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Some new machaerodonts from Makapansgat limeworks

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additional modifications in this genus are noted by Pilgrim:

(a) The occipital region of the skull is heightened, and the mastoid process strengthened.

(b) The coronoid process of the mandible is very reduced.

(c) The upper and lower canines do not come into opposition.

Species of Megantereon have been recorded from Asia, most of them of Lower Pleistocene age. From India three species are known: M. falconeri and M. palaeindicus from the Lower Pleistocene (Matthew 1929) and M. praecox from the Upper Pliocene (Pilgrim 1932). The former two have serrated upper canines, but according to Pilgrim (1932) conform to the diagnosis of Megantereon except for their larger size. In the evolution of Megantereon, there was a tendency to increase in size, and the Pleistocene forms are generally larger than the Pliocene ones (Kurten 1968).

The Chinese Lower Pliocene Machaerodus maximilliani recorded by Zdansky (1924) is considered by Chardin and Leroy (1945) to belong to the genus Megantereon, due to the absence of a P^2 and to the very narrow carnassials. The mandible of Machaerodus maximilliani is not known.

The Villafrancian of Choukoutien, China, has yielded an abundance of sabre-tooth fossils, among them one species clearly belonging to Megantereon, and called Megantereon inexpectatus (Teilhard 1939, Teilhard and Leroy 1945). The skull is described as short, high and broad, and the protocone on P^4, although still present, is extremely small. P^3 is reduced, but not as much as in other contemporary advanced forms (Chardin 1939). The glenoid process is long, bringing the jaw hinge below the level of the basi-cranium (Teilhard and Leroy 1945).

The material is very similar to Machaerodus nihowanensis from the

Villafranchian at Nihowan, China (Teilhard 1939). The Nihowan species is based upon three skulls described by Chardin and Piveteau (1930). Skull I, which is the more complete but lacks canines, has the same high, broad structure as M. inexpectatus, and the less complete skull III is identical to skull I. From the illustrations of skull I, there is a distinct protocone on P^4 and the incisor row is straight with the teeth close together. This latter feature is characteristic of this group of machaerodonts (Churcher 1966). Skull II is clearly very different from skulls I and III, mainly in the long, low skull, the very reduced P^3 and the vestigial protocone on P^4. Schaub (1934) and Teilhard and Leroy (1945) later concluded that skull II in fact belonged to a different species from skulls I and III, and the diagnosis for M. nihowanensis was therefore invalid. Chardin and Leroy (1945) named skulls I and III Megantereon nihowanensis, and in the same publication described an additional upper jaw fragment belonging to that species, from the Villafranchian of Shansi. The canine is very long, with no sign of serrations, the incisor row is a straight line, P^3 is not very reduced, and P^4 is narrow, but with a distinct protocone.

Young (1935) reported a skull from possibly the Sanmenian (Upper Pliocene) of Shansi, and referred it to Megantereon nihowanensis. The upper canine is described as broad and long, and "the inner edge, at the level of the alveolus, was so minutely serrated that it looks to be practically smooth" (p.14). P^4 has no ectostyle, and it has a distinct protocone. The mandible has a mental process and deep symphysis. P_3 though, is small, with two fused roots, indicating that it is undergoing reduction.

The genus Megantereon is also recorded from Java, from Middle Pleistocene deposits (Kurten 1962), although it is represented only by a single upper canine. The tooth has the typical long, slender shape

with rounded anterior and posterior crests, and no serrations.

The American relative of Megantereon is the single genus Smilodon, which achieved the highest degree of evolution and adaptation in the sabre-tooth line (Kurten 1963[b], 1968). Schaub (1925) first noted the similarity between the two forms.

The most extensive collection of Smilodon material occurs at Rancho la Brea in California, where large asphalt accumulations have trapped some 1,000 individuals. The age of this deposit is estimated as Upper Pleistocene, at about the level of the 4th Glaciation (Kurten 1963[b]). This is considerably more recent than the European Megantereon which was very rare above the Villafranchian. It appears that Smilodon evolved from an Asian form of Megantereon which migrated across the Bering land bridge during the Lower Pleistocene. The earlier species of Smilodon which range from Middle to Upper Pleistocene show a greater affinity with Megantereon (Kurten 1963[b]).

