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Some new machaerodonts from Makapansgat limeworks

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2015-02-13
http://hdl.handle.net/10539/16988

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M. whitei, by the longer posterior portion of M_1. A third species, M. eurynodon from Kromdraai is based upon a crushed skull and mandible, and shows affinities with M. nihowanensis (Ewer 1955). All these specimens are from small individuals.

Hendey (in press) has described an ascending mandibular ramus and various limb fragments of Megantereon sp. from Elandsfontein, South Western Cape. Also mentioned are two parts of an unnumbered mandible which was previously identified as M. gracilis (Hendey, in press, from Bone and Singer 1965). The ascending ramus described by Hendey is similar in size to M. gracilis and M. eurynodon. Hendey states that although the Elandsfontein form is more similar morphologically to M. gracilis, it is phylogenetically closer to M. eurynodon. He concludes that the distinguishing characters of M. eurynodon may be no more than temporal variation of a single species. M. whitei may possibly be included as well.

Ewer (1955) has recorded a lower carnassial belonging to Homotherium sp. from Kromdraai. An upper canine which is very compressed, serrated and slightly recurved was found at Bolts Farm and ascribed by Broom (1939) to Machaerodus transvaalensis. It has the typical appearance however, of that of Homotherium, and it may possibly belong to that genus (Ewer 1955).

A large upper canine belonging to Homotherium sp. has been recovered from Langebaanweg (Hendey, in press), and it is suggested that it is roughly contemporary with the Machaerodus material from the same locality. The tooth is very compressed, with a diametral index of 0,39 and both anterior and posterior crests are serrated. It is similar in size to the canines of sp. M8280 from Makapansgat, identified wrongly as Megantereon. The Makapansgat and Elandsfontein

specimens may possibly have been conspecific (Hendey, in press). An isolated homotherine upper canine, also from Makapansgat, briefly mentioned by Collings (1972) shows more definite affinities with the Elandsfontein type, although it is slightly smaller. There are marked serrations on both borders.

The genus Dinofelis is well represented in South Africa. Cranial and postcranial fragments of D. diastemata have been discovered from Upper Pliocene deposits at Langebaanweg (Hendey, in press). Broom (1937, 1939) recorded a skull described as Megantereon barlowi from Sterkfontein. It was later changed by Ewer (1955) to Therailurus barlowi and finally by Hemmer (1973) to Dinofelis barlowi. It is also known from Swartkrans (Ewer 1955), from Bolts Farm (Cooke pers. comm.) and from Makapansgat (Toerein 1955, Ewer 1956[a]). One skull belonging to a third species, D. piveteaui is known from Kromdraai (Ewer 1955).

D. diastemata is roughly contemporary with the European material (Hendey, in press) and the species is generally accepted as being the most primitive in the evolutionary series (Ewer 1955, Hemmer 1973). This is illustrated mainly in the larger coronoid and in the smaller carnassials relative to the size of [illegible] although the canine shows a surprisingly low diametral index (0,54) which is not in accordance with the evolutionary trends. However, the Langebaanweg specimens show a large amount of variation in the flattening of the canines, and the highest value is 0,63, with the lowest value 0,54 (Hendey, in press).

Of the Transvaal specimens, D. barlowi is definitely more primitive than D. piveteaui, shown by the wider carnassial and less reduced P^3. D. barlowi and D. piveteaui fall into a conformable sequence, although doubt is expressed whether D. barlowi follows directly from D. diastemata, due to the nature of the latter's canines (Ewer 1955, Hemmer 1973).

However, the new material from Langebaanweg shows that this may not be so inconceivable. The Chinese D. abeli is considered to have paralleled D. piveteaui whilst remaining geographically separate (Hemmer 1973), although its age (Lower Pliocene) is older than that of D. piveteaui. The carnassials of D. abeli are strongly compressed and except for the rather high diametral index for the canines, it is highly specialized (Ewer 1955, Hemmer 1973). Table I gives the relative tooth proportions for known species of Dinofelis. It is noted that the proportions for the South African D. diastemata are closest to those of D. barlowi.

