaenictitherium hyaenoides orlovi*, described by Semenov (1989). Among the material obtained by excavation at

Kalmakpai, is a *Machairodus* skull, excellently preserved, and three lower jaws. This material is described as a new species of *Machairodus*.

2. Systematic description

Order CARNIVORA Bowdich, 1821  
Family FELIDAE Gray, 1821  
Subfamily MACHAIRODONTINAE Gill, 1872  
Genus *Machairodus* Kaup, 1833

*Machairodus kurteni* sp. n.<sup>1</sup>

Holotype: Skull with I<sup>1</sup>–I<sup>3</sup>, C<sup>s</sup>, P<sup>2</sup>–M<sup>1</sup> (nasal, frontal and bullae regions crushed), PIN 2433/287.

Other material: Pair of mandibles with I<sub>1-3</sub>, C<sub>i</sub>, P<sub>3-4</sub>, M<sub>i</sub>, broken behind the tooth row, PIN 2433/524; right mandible with C<sub>i</sub>, P<sub>4</sub>–M<sub>i</sub>, broken behind the tooth row, PIN 2433/287.

Type locality: Kalmakpai, USSR, Kazakhstan, Zaisan depression, Karabulak Fm. (upper part).  
Age: Turolian (Late Miocene), MN 13.

Diagnosis: A large *Machairodus*. P<sup>2</sup> present. Diastema I<sup>3</sup>–C<sup>s</sup> small. The incisors are close to each other and form an arc. P<sup>4</sup> narrow. Lower canine

<sup>1</sup> The species is named in honour of Dr. Björn Kurtén, who has made a significant contribution to the study of fossil Carnivora.

Table 1. Measurements (mm) of *Machairodus* skulls.

	<i>Machairodus kurteni</i> sp. n.	<i>M. giganteus taraciensis</i> Riab.	<i>M. palanderi</i> Zd. (Chang 1957)
Length of skull	308.0	310.5	363.0 <sup>a</sup>
Condylobasal length	271.0	275.0	327.0 <sup>a</sup>
Basal length	251.0	255.0	297 <sup>a</sup>
Palatal length	133.0	140.0	158.0, 159.0 <sup>a</sup>
Zygomatic width	165.0	168.0	204 <sup>a</sup>
Rostral width across C <sup>s</sup> –C <sup>s</sup>	66.2	67.8	—
Width across P <sup>4</sup> –P <sup>4</sup>	101.4	110.0	113.0
Width across P <sup>2</sup> –P <sup>2</sup>	61.4	—	70.0
Postorbital width	88.0	96.0	114.0 <sup>a</sup>
Condylar width	53.8	62.7	72.0 <sup>a</sup>

<sup>a</sup> Measurements made on Plate I fig. 1 of Chang 1957.