The distinctive characters of Smilodon are clearly those of Megantereon, carried still further. The size progressively increases until it culminates in the large S. californicus (Merriam and Stock, 1932) and the South American S. neogaeus (Churcher 1967). The skull is massive, with a high occiput and a large mastoid. The sabres are extremely long, thin (with diametral index approximately 0,47) and curved, and do not appose the lower canines. Unlike Megantereon however, they bear fine serrations. P^3 is very small and P^4 is long, sectorial, with no trace of the protocone, although the internal root is present. The ectostyle is rather variable in size. The lower canines are hardly bigger than the incisors. P_3 is usually absent, although its presence or absence is rather variable. P_4 is rather complex, with an additional talonid, and sometimes another small cuspule internal to it. The lower carnassial has a small talonid, or

heel, a structure that was gradually lost by all the Felinae since the Miocene. Its re-appearance is most surprising, and its functional significance will be considered later. There is also sometimes a small basal cusp in front of the paraconid of M_1. The mandible is weak, with a very small coronoid process (Merriam and Stock 1932). The mental process, prominent in Megantereon, has disappeared, and the earlier forms like S. gracilis have a vestigial flange (Kurten 1963[b], 1965).

The skeleton is like that of Megantereon, only more extreme. The limbs are shortened, particularly the hind limb, and the phalanges rather spreading. The neck is long, the lumbar region short, with an extremely short tail, and the fore-quarters generally strong and massive (Merriam and Stock 1932).

1.1.3 The Homotherium - Dinobastis group

From the same deposits that yielded the long, slender sabres of Megantereon megantereon, there were also recovered canines that were larger, broader at the base, narrower and serrated on both sharp edges (Boule 1901). Fabrini, in 1890, described a skull with this type of canine, and named it Machaerodus crenatidens (Boule 1901, Schaub 1934). He proposed that it should be given the new generic name Homotherium, stating that there was sufficient difference between it and the contemporary Machaerodus cultridens (= Megantereon megantereon) (Ballesio 1963).

Schaub (1925) added to the distinction between the two forms in assigning to M. crenatidens a long and slender body, quite different from that of Megantereon megantereon. He, however, retained the generic name Machaerodus for the former. Kretzoi, in 1929, introduced another generic name for M. crenatidens, that of Epimachaerodus, and it was

this that was subsequently adopted. Only comparatively recently has the priority of the name Homotherium been recognised (Simpson 1945, Ballesio 1963, Churcher 1966).

The diagnosis for Homotherium is taken from Pilgrim (1932) for Epimachaerodus.

Epimachaerodus (= Homotherium) crenatidens Fabrini 1890.

(a) Upper canines long, flat and broad, lower canines much reduced.

(b) Incisors and cheek teeth with serrated edges, cheek teeth highly specialized.

(c) Upper and lower canines biting in opposition.

(d) Incisors and canines not elevated above level of cheek teeth.

(e) Mandible with weak coronoid process.

(f) Relatively shallow mandibular symphysis, strong mental crest, but no process.

(g) $P\frac{4}{4}$ with moderately developed accessory cusps.

(h) Protocone on P^4 absent, $P\frac{3}{3}$ tending to reduction, M_1 with or without a metaconid.

(i) Limbs long and slender.

Ballesio (1963) has given a detailed description of a specimen of H. crenatidens from Seneze, and in which the main differences between this and the genus Megantereon are noted. The skull is elongated and narrow, with the glenoid not depressed. The mandible is rather slender, with no mental process, and the incisors, although raised slightly above the cheek teeth are no more so than in the normal Felidae. The incisors are enormous, and the lower canines only slightly larger. Churcher (1966) has also pointed out that the incisor row in the

Megantereon - Smilodon group is straight, while in the Homotherium - Dinobastis group it lies on a distinct curve.

The upper canines are not as long as in Megantereon, but they are considerably narrower and more curved. The diametral index for H. crenatidens is 0,42, as opposed to 0,57 for Megantereon megantereon (Ballesio 1963). Kurten (1968) has given descriptive names to the two groups, which distinguishes them very well. The Megantereon group are the "dirk-toothed cats" and the Homotherium group are the "scimitar-toothed cats". $P\frac{3}{3}$ is very small (P^3 single rooted). The carnassials are more blade-like than in Megantereon, and the protocone on P^4 is completely lacking (Ballesio 1963).

