Rivista Italiana di Paleontologia e Stratigrafia	volume 113	no. 1	pp. 67-77	March 2007

AMPHIMACHAIRODUS (FELIDAE, MAMMALIA) FROM SAHABI (LATEST MIOCENE-EARLIEST PLIOCENE, LIBYA), WITH A REVIEW OF AFRICAN MIOCENE MACHAIRODONTINAE

RAFFAELE SARDELLA[1] & LARS WERDELIN[2]

Received: May 24, 2006; accepted: January 10, 2007

Key words: Africa, Libya, Carnivora, Felidae Machairodontinae, Miocene, Pliocene.

Abstract. We describe and illustrate a partial skull and mandible of a large sabertooth cat from Sahabi, Libya, and refer it to *Amphimachairodus* aff. *A. kabir.* A review shows the Miocene Machairodontinae from Africa to be a heterogeneous assemblage, with both small and large forms spanning the entire Late Miocene. The Sahabi form belongs to the group of larger sized taxa, along with *A. kabir* from Chad and some previously undescribed specimens from the Wembere-Manonga Formation, Tanzania. Both the Sahabi and Chad specimens have relatively slender lower carnassials, similarly to *Homotherium*, though derived features of the skull and mandible suggest that they are not in the direct ancestry of that genus.

Riassunto. Un cranio e una mandibola di una grande tigre dai denti a sciabola provenienti da Sahabi (Libia) sono qui descritti, illustrati e attribuiti ad *Amphimachairodus* aff. *A. kabir.* La revisione dei macairodontini africani del Miocene mostra come questi costituissero un insieme eterogeneo, comprendente forme sia di piccole sia di grandi dimensioni distribuite per tutto il Miocene superiore. La forma di Sahabi appartiene al gruppo dei taxa più grandi, insieme a *A. kabir* del Chad e ad alcuni esemplari mai descritti in precedenza provenienti dalla Formazione di Wembere-Manonga, in Tanzania. L'esemplare di Sahabi e quello del Chad hanno in comune la presenza di ferini inferiori secodonti, come si osserva in *Homotherium*, ma i caratteri derivati di cranio e mandibola suggeriscono che questi non possono essere considerati come i diretti progenitori di questo genere.

Introduction

The latest Miocene vertebrate fauna from Sahabi (Cirenaica, Libya) is a rich and diversified one. As recently emphasized by several authors (Geraads 1998; Bernor & Scott 2003), the Sahabi fauna includes a mixture of Eurasian and African vertebrates: elephantids, anthracotheres and hippos (Gaziry 1987a; 1987b; 1987c), suids (Cooke 1987), bovids (Lehmann & Thomas 1987), the short-necked giraffid *Samotherium* (Harris 1987), the rhinoceros *Diceros* (=*Ceratotherium*) *neumayri* (Heissig 1996), hipparions (Bernor & Scott 2003), several carnivores (Howell 1982; 1987; Rook & Martinez Navarro 2004), the rodent *Sayimys* (Munthe 1987; Agustì et al. 2000), and a large anatid (Ballmann 1987). As such, Sahabi is important for biogeographic reconstruction and paleoecologic comparisons (Bernor & Pavlakis 1987). Among the carnivore remains are a skull and mandible of a large-sized sabertoothed cat stored at the Paleontological Museum at "La Sapienza" University in Rome. These fossils are illustrated herein for the first time (Fig. 1) and described in relationship to other African Late Miocene Machairodontinae.

The earliest studies on the fossiliferous area of Qasr as-Sahabi (Libya) were carried out by the Italian geologist Ardito Desio, who led field activities in 1931-32. From 1934-39, further geological and palaeontological work was carried out by Carlo Petrocchi. At that time, part of the material was taken from Libya to Italy, where it was stored in different museums (Zoological Civic Museum and Paleontological Museum at "La Sapienza" University, both in Rome, and the Paleontological Museum of "Federico II", University of Naples). Petrocchi (1941; 1943; 1951) identified 62 fossiliferous localities. He mentioned the presence of a mastodon, a bovid, an anthracothere, and one skull and two mandibles of carnivores. He provided a description of the

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[1] Dipartimento di Scienze della Terra, Università di Roma La Sapienza, Piazzale Aldo Moro 5, I-00185 Roma, Italy.
E-mail: raffaele.sardella@uniroma1.it

[2] Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden. E-mail: werdelin@nrm.se