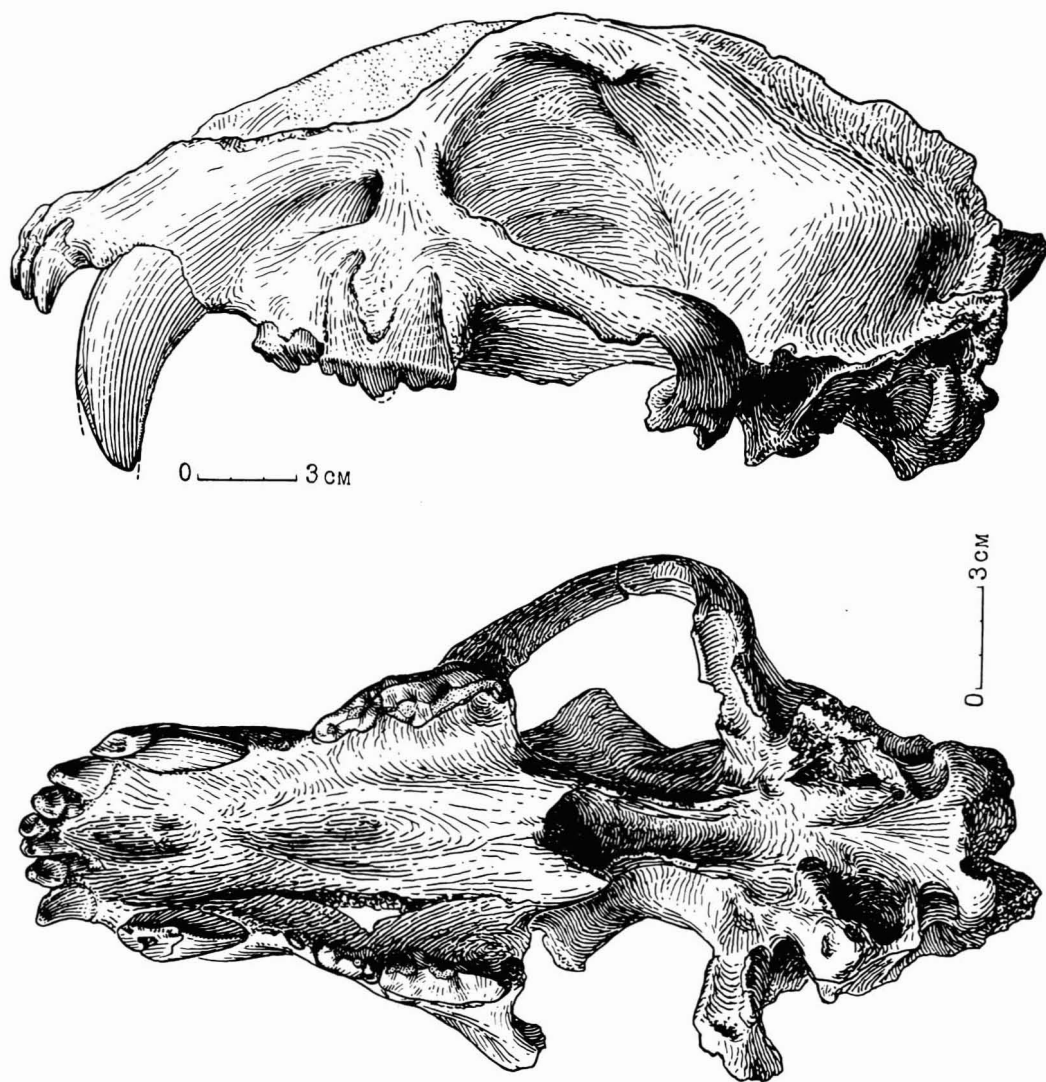


Fig. 2. *Machairodus kurteni*, Kalmakpai (PIN-2433/287), skull, ventral and lateral view.

closer to the incisor row than in other species of *Machairodus*. Lower premolars shorter than in other *Machairodus* species. Metaconid-talonid complex absent from lower carnassial.

#### Description

A large *Machairodus* (Tables 1–3).

Skull (Fig. 2) about the size of that in an African lion. The skull height in the bullae region is half as great as its basal length. Pre-maxillary massive, incisor row slightly protruding in relation to canine. Diastema  $I^3$ – $C^s$  small (5.5

mm). Infraorbital foramen above the paracone of  $P^4$  large, vertical diameter 15 mm. Postorbital processes of frontal massive and short. The bullae were presumably large, with an average length of about 39 mm. External auditory meatus rounded and large, located between mastoid process and glenoid fossa. Mastoid process well-developed, its lower dorsal edge nearly reaching the level of the glenoid fossa. Sagittal crest high. Occipital crest also well developed.

Teeth possibly initially serrated, but serration preserved only on upper and lower canines. Inci-

