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SOME NEW MACHAERODONTS FROM MAKAPANSGAT LIMEWORKS

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SOME NEW MACHAERODONTS FROM MAKAPANSGAT LIMEWORKS

BY G. E. COLLINGS

ADDENDA & CORRIGENDA

Fig. 1 - 3 Add TRANSVAAL MUSEUM Nos. TM BF 1
and DINOFELIS BARLOW 1

Page 36 LIST OF MATERIAL ADD at FOOT

15 M8279	LEFT UPPER CANINE	HOMOTHERIUM sp. GREY BRECCIA
16 M8356	LEFT LOWER CANINE	- " - - " -
17 S1(SFN 18)	LEFT UPPER CANINE	DINOFELIS sp.(LIMEWORKERS DUMPS
18 S2(SFN 19)	LEFT LOWER CANINE	MEGANTEREON sp STERKFONTEIN

All references to PERE P. TEILHARD de CHARDIN. Should read "TEILHARD" and not "CHARDIN".

INSERT NEW TABLE XIV after p118

LIST OF COMPARATIVE MATERIAL

NO	NAME	DESCRIPTION
BP1/C 188 - 199	Panthera pardus	Skulls and lower jaws ex C.D. MAGUIRE Potgertersrus District
BP1/C 258	Panthera pardus	Complete skeleton origin unknown

TYPOGRAPHICAL ERRORS

p17 4th line from bottom of the page Nimravinae is incorrectly spelled.
p30 last line of second paragraph should refer to Table III
In Table III Stirton 1957 should be 1951.
p82 should read Specimen M8357
p106 Smilodon californicus is incorrectly spelled on line 7.
p107 paragraph 2 line 5 specific is incorrectly spelled.
p112 line 3 from foot of page Leakey is incorrectly spelled.
p114 line 7 from foot of page should refer to the sub-family Hoplophoninae

p117 in Table XIII the first line of summary information should be headed "skull", not "upper canines".

ABSTRACT.

Fifteen specimens of sabre-tooth cats from the Makapansgat Limeworks are described and the skull previously named "*Megantereon problematicus*" is correctly identified as *Homotherium* cf. *nestianus*. The new material includes six cranial, numerous post cranial remains and two isolated canines. All specimens except the two teeth are referred to the genus *Dinofelis* and most can be identified as *D. barlowi*. The teeth are referred to *Homotherium* sp. Most of the skeletal fragments belong to a single individual, and a second individual can be recognised, associated with a skull. Two canines from Sterkfontein are also described.

The taxonomic position of the various sabre-tooths is discussed and an interpretation of their behaviour is attempted. An estimated age for the cave deposits is given.

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1 INTRODUCTION

1.1 Review of taxonomy

The taxonomy of the Machaerodontinae has for a long time been in a confused state. This was due, partly to the rather heterogenous nature of the group, and partly to their wide distribution, leading to a considerable amount of synonymy in the literature. Recently, comparative studies by palaeontologists in this field have cleared up most of the confusion, and a fairly clear picture has emerged.

The machaerodonts made their appearance with the Felinae at about the end of the Miocene (Teilhard & Leroy 1945, Thenius 1967). Three major groups are recognised here, and within each, not more than two genera. These groups are:

1. The Machaerodus group
2. The Megantereon - Smilodon group
3. The Homotherium - Dinobastis group

Two other unrelated groups of sabre-tooths will also be considered in this study, and they illustrate a repeated tendency for the cat family to evolve along this particular line. The additional groups are:

4. The Dinofelis group (Plio/Pleistocene)
5. The Sansanosmilus group (Pliocene)

Each represents divergence and parallel evolution from the normal feline line. Opinions vary as to the taxonomic status of these groups, but in this study, it is taken that the true Machaerodontinae are represented only by the first three groups, while the Dinofelis group represents a comparatively recent divergence, closely related to the feline stock, and the Sansanosmilus group is a remnant of the more

ancient family of sabre-tooths, the Hoplophonidae. This arrangement follows Thenius (1967).

The following list of characters for the sub-family Machaerodontinae is taken from Pilgrim (1932), although this diagnosis applies to the sabre-tooth cats as a whole.