The skeleton is not short and stocky as in Megantereon, although the fore-quarters are strengthened. The tendencies in Megantereon and Smilodon to lengthen the neck region and shorten the lumbar region are only very slight in Homotherium, and it is closer to the feline build. The tail, however, is as short as it is in Megantereon.

A number of different European species have been recorded for this genus, but they are probably all a single species (Kurten 1968). Kurten actually refers to H. sainzelli, but this is synonymous with H. crenatidens.

In China, the Lower Pliocene Machaerodus palanderi and M. tingii are considered by Teilhard and Leroy (1945) to be Homotherium, in view of the very narrow upper canines and highly specialized carnassials (diametral index 0,37). Churcher (1966) however, does point out that they are rather primitive forms of Homotherium, shown by the small protocone on P^4 and the presence of a P^2 in M. palanderi. In addition they are of a greater age.

The Chinese Villafranchian deposits at Choukoutien have yielded

large specimens of Homotherium ultimus (Teilhard, 1939, Teilhard and Pei 1941), of which the skull is almost identical to H. crenatidens. Pei (1934) had previously described a number of isolated teeth, all serrated and highly specialized, and which can be referred to the genus Homotherium (Teilhard and Leroy 1945).

Homotherium sp. has also been recorded from the Middle Pleistocene of Java (Kurten 1962).

In addition to Homotherium crenatidens, Fabrini distinguished another, similar type of skull, but which for certain reasons he set apart, and gave it the name Machaerodus nestianus. The skull and dentition of this form are identical to H. crenatidens, except that serrations are lacking on the anterior border of the upper canine, and there is a diastema between P_3 and P_4 (Boule 1901). Boule considers this as merely an individual or sexual difference, and M. nestianus may be identified with H. crenatidens. Schaub (1934) however, cites several other occurrences of this type of canine, which also appears slightly different in shape and size, and he believes it to be separate from H. crenatidens. A similar situation exists between Machaerodus palanderi and M. tingii of the Chinese Pontian (Zdansky 1924). M. tingii lacks serrations on the anterior border of the canine, but in all other respects is similar to M. palanderi. Churcher (1966) suggests they may be conspecific.

The homotheriines are well represented in North America, although for a long time they had been confused with Smilodon (Churcher 1966). The genus Dinobastis is recorded from Pleistocene cave deposits (Hay 1920, Churcher 1966) and the similarity with Homotherium is notable. The age of the American form is roughly contemporaneous with the Choukoutien H. ultimus. These younger forms, Kurten (1963^b) prefers to retain in the genus Dinobastis, as distinct from the Villafranchian

(or upper Pliocene) Homotherium. The only known European form above the Villafranchian is H. latidens from Middle Pleistocene cave deposits in Britain (Dawkins and Sanford, 1866 - 1871). This Kurten (1963[b]) also considers as Dinobastis. D. latidens differs from H. crenatidens in the smaller size and the coarser serrations on the upper canine. Churcher (1966) however, considers Dinobastis to be synonymous with Homotherium.

Fragmentary remains of a highly specialized Homotherium, H. moravicum are recorded from different aged layers from Hungary (Thenius 1972), and which appear to be an evolved type of H. crenatidens.

1.1.4 The Dinofelis group

Zdansky (1924) described a new type of felid from the Chinese Lower Pliocene which seemed to be intermediate between the Felidae and the Machaerodontinae. For this form, based upon a complete but rather badly preserved skull, he proposed a new genus and species, Dinofelis abeli.

In general form the skull is felid in character, with the occiput on the same line as the frontals and not raised above as in the machaerodonts. The mastoid process though, is relatively large and well developed, and the infra-orbital foramen large. There is no mental process or crest on the mandible, although the coronoid process is noticeably smaller than in the Felidae.

In the dentition, Dinofelis presents the closest similarity with the sabre-tooths. The upper canines are relatively long, compressed and with sharp anterior and posterior crests, but there are no serrations. The incisor row is curved and the lower canine much smaller than the upper. There is no P^2. P^3 has a large posterior talon, and although damaged, it appears that P^4 had a reduced protocone.

The lower carnassial is specialized with the protoconid longer than the paraconid. A distinguishing feature of the sabre-tooths is the increase in length of the posterior lobe of the carnassial. Dinofelis thus seems to have been a normal felid showing distinct machaerodont tendencies.