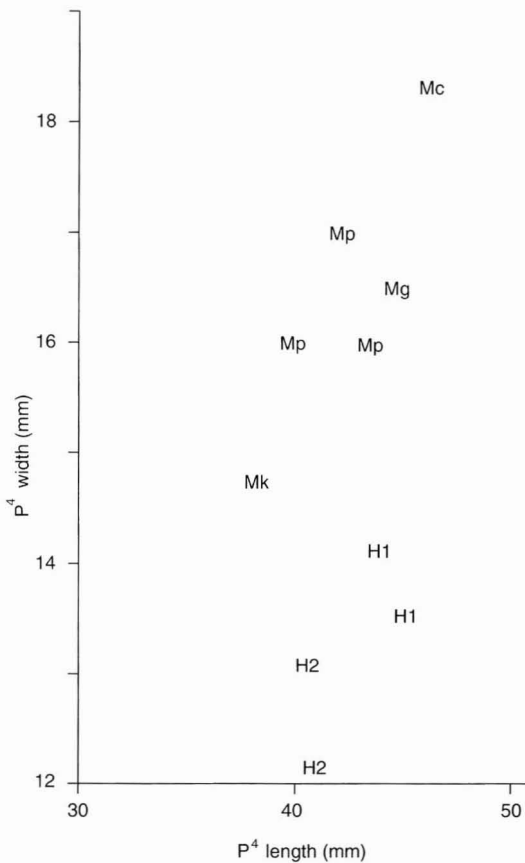


Fig. 3. Relationship between width and length of  $P^4$  in *Machairodus* and *Homotherium*. — Mc: *Machairodus copei* (Grebeniki), Mp: *Machairodus palanderi* (China,) Mg: *Machairodus giganteus* (Taraklia), Mk: *Machairodus kurteni* (Kalmakpai), H1: *Homotherium* (Upper Valdarno and Olivola), H2: *Homotherium* (Kuruksay).

sors large, set in an arc with width ( $I^3-I^3$ ) 49 mm, and closer to canine than in other species of *Machairodus*. The third incisor in close contact with  $I^2$ . The upper canines broken and worn, possibly during the animal's life, large, with serrated anterior and posterior edges. The diastema between the canine and  $P^3$  is 17 mm. Left  $P^2$  present, single-rooted and unicusped, possibly non-functional, not worn. Diastema  $C^s-P^2$  is 9.5 mm,  $P^2-P^3$  is 3.5 mm.  $P^3$  with four cusps. Anterior cusp large and set well apart from the main one. There are two distinct posterior cusps on  $P^3$  behind the main one. Anterior width of  $P^3$  7.7 mm,

posterior width 9.4 mm. The blade of  $P^4$  (carnassial) consists of four cusps, preparastyle present, protocone weak with a flat tip, inner root closely pressed to the other roots.  $P^4$  in *M. kurteni* is proportionally narrower than that in other species of the genus *Machairodus* (Fig. 3).  $M^1$  small, single-rooted, situated at right angles to  $P^4$ .

Mandible (Fig. 4) high (symphyseal height 72.5 mm). Incisors and canine situated high above the level of the cheek teeth. Incisors close to each other, their tips directed upward to form a single contact system with the lower canine (Fig. 5A). In *Homotherium* the incisors are morphologically similar. Early Turolian *Machairodus*, i.e. *M. giganteus* (Wagner) from Taraklia (Fig. 5B), has a broader symphysis, incisors set in a broad arc, their tips directed forward, the canine separated from the incisor row by a small diastema. There are two large mental foramina, one under the first root of  $P_3$  the other under the middle part of the diastema  $C_1-P_3$ . Mandible flange for protection of upper canine sabre present and bounded by distinct mental crests trending along the dorsal and posterior border of the flange. Masseteric fossa relatively deep, its anterior margin reaching the level of the posterior root of  $M_1$ .  $P_3$  four-cusped, the fourth posterior cusp weak, formed by the basal cingulum. Blade of  $P_4$  is also four-cusped. Anterior cusp in close contact with the main one, with a slightly backward inclination; two posterior cusps also inclined. Anterior edge

Table 2. Measurements (mm) of upper dentition of *Machairodus kurteni* (PIN 2433-287).

	Right		Left	
	length	width	length	width
$I^1$	9.0	5.6	8.9	6.0
$I^2$	10.5	8.0	11.0	—
$I^3$	14.1	11.5	14.5	—
$C^s$	—	13.0	33.3	13.0
$P^2$	5.5	3.0	absent	
$P^3$	—	9.2	21.0	9.1
$P^4$	38.2	14.8	38.5	—
$M^1$	—	—	5.0	7.5
$I^3-M^1$	134.1		131.0	
$C^s-M^1$	—		110.0	
$P^3-M^1$	61.0		59.2	
Diastema $I^3-C^s$	—		5.5	
Diastema $C^s-P^3$	17.1		17.0	