The post cranial material belonging to D. diastemata and D. barlowi have also been described. D. diastemata shows distinct modifications in the machaerodont direction (Hendey, in press) whilst D. barlowi is described as essentially felid in character, with the proportions of a tiger (Cooke pers. comm.).

1.3 The correct identity of Megantereon problematicus

Collings (1972) described a large sabre-tooth skull and mandible, sp. M8280 from Makapansgat Limeworks, and according to the information at the time, it seemed most likely to belong to the genus Megantereon. Unfortunately, the only knowledge pertaining to Homotherium was that of Epimachaerodus from Pilgrim (1932) and Ewer (1954, 1955). The reasons for placing it into the genus Megantereon were as follows: The diagnosis for Epimachaerodus states that the protocone on P^4 is absent, $P\frac{3}{3}$ tending to reduction, the mandible has a relatively shallow symphysis with no mental process, and the incisors are not raised above the level of the cheek teeth (Pilgrim 1932). In sp. M8280, a bulge on the lingual side of P^4 shows the presence of a small protocone in

the unworn state, $P\frac{3}{3}$ are greatly reduced, the symphysis is very deep, with what seems like a mental process, and the incisors are raised above the level of the cheek teeth. These points all correspond to the diagnosis for Megantereon (Pilgrim 1932). Ewer (1954, 1955) states that the upper canine of Epimachaerodus is double edged and highly serrated, whilst in sp. M8280, the serrations on the anterior of the left canine are barely visible, and on the right, only present on the posterior border. Moreover, Pilgrim (1932) records a species of Megantereon, M. falconeri, which has serrations only on the posterior edge of the canine.

In view of the points in favour of Megantereon, sp. M8280 was identified accordingly, but since it did not correspond to any of the previously recorded species, particularly in respect of the highly compressed carnassials, it was given a new species name, M. problematicus.

Since obtaining much of the European literature on the machaerodonts, the synonymy of Epimachaerodus with Homotherium is realised, and also its more correct definition. In this genus, the canines and carnassials are more compressed than in Megantereon but the protocone on P^4 often remains as a bulge on the inside of the paracone. $P\frac{3}{3}$ are relatively much smaller than in Megantereon. The symphysis is deep and usually extends somewhat beneath the lower border of the rami (Ballesio 1963, Churcher 1966 and others).

It is immediately clear that sp. M8280 belongs to the genus Homotherium. The absence of serrations on the anterior border of the right canine is due to a heavy wear facet with the lower canine, which was thought to be an abnormality. The extremely faint serrations on the anterior of the left canine are probably a result of wear, since

this was a very old individual, although they are more prominent on the posterior border. Table I is a list of important tooth proportions for various known machaerodonts, and sp. M8280 compares well with H. crenatidens and H. nestianus from Europe.

Piveteau (1948) has recorded a skull from the European Villafranchian, which was initially described as H. crenatidens, but because of certain characters, such as the less curved upper canine, it was changed to H. nestianus. On this specimen, the canine is serrated on both edges, but the serrations on the anterior edge are weaker, and stop before the distal end. These are almost exactly the same conditions as in sp. M8280, in which case it could be ascribed to H. nestianus. But the very worn nature of the teeth would imply that serrations might have been more distinct in the unworn state.

The Chinese H. ultimus is too specialized. (The very low reading for P^4 width on sp. M8280 is probably also a result of wear). None of these species has been recorded so far from Africa, although some of the more complete material from East Africa is similar to H. crenatidens (M. Leakey pers. comm.). Until more material is known however, sp. M8280 will remain identified as Homotherium c.f. nestianus.

Table II shows the more important tooth ratios for various recorded species of Machaerodontinae. H. "problematicus" seems a little more advanced than H. crenatidens and H. nestianus.