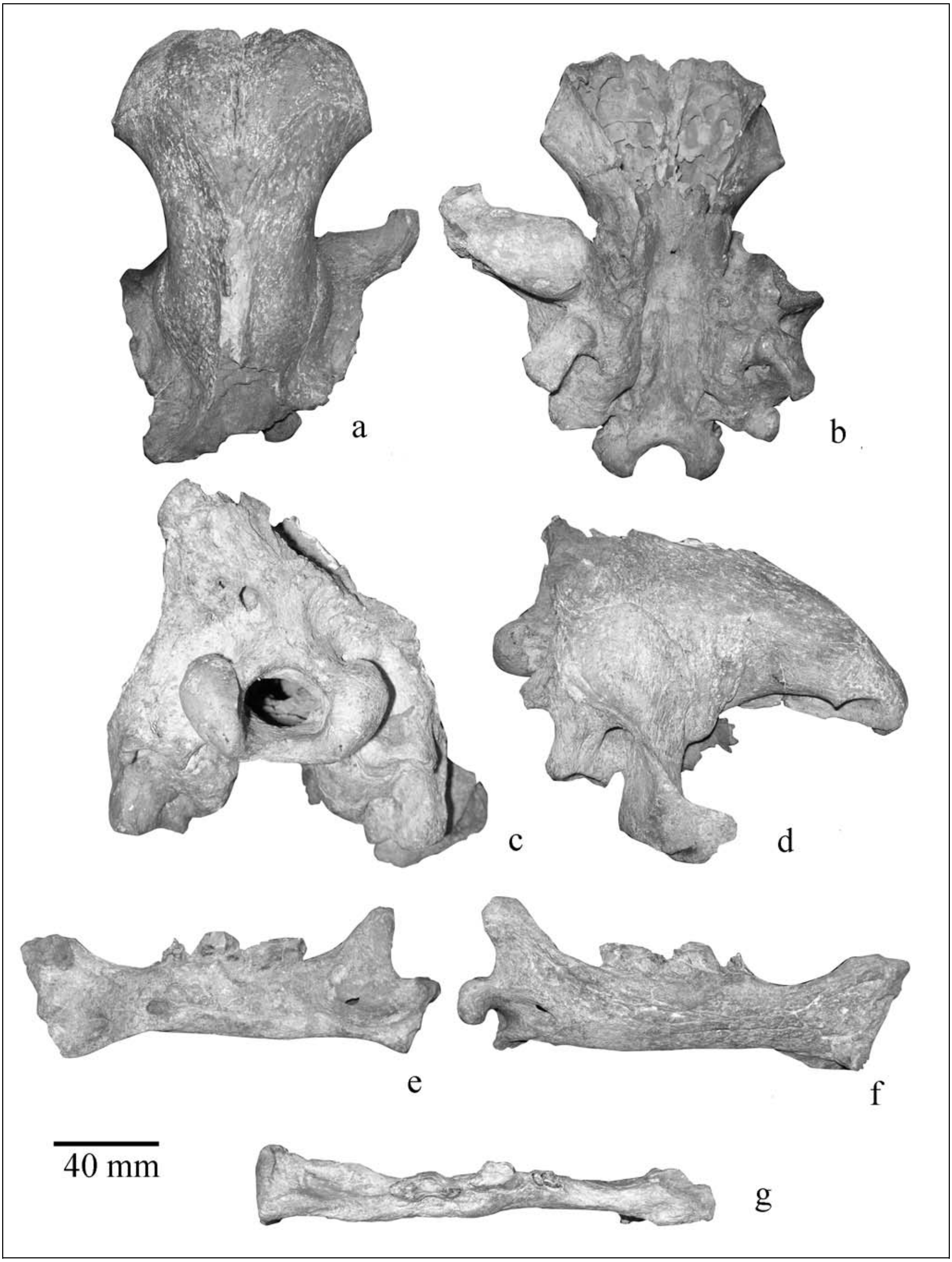

Fig. 1 - *Amphimachairodus* aff. *A. kabir* from Sahabi: skull in a) sagittal, b) palatal, c) occipital and d) lateral view; left mandible in e) buccal, f) lingual and g) occlusal view.