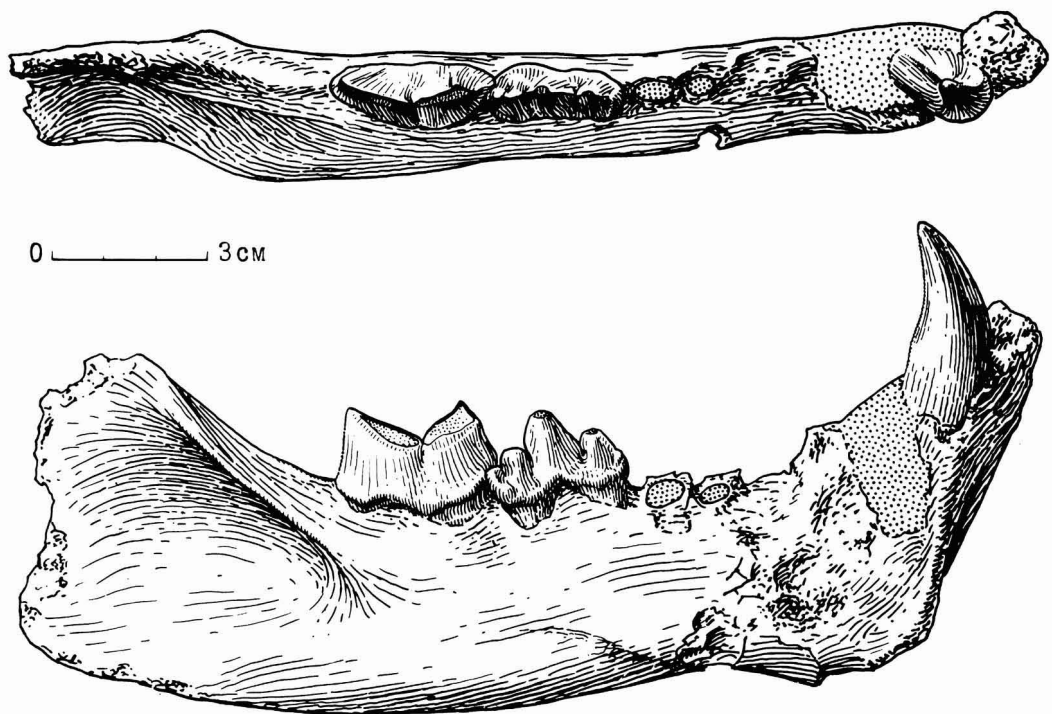


Fig. 4. *Machairodus kurteni*, Kalmakpai (PIN-2433/287), right mandible, external and dorsal views.

of  $M_1$  overlapping posterior edge of  $P_4$  in all the three specimens. Similar (though more pronounced) overlapping occurs in *Homotherium*. In

other species of *Machairodus*,  $P_4$  and  $M_1$  overlap to a lesser degree.  $M_1$  is relatively narrow, no traces of metaconid or talonid present.

Table 3. Measurements of lower dentition and mandible of *Machairodus kurteni*.

	PIN 2433-287		PIN 2433-524			
	length	width	left length	left width	right length	right width
$I_1$	—	—	7.3	—	7.3	3.6
$I_2$	—	—	8.3	6.1	8.2	5.8
$I_3$	—	—	10.1	8.5	10.4	8.6
$C_1$	16.2	11.6	—	—	15.2	12.2
$P_3$	17.5 al.	—	17.0	—	17.5	7.9
$P_4$	26.8	11.5	25.0	—	25.5	11.1
$M_1$	31.2	13.0	31.5	14.5	31.3	13.5
$C_1-M_1$	128.2	—	136.0	—	135.0	—
$P_3-P_4$	46.1	—	43.5	—	42.0	—
$P_3-M_1$	76.4	—	73.2	—	73.0	—
Diastema $C_1-P_3$	37.7	—	—	—	46.9	—
Ramus depth behind $M_1$	40.5	—	46.1	—	45.0	—
before $P_3$	39.0	—	41.1	—	41.5	—