Sub-family Machaerodontinae Gill 1872

Felidae having teeth for the most part with crenulated crests; incisors progressively enlarging; upper canines progressively increasing in size and lower canines progressively diminishing; upper and lower carnassial teeth only slighly notched between the lobes; P^3 frequently with strong anterior accessory cusp; P^4 mostly with reduced protocone, with the exception of the most primitive forms; well developed paracone, with or without well developed parastyle ..... Concurrently with the increase in length of the upper canines, the muzzle lengthens; the infra-orbital foramen widens; the occipital is heightened; the mastoid process is progressively strengthened; the glenoid fossa depressed; the zygomatic arches become shorter and stouter; the coronoid process of the mandible becomes reduced; a mental crest or process on the mandible present in most; skeletal structure rather massive; hallux strong.

Not all the characters would be present in any one group. and the absence or presence of a certain character might distinguish between one genus and another. In many cases however, there is a high degree of parallelism and, in incomplete or badly preserved specimens, this often leads to a difficulty in identification.

1.1.1 The Machaerodus group

In the past, any sabre-tooth fossil found in Europe was given the generic name Machaerodus although it was recognised at quite an early stage that there were, at least, three different types (Boule 1901). Their localities were numerous and widespread, and they aged from Upper Miocene to Middle Pleistocene (Boule 1901, Dawkins and Sanford 1881, and others).

The geologically earliest type was Machaerodus aphanistus from Upper Miocene European localities, such as Eppelsheim, Pikermi, Maragha, based upon various isolated upper canines (Boule 1901). Kaup originally named the type specimen Felis aphanistus, and at about the same time, the generic name Machaerodus was being used for sabre-tooth specimens from more recent deposits, and which were somewhat different from F. aphanistus. However, these younger specimens were identical to the skull described as Felis Megantereon by Bravard in 1828, from the Villafranchian of Mont Perrier (Matthew 1929). This was changed, in the same year, to the genus Megantereon by Croizer and Jobert. Boule (1901) therefore assumed the name Machaerodus for Kaup's aphanistus specimens since they were clearly not Felis but some type of sabre-tooth.

In 1929, Matthew stated that the generic name Machaerodus should only be applied to a single European species, that of M. aphanistus, and this view has been followed by more recent palaeontologists. Matthew's (1929) diagnosis for Machaerodus aphanistus is:

(a) $P\frac{3}{3}$ little reduced, P_3 similar in construction to P_4.

(b) Accessory cusps only moderately developed on P_3- 4, and with little backward pitch of cusps.

(c) Accessory cusps of P_4 well developed.

(d) M^1 long, transverse, less reduced than in other genera.

(e) Lower canine stout, rather compressed, oval, no dependent flange on jaw, but prominent angulation of surface at symphyseal region in front and beneath.

(f) Upper canine very large, stout, flattened. Not as long as in others.

(g) Size medium to large.

(h) Lower molar has mostly a vestigial metaconid.

In 1924, Zdansky recorded several skulls from the Chinese Pontian (Lower Pliocene), which he distinguished as three species of Machaerodus: M. palanderi, represented by a number of individuals, M. tingii, and M. maximilliani. All these species seem justifiably to fit that genus, although because of some surprisingly advanced characters, some authors place them into the later more specialized genera. M. palanderi and M. tingii are considered as belonging to the Homotherium group, and M. maximilliani to the Megantereon group (Chardin & Leroy 1945, Churcher 1966).

Chang (1957) has recorded additional specimens of M. palanderi and M. tingii from different Chinese localities but still Pontian in age. His M. tingii does not quite agree with Zdansky's (op.cit.), although it is much damaged, and was an extremely old individual. A notable feature the two specimens have in common, however, is the upper canine with serrations only on its posterior border.

Burt (1934) has described specimens of Machaerodus catocopis from the Pliocene of North America. This genus is rather rare in America, but M. catoccpis may add to the rather uncertain definition of the true Machaerodus. Numerous fragments of post crania are represented, as well as cranial material. From this study, the following points may be added to Matthew's (1929) diagnosis:

(a) P^2 may or may not be present.

(b) The premolars are less reduced than in Pleistocene genera.

(c) Upper and lower carnassials narrower than those of Smilodon.

(d) A small mental process, not as large as in Megantereon, but larger than in Smilodon.

(e) Coronoid process slightly reduced.

(f) Ramus of jaw narrow and straight.