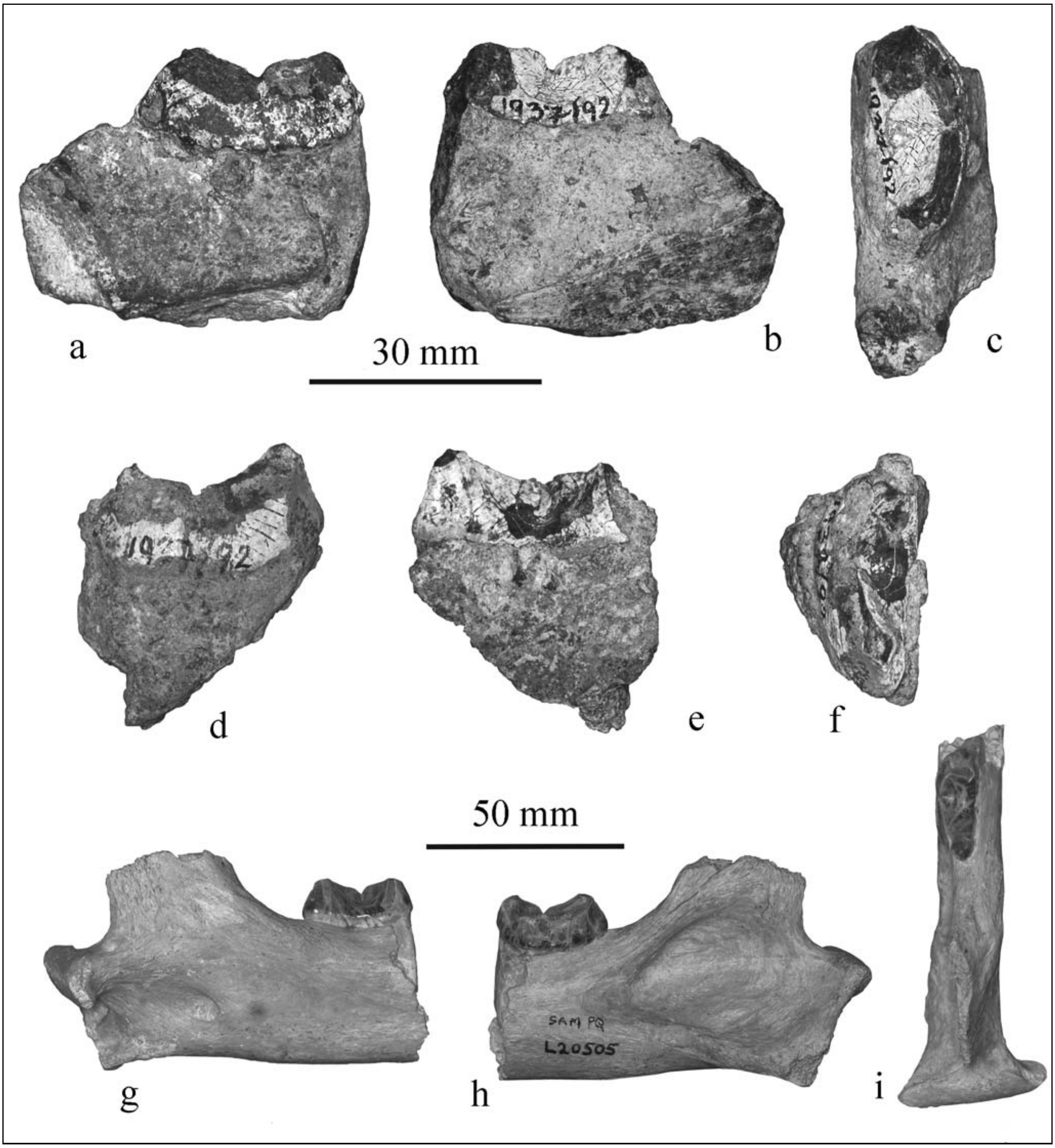

Fig. 2 - Lower right m1, WM 1937/92a, Wembere-Manonga Fm., Tanzania, in a) buccal, b) lingual, c) occlusal view; d-f: lower left m1, WM 1937/92b, Wembere-Manonga Fm., Tanzania, in d) buccal, e) lingual, f) occlusal view; g-i: left mandibular fragment, SAM-PQ L20505, Langebaanweg, South Africa, in g) lingual, h) buccal, i) occlusal view.

elephantid *Stegotetrabelodon syrticus* (see Ferretti et al. 2003 for a discussion), but no taxonomic consideration of the carnivore remains

In 1980, Esu & Kotsakis described one of the two carnivore mandibles and referred it to *Ictitherium arkesilai*, a new species of hyaenid. Werdelin & Solounias (1991) revised hyaenid systematics and reassigned the species to "*Hyaenictitherium*" *namaquensis*, otherwise known from South Africa (Stromer 1931; Hendey 1974) and Kenya (Morales et al. 2005). During the 1970 and 1980s further field campaigns organized by Boaz and El-Arnauti (International Sahabi Research Project) were carried out by an international team of geoscientists and 141 new fossiliferous localities were documented in the area (De Heinzelin & El-Arnauti 1987).

In his 1987 analysis of the Sahabi carnivores, Howell presented a synthetic description without illustrations of the skull and mandible of the Petrocchi collection. He referred them to *Machairodus* sp., together with a p3, a dP3 and a few postcranial bones recovered in the 1980s. In his PhD dissertation Sardella (1994) underlined the peculiar morphological features of the Sahabi machairodontine cat, suggesting that it might belong to a new species.

The taxonomy of Neogene machairodontine cats has been discussed in a series of recent papers (Antón et al. 2004; Geraads et al. 2004; Peigné et al. 2005; Sotnikova & Noskova unpublished). In particular, analysis of a rich sample of craniomandibular elements of *Machairodus aphanistus* from Batallones-1 (Spain) (Antón et al. 2004) shows that this species, which is the type species of the genus, differs markedly in morphology and adaptations from "*Machairodus*" *giganteus*. These authors suggest restricting the use of the genus *Machairodus* to the type species and thus "*M.*" *giganteus* can be placed the genus *Amphimachairodus* Kretzoi, 1929, as also suggested by Beaumont (1978).

African larger Machairodontinae

With the recent removal of *Afrosmilus* from the Felidae (Morales et al. 2001; Morlo et al. 2004), the fossil record of pre-Pliocene larger Machairodontinae (excluding *Dinofelis* and *Metailurus*) in Africa has become very limited. The oldest record is a left mandibular ramus and upper canine fragment from Bled Douarah in Tunisia (?Early Vallesian). These specimens were referred to *Machairodus robinsoni* by Kurtén (1976). This species is of uncertain affinities, though it is likely to be close to the coeval Eurasian form *M. aphanistus*.