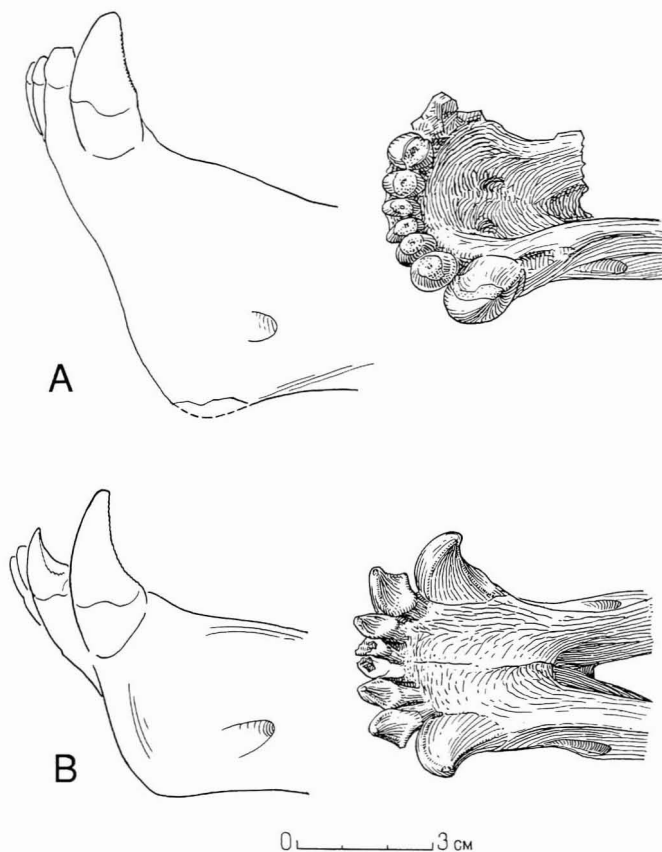


Fig. 5. *Machairodus* mandibles, anterior part in occlusal view. — A. *Machairodus kurteni*, Kalmakpai (PIN-2433/524). — B. *Machairodus giganteus tarakliensis*, Taraklia (PIN-1256/3084)

### 3. Discussion

*Machairodus* appears in Eurasia at the end of the middle Miocene and is reliably traced up to the close of the late Miocene. Remains of machairodonts are very rare in the early Pliocene. At the end of the early Pliocene a new, scimitar-toothed, felid, *Homotherium*, appears in Africa and Eurasia.

The earliest *Machairodus* have been reported from North Africa and Asia. They are known from assemblages of an age transitional between the Astaracian and Vallesian or early Vallesian and include *Machairodus robinsoni* Kurtén from the Beglia Formation of Bled Douarah, Tunisia, and *M. pseudailuroides* Schmidt-Kittler from the locality Yeni Eskihsar in Turkey (Kurtén 1976, Schmidt-Kittler 1976). The most primitive forms were referred to the subgenus *Miomachairodus* Schmidt-Kittler, while the later species from the European Vallesian were grouped in the subgenus *Machairodus* (Beaumont 1978).

The specimens referred to *Machairodus* from the Vallesian of Europe form a relatively homogeneous group, which is currently treated as a single species, *Machairodus* (*Machairodus*) *aphanistus* (Kaup). Among the main characteristics of this group are: small incisors in the lower jaw forming a straight row, a large lower canine, a small diastema between  $C_1$  and  $P_3$ , large premolars with a complete set of additional cusps, a lower carnassial with a well-developed metaconid-talonid complex and a strong protoconid. The lower jaw is massive and high, while the mandibular flange is practically undeveloped. The upper carnassial has a distinct protocone. A preparastyle is present on  $P^4$ . All the teeth were probably serrated.

In Western Europe *M. aphanistus* is reported from such localities as Eppelsheim, Charmoille, Montredon, Soblay and Zillingdorf (Beaumont 1975).

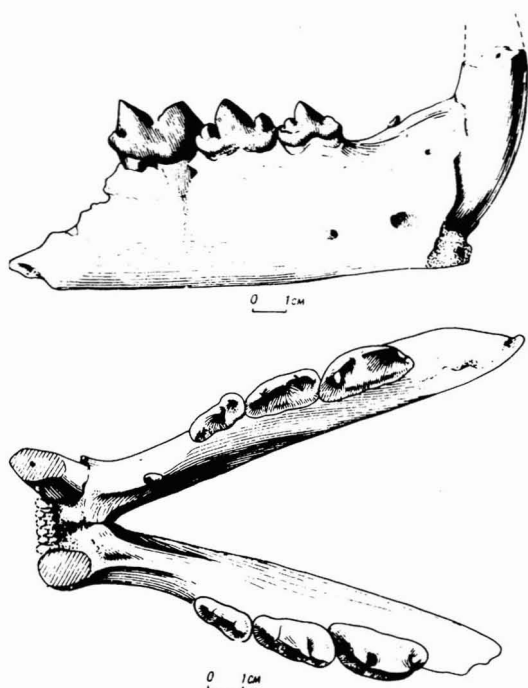


Fig. 6. *Machairodus laskarevi*, Kalfa (TGPI-1/2257), mandible, external and occlusal view (Lungu 1978).