(g) Condyle actually and relatively with smaller diameter than in Smilodon.

The presence of P^2, the less reduced pre-molars and the only slightly reduced coronoid are all indicative of a primitive machairodont. The extremely narrow carnassials are surprising, as the blade-like carnassial is considered a highly advanced feature among the sabre-tooths, evolved from a basically triangular tooth.

This material is comparable to Zdansky's (1924) M. palanderi, particularly in the presence of P^2 and the extremely narrow carnassials.

Associated with the skull fragments of M. catocopis were a number of incomplete limb bones, which were taken almost certainly as belonging to the same species (Burt 1934). These indicate a long-limbed cat, with about the same proportions as the extant mountain lion. Pilgrim (1932) states, in his diagnosis of Machaerodus, that the skeleton is unknown, "but assumed to be robust with stout limbs" (p.194). Ballesio (1963) considers that the European M. aphanistus had short stocky limbs, but does not give his reasons.

1.1.2 The Megantereon - Smilodon group

Cuvier, in 1835, described a large flattened canine from the Villafranchian of Europe, and which he initially named Ursus cultridens, believing it to belong to a bear, (Boule 1901, Matthew 1929).

He later changed the name to Machaerodus cultridens. It differs from the canine of the Upper Miocene M. aphanistus in its smaller size, slender elegant shape, and lack of serrations. This canine is identical to that belonging to the skull from Mont Perrier, and which Croizet and Jobert had named Megantereon megantereon in 1828. Boule (1901) considered the latter as synonymous with Machaerodus cultridens, but it was not until 1929 that Kretzoi pointed out the priority of Megantereon megantereon over Machaerodus cultridens (Ballesio 1963)

Schaub (1925 described a nearly complete skeleton of M.cultridens from Senezc (Villafranchian) and another from Val d'Arno, of the same age. He described the body as heavy and clumsy, with short stocky limbs. The neck is elongated, with the cervical and thoracic vertebrae strengthened, but the lumbar region relatively short. The sacrum is very strong, massive and shortened, and the tail short. The fore-limb (and the fore-body in general) is strengthened and the hind-limbs rather short and weak although, strangely, not the cancaneum. The foot is short and broad, only slightly longer than the hand. M. cultridens was clearly not built for running but for strength and holding power.

The first author to attribute short stocky limbs to sabre-tooth cats was Deperet, in 1890 when he figured limb bones of M. cultridens from the Lower Pliocene of Mont Pellier and Rousillon (Schaub 1934). This is considerably older than the later, more common, forms of M. cultridens from the Villafranchian and the two limb bones in question, the humerus and radius, are slightly weaker than the Seneze ones. Schaub (1934) considers a direct relationship between the two forms. This means that the earliest forms must have been contemporary with the rather different M. aphanistus.

In 1929, Kretzoi reviewed the existing classification and considered Machaerodus cultridens synonymous with Megantereon megantereon, on the grounds that it differed sufficiently from Machaerodus aphanistus for generic distinction (Matthew 1929). Matthew was of the same opinion, and his diagnosis for the genus Megantereon follows:

Megantereon megantereon Croizer and Jobert 1828.

(a) Upper canines long, slender, not serrated.

(b) Lower jaw with well developed mental process.

(c) $P\frac{3}{3}$ reduced, P_3 much smaller than P_4, double rooted.

(d) P_4 with moderately developed accessory cusps smaller than main cusp, well developed talonid, cusps all pitch backward.

(e) Minute vestigial heel on M_1.

(f) P^4 with rudimentary 4th cusp (ectostyle) anterior to parastyle. No inner cusp (protocone).

(g) M^1 small, round to oval.

Matthew (1929) did not consider the presence or absence of serrations on the upper canine as diagnostic, and their absence in Megantereon megantereon may be specific or accidental. Pilgrim (1932) is of the same opinion. Up until this time, a number of fossils ascribed to Machaerodus cultridens had been recovered from European localities, and these should all be referred to the single genus and species Megantereon megantereon (Matthew 1929).

The genus Megantereon was recognised as a more advanced sabre-tooth than Machaerodus, mainly seen in the more sectorial carnassials (loss or reduction of inner cusp), more reduced anterior pre-molars, the greatly reduced lower canines, set at a higher level than the cheek teeth, and the heavily built body (Pilgrim 1932). The following

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