1.4 The age of the Transvaal cave deposits

The sites of the various fossil bearing caves in the Transvaal are:

Sterkfontein

Kromdraai

Swartkrans

Makapansgat Limeworks

Schurveberg

Bolts Farm and Bolts Workings

In addition, the site of Taungs in the Cape Province can be included as roughly contemporary. There has been no proved and accepted date placed on these deposits, although it is generally accepted that the fauna is broadly Villafranchian in age. The precise date is still the source of much debate and the only reliable method is that of fossil correlation with other datable localities (Ewer 1956[b], Cooke 1970).

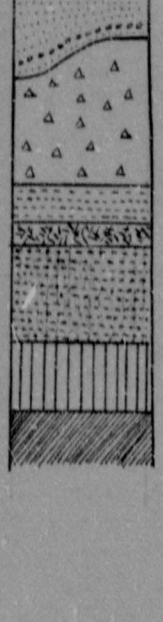
The reason for the uncertain date is due to the nature of the deposits. A brief summary of the method of accumulation and type of sediments found at Makapansgat is taken from Brain (1958). The cave is formed in ancient dolomitic limestone, which is attacked by rainwater draining through it to form an underground solution cavity. This is first filled with water until land uplift lowers the water table to a level underneath the cavern. Joints and fissures formed in the overlying dolomite facilitate the rapid downward passage of water into the cave, and calcium and magnesium carbonate are deposited as travertine on the walls of the cave, and as stalactites and stalagmites.

With the widening of the joints connecting the cave to the surface, small amounts of surface material begin to enter and are deposited as a very calcified red mud, or "basal red" breccia. This contains a few fossils, and since the cracks open to the surface were at this stage rather like vertical pot-holes, the animals probably fell in by accident (Kitching pers. comm.). Within the "basal red" breccia is a thin band of buff-coloured or "grey" breccia which is extremely bone rich, showing that the cave opening was sufficiently wide to allow animals to enter, but still small enough to prevent rapid accumulation of sediment.

At this stage, the cave was probably used as a shelter, and the numerous rodent bones in the "grey" breccia indicate that owls used it as a roosting place. Many of the bones have been mineralised by manganese and carbon, staining them black. A great deal of the bones also appear to have been fashioned into tools, indicating the work of Australopithecus. These breccias are called Lower Phase I breccias.

As the cave opening becomes wider, more surface material comes in, and the overlying Upper Phase I breccia contains a lot of sand grains and blocks of dolomite. Fossils are rare and the breccia is a hard, light pink sediment, highly calcified. Above this, Phase II breccia is easily distinguished by a marked contact, and the cave was suddenly exposed by a collapse of the roof, allowing a great influx of surface material. The breccia is a brown loose-textured one, only lightly calcified and containing mostly worn dolomite pebbles with two quartzite bands. Continued erosion gradually removes the rest of the cave roof and exposes the breccias to the surface.

The following diagram is a composite profile for the Limeworks deposit (from Brain 1958).



Phase II
Sandy breccia with gravel bands

Upper Phase I
Highly calcified with weathered dolomite blocks

Lower Phase I
Contaminated travertine and calcified red muds ("basal red" breccia) often bone rich

Floor travertine

Dolomite floor

(not to scale)

The particular environment of deposition in these caves makes correlation with other sites difficult, and many of the zone fossils are lacking (Arambourg 1947, Cooke 1968). In the past, attempts to synchronise evidence of high and low rainfall in South and East Africa with glacial events in Europe have proved unreliable (Cooke 1955). However, Brain (1956) has estimated an age sequence for 4 of the main caves, based on climatic evidence from analyses of the cave deposits, and correlating them with the "pluvials" and "interpluvials" that were thought to occur in Africa's Lower Pleistocene. Brain's sequence was, from the oldest to the youngest: Sterkfontein, Makapan, Swartkrans, Kromdraai.

Even in Europe, the exact position of the beginning of the Pleistocene is not fixed. Palaeontologically, it is taken as the first appearance of Bos, Elephas and Equus, but geologically, as the beginning of the first Ice Age. Neither of these criteria coincide, as the palaeontological "Villafranchian" falls in the geological "Pliocene" (Cooke 1948).