In the USSR, this group of sabre-tooths includes a *Machairodus* from the Vallesian locality Kalfa in Moldavia. The combined geological, palaeontological and palaeomagnetic data allow us to date the Kalfa fauna to the upper part of zone MN 9 (Lungu 1978). Lungu described a new species, *Machairodus laskarevi*, on the basis of a well-preserved pair of mandibles from Kalfa (Fig. 6). This form shows all the characters typical of *M. aphanistus*: flange virtually absent, lower jaw high, incisors small, canine large and  $M_1$  with a well-developed metaconid-talonid complex.

The measurements of *M. laskarevi* are similar to those of *M. aphanistus* from Eppelsheim. The length of  $P_3$ ,  $P_4$  and  $M_1$  are 19, 25 and 29 mm, respectively, while the corresponding measurements reported for the *Machairodus* of Eppelsheim are 21, 27.4 and 30.2 mm. However,  $P_2$  is generally absent from the *M. aphanistus* mandible. In *M. laskarevi* it occurs in the right branch of the mandible.  $P_2$  is small, unicuspid and single-rooted, and is located in the middle of the diastema

between  $C_1$  and  $P_3$ . The presence of  $P_2$  in the Machairodontinae is regarded as a primitive character. The Kalfa *Machairodus* may confidently be considered the earliest form of the Vallesian *Machairodus* group in Europe.

Turolian species of *Machairodus* are referred to the subgenus *Amphimachairodus* Kretzoi (Beaumont 1978). The latter includes the majority of sabre-toothed felids reported from the Late Miocene of Eurasia. The Turolian sabre-tooths from Eurasia are characterized by curved, large and strong upper sabres, a more prominent mandibular flange than in *Machairodus aphanistus*, all teeth serrated, large incisors set in a weak arc,  $P^1$  with a weaker and lingually less protruding protocone than in *Machairodus aphanistus*, the lower carnassial with weak or absent metaconid-talonid complex. The above characters allow us to differentiate two distinct groups within the Vallesian and Turolian species of *Machairodus*.

Beaumont (1975) suggested that the Turolian sabre-toothed cats belong to the species *Machairodus giganteus* (= *M. leoninus*). *Machairodus giganteus* (Wagner) was described from the Turolian fauna of Pikermi (Greece), and a similar form has been reported from the same stratigraphic level of Samos. Beaumont (1975) also treated the following as synonyms of *M. giganteus*: *Pogonodon copei* Pavlov and *Machairodus aphanistus taracensis* Riabinin from Moldavia, USSR, and *Machairodus palanderi* Zd. and possibly *M. tingii* Zd. from China.

The above forms were referred to a single species on the basis of the characters shared by all the Turolian sabre-tooths. However, Beaumont (1975) indicated a high degree of variability in some of the characters used for the subdivision of machairodonts, e.g. the height of the mandibular symphysis region, the extent of the flange development, the length of the diastema between  $C_1$  and  $P_3$ , and the size of the third lower premolar.

Hence, the attempts to recognize evolutionary changes in the Turolian *Machairodus* of Eurasia were unsuccessful. This was partially due to the incompleteness of the fossil material available and to the lack of detailed stratigraphic data, particularly for the Asian finds. For instance, in Western Europe the most complete material of sabre-toothed cats is known from Samos and Pikermi, but it consists largely of lower jaw re-



mains. The fossils from other localities are even more fragmentary. Although the material of Asian machairodonts is somewhat richer, the North Chinese localities yielding fossils have not been dated with sufficient accuracy. The fauna recovered from these localities is dated to the latest Miocene (Baodean), which corresponds to the Turolian *sensu lato* (Li et al. 1984).

The richest material of sabre-toothed cats from a variety of Turolian levels is currently available in the USSR. *Machairodus* has been reported from the localities Grebeniki (Ukraine), Taraklia (Moldavia), and Kalmakpai (Kazakhstan). The stratigraphic age of the above localities was tentatively dated as late Vallesian to early Turolian (Grebeniki) and the second half of the Turolian (Taraklia). The genus *Hipparion* provides detailed knowledge of the faunal age. The presence of *Hipparion giganteum* Gromova and *Hipparion verae* Gabunia in Grebeniki, and the occurrence of the more progressive *H. moldavicum* Gromova in Taraklia, allowed Gabunia (1986) to date the former fauna as earliest Turolian and the latter as Middle Turolian.