In 1929, Astre described a mandibular ramus belonging to a new species of "Felis", Felis diastemata, from the European Upper Pliocene (Schaub 1934, Piveteau 1948). Schaub however, considered that the material was more machaerodontine than felid. Piveteau (1948) described a more complete skull from Rousillon (Lower Pliocene) which was identical with F. diastemata, and in which he noticed a combination of machaerodontine and felid characters. For this new form, he gave the name Therailurus diastemata.

The similarity between the two genera Dinofelis and Therailurus was recognised by Hemmer (1965), who decided that Therailurus was synonymous with Dinofelis although the species D. abeli and D. diastemata were distinct. D. abeli is, in every respect other than the upper canines, more advanced than D. diastemata. The canines are less compressed than in the European form, although the cheek teeth are more blade-like (Hemmer 1965).

Two fossil species of the Felidae, previously identified as Felis cristata and Panthera palaeonca have been revised and found to be identical to Dinofelis (Hemmer 1973). D. cristata from the Pinjor stage of India shows the same shape of skull and tooth proportions as Dinofelis. D. palaeonca, from the American Pliocene has similar lengthened upper canines. It thus appears that the "false sabre-tooths" were as wide spread as the true sabre-tooths.

1.1.5 The Sansanosmilus group

The genus Sansanosmilus illustrates an entirely independent machaerodontine evolution that took place at a geologically earlier date. It is known, so far, only from the region of Sansan in France, of Middle Miocene age (Filhol 1891, Ginsburg 1961).

Two species are recognised, S. palmidens and S. jourdani (Ginsburg 1961), the first one described by Filhol (1891) under Machaerodus, in which certain similarities with Megantereon were pointed out. Ginsburg finally distinguished their true phylogenetic position.

In spite of its highly specialized nature, Sansanosmilus is structurally close to the Oligocene Hoplophonidae. Certain features of the skull, such as the possession of an alisphenoid canal, the posterior lacerate foramen well separated from the condylar foramen, the anterior palatine foramen positioned on the maxilla, are all characteristic of primitive cats generally (Ginsburg 1961). However, there are also features paralleling Homotherium and Smilodon such as the long, flattened, serrated upper canines, reduced anterior pre-molars, and long compressed carnassials (P^4 has even lost the protoconid). There is also a mental process and the incisors are raised above the level of the cheek teeth (Ginsburg 1961).

It could be argued that Sansanosmilus is descended from Eusmilus, an extreme Oligocene sabre-tooth, but the latter is far too specialized. Neither can Sansanosmilus be considered ancestral to the plio-Pleistocene machaerodonts, as it is still structurally very primitive (Ginsburg 1961). Ginsburg concludes that Sansanosmilus is a particular type of Minravinae, showing convergence with the Machaerodontinae.

Different opinions are expressed regarding the phylogenetic status of Sansanosmilus. Pilgrim (1932) believes it to be a possible

ancestor for Megantereon. Thenius (1967) considers it an evolved type of Hoplophoneus.

1.2 Sabre-tooths previously recorded from Africa, with particular regard to those from South Africa.

The genus Machaerodus is recorded from the Upper Pliocene of Langebaanweg, South Western Cape Province (Hendey in press). The material consists of cranial remains and is typical of Machaerodus. Especially notable is the upper canine whose anterior crest curves lingually at the base, the same trait noted for the Chinese M. maximilliani (Teilhard and Leroy 1945).

The Lower Pleistocene deposits of East Africa have yielded abundant remains of sabre-tooths. Arambourg (1947) reports a mandibular fragment and humerus of Homotherium ethiopicum from Omo, Ethiopia. Another anterior jaw fragment has been recorded from Bed I of Olduvai, belonging to Megantereon sp., and a large upper canine root from Bed II, possibly belonging to Homotherium (Leakey 1961). Cooke (1964) reports a questionable Homotherium from Kaiso.

Recent excavations on the Eastern shores of Lake Rudolf have revealed a number of specimens of Megantereon eurynodon and Homotherium sp. (Maglio 1972, M. Leakey pers. comm.). The Homotherium material is similar to both H. crenatidens and sp. M8280 from Makapansgat (M. Leakey pers. com). Dinofelis specimens are also recorded (Maglio 1972), including some post crania (M. Leakey pers. comm.).

In South Africa, three species of Megantereon are recognised. M. whitei from Schurveburg (Broom 1937, 1939, 1948) and M. gracilis from Sterkfontein (Broom 1948) are both based on single mandibular fragments. It appears that M. gracilis is more advanced than

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