The most likely sites for correlation with South Africa are those in East Africa. The more important ones are Omo and Lake Rudolf in Ethiopia, Kaiso in Uganda, the Kavirondo gulf area of Lake Victoria, the Eastern rift of Kenya, and the Olduvai gorge - Laetolil - Peninj area of Serengeti in Tanzania (Cooke 1968). Especially significant among the fossils are the australopithecines which are common to both East and South Africa. Two types of these early hominids are known from the South African localities: a robust type, Australopithecus (= Paranthropus) robustus, and a gracile type, A. africanus, which is thought to have led ultimately to Homo sapiens. Both types are also known from the East African sites: A. (=Zinjanthropus) boisei, the robust form, and Homo (=Australopithecus) habilis the gracile form (Cooke 1970).

A number of other mammalian genera are also common to both regions, and a considerable amount of work has been done on their correlation. This has resulted in varying conclusions which are summarised below.

The abundant and rapidly changing species of Suidae provide a good means of linking different sites fairly accurately (Cooke 1964). According to Ewer (1958), Makapansgat has yielded Notochoerus euilus, which has also been recorded from Kaiso, Omo, Laetoliland Bed I of Olduvai (Cooke 1964). A giant pig, Phacochoerus antiquus, recorded from Makapansgat, is also recorded from the Omo basin and Koobi Fora (Cooke 1970).

The relative ages of the cave deposits have been placed by analysing the number of synchronous species from one site to another, together with a consideration of the antiquity of the fauna (Ewer 1956[b]). This resulted in the following sequence:

Kromdraai (younger)
Swartkrans
Makapan
Taung
Sterkfontein (older)

To obtain a correlation with the East African deposits, Ewer (1956[b]) compared the relative number of extinct genera against the number of genera closely related to living forms. This gave the Transvaal caves the oldest age, then Omo, followed by Laetolil and finally Olduvai. As a whole, they all have a Villafranchian age (Ewer 1956).

Cooke (1968) agreed with the above sequence for the cave deposits, but separated them into an older "Sterkfontein faunal span" and a younger "Swartkrans faunal span". Cooke's (1964, 1968) correlation with East Africa was rather different, as he placed Sterkfontein, Taung and Makapan roughly contemporary with Omo, Laetolil and Olduvai bed I.

Kromdraai, Swartkrans and Sterkfontein extension (which is not contemporary with Sterkfontein type site) were placed parallel with part of Olduvai bed II. From Bed II to Bed IV of Olduvai and higher, the palaeontological and archaeological evidence was Middle to Upper Pleistocene, and contemporary with South African Vaal gravels, Cornelia and Hopefield localities (Cooke 1964, 1968). The deposits at Kaiso were the oldest with a rather archaeic fauna, such as Archidiskodon subplanifrons, Anancus and Stegodon (Cooke 1968).

More recent and conclusive evidence of age is from the potassium/argon (K/A) radiometric method (Cooke 1970, Leakey 1967, Maglio 1972). The Omo beds are particularly satisfactory, being lacustrine deposits interbedded with volcanic ash, tuff and lavas, which provide the radiometrically datable material. These beds are dated at 4,0 to 1,4 million years, and the Makapansgat fauna seems to correspond to the oldest of these beds. The evidence is in the giant Suids, as the other sites where they are also recorded are all dated at 3,0 to 4,0 million years (Cooke 1970).

Recently, the nearby deposits at Koobi Fora and East Rudolf have also been given a radiometric date of 4,5 to 1,3 million years, which corresponds approximately with that of Omo (Maglio 1972). The conformable beds can be separated into faunal zones, with zone 1 being the youngest. This is notable for very advanced stages of Mesochoerus limnetes and Metridiochoerus andrewsi. Also present are the living elephant, Loxodonta africana, and modern stages of hippo and white rhino (Maglio 1972). Four species of Felidae have been recorded. These are:

	No. of specimens
Panthera sp.	6
Therailurus (=Dinofelis) sp.	1

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Name of thesis Some New machaerodonts from Makapansgat limeworks 1973

PUBLISHER:
University of the Witwatersrand, Johannesburg
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