A machairodont specimen, most recently referred to *M. aphanistus* (Geraads et al. 2002) is known from the Chorora Fm., Ethiopia (ca. 10.5 Ma). The specimen consists of the symphyseal region of a left mandibular ramus.

Petter (1994) referred an upper canine and right MT III from the Nkondo Fm. of the Albertine Rift, Uganda to *Homotherium* sp. The attribution is mainly based on the similarity between the MT III and that of *Homotherium* from Senèze (Ballesio 1963) and on the reported presence of *Homotherium* sp. at Langebaanweg (Hendey 1974).

Three lower carnassials of machairodonts are known from the Ibole Mb. of the Wembere-Manonga Formation, Tanzania (Harrison 1997; LW personal observations). Two of these, possibly belonging to the same individual, from Shoshamagai 2, are large (Fig. 2a-f), and the third, from Inolelo 1, is considerably smaller. Only the former two are considered herein, as the latter likely belongs to *Dinofelis* or a related taxon.

Werdelin (2003) described a new genus and species of machairodont, *Lokotunjailurus emageritus,* from the Nawata Fm., Lothagam, Kenya (ca. 7.5-6.5 Ma). This species is known from a partial skeleton and assorted other skeletal elements. It is quite distinct from other Machairodontinae known from Africa in its derived dentition and slender mandible.

Haile-Selassie (2001; Haile-Selassie et al. 2004) described as *Machaidorus* sp. an extensive material from the Late Miocene Adu-Asa Fm., Middle Awash, Ethiopia (dated 5.8-5.2 Ma). This material includes both craniodental and postcranial elements, but is quite fragmentary, especially the craniodental material.

Recently, Peigné et al. (2005) described machairodont specimens from Toros-Menalla, Chad (Late Miocene, about the same age as Lothagam), as the new species *Machairodus kabir.* This species is large and has a robust mandible, quite different from that of *Lokotunjailurus*, but similar to the material from Sahabi described herein.

Finally, Hendey (1974) described as *Machairodus* sp. a considerable material from Langebaanweg, South Africa (earliest Pliocene) (Fig. 2g-i). This material resembles *Lokotunjailurus* in some respects, yet differs significantly from it in others. Its affinities remain to be established. In the same publication, Hendey described an upper canine as belonging to *Homotherium* sp. This specimen and some postcranial bones were recently reassigned by Werdelin & Sardella (2006) to *Amphimachairodus*. It is considerably different from the material referred to *Machairodus* sp., making Langebaanweg the only African site with remains of more than one species of machairodont cat larger than *Dinofelis*.

African machairodont material younger than that from Langebaanweg can be referred to the Plio-Pleistocene genera *Homotherium* and *Megantereon*. The former has its earliest appearance in the Lonyumun Mb. of the Koobi Fora Formation, Kenya, while the earliest occurrence of the latter is from South Turkwel, Kenya (Werdelin & Lewis 2000). The record of the former may be and the latter is the globally earliest record of the respective taxa.

Material and Methods

Apart from the Sahabi fossils described herein, a large amount of comparative material has been studied. African fossil machairodonts from Lothagam, Langebaanweg and the Wembere-Manonga Fm., as well as all African *Homotherium* sp. used in Fig. 3, have been studied by one of us (LW) from original specimens. Information on specimens from Bled Douarah, the Albertine Rift, Toros-Menalla and Chorora has been obtained from the relevant publications (Kurtén 1976; Petter 1994; Geraads et al. 2002; Peigné et al. 2005). Comparative material of *Amphimachairodus giganteus* from Eurasia has been studied by both of us from original specimens in collections in Uppsala (Palaeontological Division, Museum of Evolution), Beijing (Institute of Vertebrate Paleontology and Paleoanthropology), Rome (Museum of Paleontology, La Sapienza University), Florence (Museum of Paleontology), London

(The Natural History Museum) and Paris (Natural History National Museum). Information on *Machairodus aphanistus* from Batallones-1 and *Machairodus kurteni* has been obtained from the literature (Sotnikova 1991; Antón et al. 2004). All measurements used in Fig. 3 are original except for those on *M. aphanistus, M. kurteni, M. robinsoni,* and *M. kabir.*

Abbreviations used: KNM: Kenya National Museums, Nairobi; NMT: National Museum of Tanzania, Dar Es Salaam; SAM: Iziko South African Museum, Cape Town; TMM: Texas Memorial Museum, University of Texas, Austin; BM: The Natural History Museum, London; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; PMU: Palaeontological Division, Museum of Evolution, Uppsala; PIN: Paleontological Institute, Moscow; BPI: Bernard Price Institute, Johannesburg.