On the basis of the literature, Beaumont (1975, 1978) referred the *Machairodus* from Grebeniki and Taraklia to the subgenus *Amphimachairodus* Kretzoi and identified them as the species *Machairodus giganteus* (Wagner). A study of the *Machairodus* remains from these localities (*Pogonodon copei*<sup>1</sup> and *Machairodus aphanistus taracliensis*<sup>2</sup>) shows that both forms have typical features of the genus *Machairodus*, but that they must be attributed to different species.

Comparison of the upper teeth of these specimens yields the best information. The teeth of *Machairodus copei*, especially the premolars, have a more complicated structure than those of the other species of Turolian *Machairodus*. This sabre-tooth has the following characteristics: It is large, the third premolar has an extremely strong basal cingulum, which forms three transverse plaits on the anterior end of P<sup>3</sup> and a fifth

accessory cusp on its posterior end. The upper carnassial has an accessory cusp on the anterolabial side of the tooth in front of the preparastyle, and the protocone is better developed than in other Turolian *Machairodus* (Fig. 3).

The evolutionary changes traceable in the teeth of the Turolian *Machairodus* suggest that they may have evolved from forms with large, well developed premolars with complicated structures, towards forms with smaller and simpler premolars. The structure of the premolars makes it probable that *Machairodus copei* from Grebeniki represents the earliest stage of Turolian *Machairodus* in Eurasia.

The *Machairodus* from Taraklia is similar to *Machairodus giganteus* from Samos and Pikermi. It differs from the latter only in the lack of a distinct metaconid and talonid on the lower carnassial. This *Machairodus* may be regarded as a separate subspecies, *M. giganteus taracliensis* Riabinin.

*Machairodus palanderi* and *Machairodus tingii* from China were referred by Beaumont (1975) to the species *M. giganteus*. Analysis of the material showed that the majority of the specimens described by Zdansky (1924) and Chang (1957) from the late Miocene of China have many features in common with *Machairodus* from Taraklia. Their dentition is characterized by incisors set in a weakly-rounded arc and slightly separated from each other. The upper canines are variable in size and separated from the incisors by a relatively large diastema. The second upper premolar is small and single-rooted, if present. The carnassial has a relatively well developed protocone (Fig. 4) and double parastyle. If present, the metaconid-talonid complex on the lower carnassial is weak. The lower premolars are large in comparison with M<sub>1</sub>.

When I compared *Machairodus kurteni* with machairodonts of the *giganteus* group, especially with *Machairodus* from Taraklia and *Machairodus irtyschensis* Orlov (1936), it became clear that it has a different arrangement of the lower incisors (Fig. 5A). In addition to the smaller premolar length compared with that of M<sub>1</sub> and the reduction of the protocone on P<sup>4</sup>, the complete loss of the metaconid and talonid on the lower carnassial are characteristic. Among the scimitar-tooths a similar structure of the incisor region of

<sup>1</sup> In addition to the skull described by Pavlov (1914), another better preserved specimen from Grebeniki was studied by the author in the Odessa State University collection (OGU-2638).

<sup>2</sup> Riabinin (1929) examined the unprepared skull with jaw. The present author analysed this material after the cranium was separated from the mandible.



the mandible is seen in the Pliocene-Pleistocene genus *Homotherium*, e.g. in *Homotherium crenatidens* (Fabrini) from the Kuruksay locality in Tadjikistan, described by Sotnikova (1989: table 8, fig. 1). All the peculiarities of the teeth of *Machairodus kurteni* are present in more specialized form in the Pliocene scimitar cats. *Homotherium* always lacks the  $P^2$ ,  $P^3$  is small and single-rooted and  $P_3$  and  $P_4$  are small compared to  $M_1$ . The lower carnassial lacks the metaconid and talonid, the protocone of the upper carnassial is weakly developed and the preparastyle is small or lacking.

Kurtén & Anderson (1980) suggested that *Homotherium* might be derived from *Machairodus*. Among all the known species of *Machairodus*, *M. kurteni* is most similar to *Homotherium*. It is a typical representative of the genus *Machairodus*, but differs from the other Turolian sabre-toothed cats in its morphology, which shows an evolutionary trend leading to *Homotherium*. In the *Machairodus* lineage, the sabre-toothed cat from Kalmakpai appears to represent the latest evolutionary stage of this genus.

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