Description of the Sahabi machairodont material

Cranium (Fig. 1a-d). The well preserved neurocranium lacks the left zygomatic and glenoid processes, the posterior part of the sagittal crest and the right part of the occipital crest. The occipital plane is vertical. Anteriorly, the skull is broken just above the orbit. The lambdoid crest is strongly developed, while the temporal fossa is wide, vertically high, and delimited by a massive zygomatic-glenoid process. The glenoid fossa is very wide and deep. The paroccipital processes are large and posterolaterally oriented relative to the mastoid processes, which are broad and massive. The latter extend vertically below and partially behind the respective external auditory meatus, which is located medially below and behind the zygomatic root and anterodorsal to the root of the mastoid process. Furthermore, the glenoid process protrudes ventrally below the lower end of the mastoid process, approximately as much as the mastoid processes extend below the lower margin of the external auditory meatus.

Mandible (Fig. 1e-g). The almost complete left mandible shows evidence of weathering, especially on the lingual side. The incisors and the lower canine are lacking; the cheek teeth, p4 and m1 in particular, are heavily worn. Moreover, the anterior half of p3 was accidentally broken in the late 1980s. The broad wear surfaces on p4 and m1 indicate that the specimen is an old individual.

The horizontal ramus is slender, in particular at the c-p3 diastema. A marked mental flange, slightly damaged in its anterior part, is present. Judging by its alveolus, the lower canine was quite large, and elevated relative to the level of the cheek teeth. Even if partially damaged, the reduced size of the double-rooted p3 is evident. Howell (1987) described it as follows: "p3 is present and it is quite worn, but the cusps are preserved; the main cusp is pointed and canted rather backward, and there are substantial anterior and posterior accessory cusps and a seemingly low distal cingulum. The p3 is quite closely approximated to p4."

Both p4 and m1 are large and worn, especially on the lingual side. Nevertheless, there is overlap between the anterior edge of m1 and the posterior edge of p4. In m1, the metaconid-talonid complex is missing.

Other dental remains referred by Howell (1987) to *Machairodus* sp. are a right p3 (185P28A) from locality P28A and a dP3 from locality P29A. We have not seen these specimens and they are not figured by Howell (1987). He does, however, figure several postcranial elements (Howell 1987, Fig. 8) referable to Machairodontinae. These will be compared to material from Lothagam and Langebaanweg in a separate contribution.

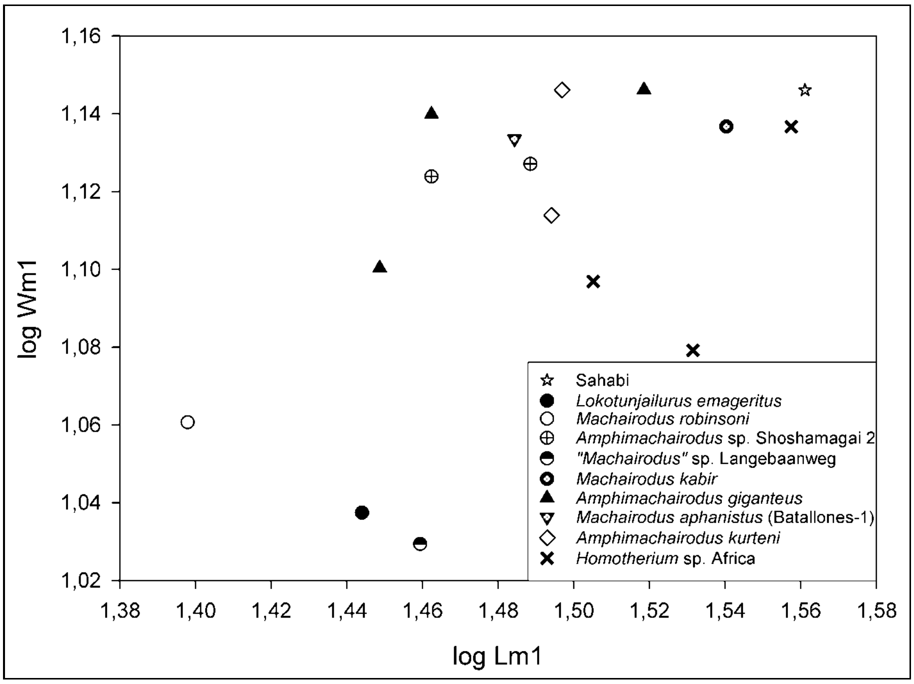

Fig. 3 - Bivariate diagram of length versus width of the lower carnassial of some Mio-Pliocene machairodonts as labeled.

Comparison of the Sahabi machairodont material to other Late Miocene machairodonts

The *Amphimachairodus* from Sahabi shows advanced characters in its basicranium and lower cheek teeth. Among Turolian sabertoothed cats, only a few skulls with well preserved basicrania are known, and some of these are juvenile specimens. Among European *A. giganteus* specimens, the morphology of the mastoid and occipital area can be observed in the almost complete adult skull from Halmyropotamos described and figured in Melentis (1970) (at that time referred to *M. aphanistus*) and in a juvenile specimen from Samos published and figured by Beaumont (1978). Further information on the cranial morphology of these felids can be obtained from skulls from different localities of the former Soviet Union, among them the recently prepared skull with mandible of *Amphimachairodus taracliensis* (holotype), a previously unpublished skull of *Amphimachairodus copei* (OSU 2638) from Grebeniki and the skull with mandible of *Amphimachairodus kurteni* (Sotnikova 1991; Sotnikova & Noskova personal communication).

The Chinese fossil record also includes some very well preserved complete skulls, such as that referred to *A. palanderi* (= *A. giganteus*) by Chang (1957) and the subadult specimen from loc. 113 of Baode, Shanxi, China) (Zdansky 1924). The Sahabi *Amphimachairodus* has also been compared to a cast of a quite complete, though slightly crushed, skull with articulated mandible of *A. giganteus* from an unknown locality in China (stored at the Swedish Museum of Natural History, Stockholm).

In comparison to all the specimens listed above, the Sahabi machairodont shows the most derived occipital and mastoid area, with larger paroccipital processes and a broader mastoid process that is more ventrally oriented and is located approximately midway along a line separating the paroccipital process from the glenoid process. Such features in the Sahabi specimen suggest an adaptative set converging on smilodontine cats.

The available data indicate considerable similarities between *A. giganteus* and *Homotherium*, in particular in the shape and development of the paroccipital and mastoid processes. Such features can be seen on a well preserved and complete skull of *H. nestianus* from the Late Pliocene of Rocca Neyra (France) (Bonis 1976) and on a cast of a skull of *H. crenatidens* from Seneze (France) (Ballesio 1963). A neurocranium from Pirro Nord (Early Pleistocene, Italy) has also been used for comparison (Sardella 1994). A detailed study of the basicranial morphology of well preserved specimens of *Homotherium* from Incarcal (Early Pleistocene, Spain) was recently published (Antón & Galobart 1999) and provides a good comparative sample. The different specimens of *Homotherium* listed above differ in size and in some craniodental features, but the general setting of the mastoid area is quite homogeneous.

Compared to *Homotherium*, the Sahabi specimen has a larger paroccipital process, related to a powerful m. digastricus, a broader mastoid process, with a wide insertion area for the m. obliquus capitis cranialis. Lateral to this area are the insertions for mm. splenius, longissimus capitis, and sterno-cephalicus. The brachiocephalicus and part of the sternocephalicus insert on the tip of the process. Judging by the basicranial morphology, these muscles are very strong and more anteroposteriorly oriented in the Sahabi specimen than in *Homotherium*. The occiput is more vertical than in *Homotherium* and the other species of *Amphimachairodus*. In this feature and in the set of the mastoid-glenoid area, the Sahabi specimen seems to parallel the smilodontine cats. A great development of the upper canine may be expected in the Sahabi species. The mandible from Sahabi also has some features of interest, including a relatively slender horizontal ramus, in particular at the level of the c-p3 diastema, a strong mental flange, reduced p3 and wide wear surfaces on the lingual side of both p4 (posterior half) and m1.

The occurrence of such a distinct mental flange is variable in Turolian machairodonts. Judging by the illustrations, it is present in the specimens referable to *A. giganteus* from Pikermi and Samos (Beaumont 1978), in *A. giganteus* figured by Chang (1957) and in *A. kurteni* (Sotnikova 1991), but not in specimen M3851 from Baode loc. 30 (Zdansky 1924). A direct comparison with the almost complete lower jaw from loc. 113 referred to *A. palanderi* (= *A. giganteus)* (Zdansky 1924; Kurtén 1952), which belongs to a subadult individual, and with *A. giganteus* from an unknown locality in China, demonstrates marked differences in the general morphology of the coronoid process (more reduced in the Sahabi specimen) and in the shape of the masseteric fossa, which is quite rounded in *Amphimachairodus* from Sahabi and more trapezoid in the other specimens. The Libyan sabertoothed cat also has a more reduced p3.

Affinities with *"Machairodus" kabir* from Toros Menalla (Peigné et al. 2005) are evident. The Chad specimen is somewhat smaller than the Libyan one, though they are closely similar in dental measurements. The mandible TM 266-02-102 shows a developed mental flange and a reduced p3, but differs in having a larger coronoid process (judging by the photo) and evidence of a small metaconid/talonid complex. In these features, *"M." kabir* seems to be slightly more primitive than the Sahabi specimen as would befit it's somewhat greater age.

A very wide wear surface can be seen on the lingual side of the lower carnassial, as well as on the posterior cusp of p4. Such a condition is seen in the *A.*

Tab. 1 - Measurement data for the lower dentition of African and Eurasian machairodonts as used in Fig. 3.

Catalog number	**Species**	**Locality**	**Lp3**	**Wp3**	**Lp4**	**Wp4**	**Lm1**	**Wm1**
La Sapienza -	*Amphimachairodus* cf. *A. kabir*	Sahabi	18.9	6.5	21.2	11.2	36.4	14.0
KNM-LT 26178	*Lokotunjailurus emageritus*	Lothagam	8.1	5.2	17.9	8.5	27.8	10.9
T-491	*Machairodus robinsoni*	Bled Douarah					25.0	11.5
NMT WM 1937/92a	*Amphimachairodus* sp.	Shoshagamai 2					29.0	13.3
NMT WM 1937/92b	*Amphimachairodus* sp.	Shoshagamai 2					30.8	13.4
SAM-PQ L20505	*"Machairodus"* sp.	Langebaanweg					28.8	10.7
TMM 266-02-102	*Amphimachairodus kabir*	Toros-Menalla					34.7	13.7
BM M 48437	*Amphimachairodus giganteus*	Siwaliks			24.5		29.0	13.8
Composite, from Antón et al. 2004	*Machairodus aphanistus*	Batallones 1			26.3	10.2	30.5	13.6
IVPP V.906	*Amphimachairodus giganteus*	Yushe	21.0	10.0	29.0	12.0	33.0	14.0
PMU – (Ex2)	*Amphimachairodus giganteus*	Loc 113, Baode	15.6	7.4	26.1	10.3	28.1	12.6
PIN 2433/287	*Amphimachairodus kurteni*	Kalmakpai			26.8	11.5	31.2	13.0
PIN 2433/524	*Amphimachairodus kurteni*	Kalmakpai	17.3	7.9	25.3	11.1	31.4	14.0
BPI M8280	*Homotherium problematicum*	Makapansgat					34.0	12.0
KNM-ER 931	*Homotherium* sp.	Koobi Fora, KBS Mb.					36.1	13.7
KNM-KP 30420	*Homotherium* sp.	Kanapoi					32.0	12.5

giganteus complex, including the derived *A. kurteni*, and is typical of the genus *Homotherium*.

Nevertheless, the advanced features of the basicranial morphology in the Sahabi specimen compared to the less derived characters occurring in *Homotherium* suggest that the Libyan taxon should be considered a very advanced form in the evolutionary trend of the *A. giganteus* group, but not the direct ancestor of *Homotherium*.

Similar considerations have been pointed out also for *Amphimachairodus kurteni* (Sotnikova 1991), which shares with the Sahabi specimen a distinct mental apophysis and absence of the metaconid/talonid complex.

Reassessment of African Late Miocene machairodonts

The most commonly preserved element in the African machairodont material that is currently available is the m1. In Fig. 3, the length and width of the available lower carnassials are compared to lower carnassials of some Eurasian Miocene large machairodonts, as well as some African *Homotherium* sp. (Tab. 1). From this it is evident, first of all that the African Miocene machairodont material can be separated into two size classes. A group of small forms includes *M. robinsoni*, *L. emageritus* and "*M.*" sp. from Langebaanweg (it should be noted that the m1 from Inolelo 1, Wembere-Manonga Fm alluded to above is considerably smaller than this group), while a group of larger forms includes "*M.*" *kabir*, *Amphimachairodus* sp. from Shoshamagai 2, and the Sahabi specimen described above.

Within each of these groups there are differences between specimens, however and these differences can be related to similar differences in the comparative material. In the group of small specimens, *M. robinsoni* has a broad m1, while the much younger Lothagam and Langebaanweg specimens have slender lower carnassials. It is tempting to suggest that the former is broad because it is older and more primitive, since there is a trend at least in later machairodonts (see below) for the m1 to become progressively more slender. This tends to be confirmed by the broad m1 in the similarly aged *M. aphanistus* (in the plot this species is represented by the mean of the Batallones-1 sample from Antón et al. 2004). The similarity between the Lothagam and Langebaanweg forms lends credence to suggestions that they are closely related, though differences in other dental and cranial proportions, as well as in skeletal features preclude specific identity. Curiously, the older Lothagam form appears more derived than the younger Langebaanweg form, but again, this requires further analysis.

In the group of larger forms there are also specimens with broad lower carnassials and specimens with more slender ones. In the first group we have the two specimens from Shoshamagai 2 and in the latter group we have "*M.*" *kabir* and the Sahabi specimen. It should be emphasized that the difference between these specimens in m1 width has no obvious stratigraphic component, as all specimens are between 5 and 7 million years old. Instead, the differences may reflect a taxonomic distinction and differential history of the taxa involved. The Shoshamagai 2 specimens match Eurasian *A. giganteus* closely in m1 proportions, while the other two specimens approach *Homotherium* sp. in proportions. It thus seems plausible to suggest that, given the similar ages of the specimens, the more slender Libyan and Chadian specimens either represent a secondary immigration of *Amphimachairodus* into Africa or are descendants of an African form similar to that represented in the material by the specimens from Shoshamagai 2. Basicranial morphology seems to preclude the presence of the Sahabi form in the direct ancestry of *Homotherium* whose first (global) occurrence is in the Lonyumun Member of the Koobi Fora Formation, dated 4.35-4.1 Ma (Werdelin & Lewis 2005), but the group that did give rise to *Homotherium* must surely be very close in time and morphology to the Sahabi form. For taxonomic purposes it is also quite clear that the Chad form must be referred to *Amphimachairodus*.

Of material that is not included in the discussion above, the specimen from the Chorora Fm. is specifically indeterminate, but broadly similar to the *M. aphanistus*/*M. robinsoni* group. The material from the Nkondo Fm. has not been available for study. However, the dimensions and morphology of the specimens, as well as the illustrations in Petter (1994) provide no indication that this material could not be referred to *Amphimachairodus* sp., which would be more in line with its Late Miocene age. As we have shown elsewhere (Werdelin & Sardella 2006), the larger machairodont from Langebaanweg would fit comfortably in the group of larger specimens discussed above, but in the absence of dental material other than the upper canine it cannot be determined if it belongs with the broad lower carnassial form represented by the Shoshamagai 2 specimens or the slender lower carnassial form represented by the material from Libya and Chad.

Finally, Haile-Selassie et al. (2004) note that the "*Machairodus*" sp. material from the Adu-Asa Fm. "is larger in size [than *L. emageritus* from Lothagam, i.e., the size of *M. giganteus*], with a shorter and wider m1". Given the length of m1 stated in Haile-Selassie (2001), we assume the latter to mean relatively shorter and wider. These statements suggest that the Adu-Asa Fm. m1 is most similar to the two lower carnassials from Shoshamagai 2. Clearly, the Adu-Asa Fm. specimens should at least provisionally be referred to an *Amphimachairodus* sp. similar to that from Shoshamagai 2 but different from the Libya/Chad species.

Conclusions

The vertebrate fauna of Sahabi has been variously interpreted as being of latest Miocene (on the biochronology of its faunal elements) or basal Pliocene age (based on regional geology considerations). At present, most authors seem to consider Sahabi to lie very near the Miocene-Pliocene transition (MN 13). Paleoecological studies suggest that at Sahabi wooded habitats occurred along adjacent banks of a large river contrasting with semiarid conditions away from the river. Such conditions probably became intensified during a well marked dry season (Boaz 1987). *Amphimachairodus* was the largest specialist predator in the Sahabi fauna, with an adaptation for killing large prey (young proboscideans or rhinos, hippos, antracotheres, etc.).

The Sahabi *Amphimachairodus,* with its strongly developed mastoid and glenoid processes, and reduced p3 and coronoid process can be considered as a derived form within the para- or polyphyletic *Amphimachairodus* species complex. In some cranial features it converges on smilodontine cats. The Libyan species seems too derived to be considered ancestral to the genus *Homotherium*. Compared to other Neogene African specimens the Sahabi form differs greatly in both size and morphology from *Lokotunjailurus emageritus* of Lothagam (Kenya), while it shows clear affinities with the large *Amphimachairodus kabir* from Toros Menalla (Chad). The latter seems more primitive in having a more developed coronoid process and retaining a metaconid/talonid complex on m1. It seems probable that the two forms are related, and should be placed in a different taxonomic group than the Eurasian large *A. giganteus*. Whether the Toros-Menalla and Sahabi specimens represent the same species is not possible to determine with certainty on the basis of the material available, but indications are that the differences present can be ascribed to ontogeny, interspecific variation and stratigraphic age. Toros-Menalla and Sahabi are not very different in age in view of the occurrence of a similar faunal complex in both localities (e.g. the antracothere *Lybicosaurus petrocchii*) (Vignaud et al. 2002), but overall the Toros-Menalla fauna must be considered somewhat older than that of Sahabi. We provisionally refer the Sahabi specimens to *Amphimachairodus* aff. *A. kabir*.

The presence of a derived *Amphimachairodus* at Langebaanweg (earliest Pliocene, South Africa) (Werdelin & Sardella 2006) and the Wembere-Manonga Fm. (latest Miocene, Tanzania) suggests that the evolution of sabertoothed cats in Africa at the Miocene-Pliocene transition is more complex than previously envisaged.

Acknowledgements. We would like to thank all those museum curators who have provided access to specimens, especially Solweig Stuenes, Uppsala, Elisabetta Cioppi, Firenze, Margaret Avery and Derek Oland, Cape Town, the government of the Republic of Kenya, Meave Leakey, Emma Mbua, Fredrick Kyalo Manthi, Mary Muungu and many others for permissions and assistance in the study of material housed in Nairobi, and COSTECH, Terry Harrison and Amandus Kwekason for permissions and assistance with the study of material housed in Dar Es Salaam. We thank the referees Lorenzo Rook and Manuel Salesa for critical reading the manuscript and the useful suggestions. We also thank Marina V. Sotnikova for access to an unpublished manuscript, Stephane Peigné for discussions about *A. kabir*, Luca Bellucci and Alessia Cipullo for technical assistance. RS acknowledges funding through the "High Lat" program which was made available by the European Community - Access to Research Infrastructure action of the Improving Human Potential Program, as well as through SYNTHESYS, project SETAF-1042, which was made available by the European Community - Research Infrastructure Action under the FP6 "Structuring the European Research Area" Program. LW gratefully acknowledges funding from the Swedish Research Council, VR.

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