New Dinofelis (Carnivora: Machairodontinae) remains from Sterkfontein Valley sites and a taxonomic revision of the genus in southern Africa

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Several new specimens attributed to the genus Dinofelis Zdansky, 1924 have been recently recovered from three limestone caves within the Sterkfontein Valley. The new site of Motsetse has yielded in situ isolated dental remains and postcranial elements assigned to D. piveteaui. Cooper’s Cave has yielded a number of taxonomically inconclusive cranio-dental and postcranial elements from in situ deposits which we assign to Dinofelis sp. A crushed skull and associated mandible of Dinofelis from the Gladysvale Cave was recently located in the collections housed at the Geological Survey in Pretoria, South Africa. The specimen had apparently been recovered in the early 1990s during initial surveys of the site. It was partially prepared and has remained undescribed. Further preparation of the specimen revealed a complete set of the lower jaw and maxilla with dentition. The cranial base, although distorted, is also preserved. This material is here assigned to D. piveteaui and represents the first ever discovery of an associated skull and mandible of this taxon. Following the discovery of all this new material, a reassessment has been made of the taxonomic status of the genus Dinofelis in southern Africa.

Keywords: Dinofelis, Plio-Pleistocene, Coopers, Gladysvale, Motsetse.

INTRODUCTION

The machairodont fossil record represented at the Plio-Pleistocene cave deposits of the Sterkfontein Valley is relatively abundant and diverse. In recent years, field work conducted at these cave sites has yielded new specimens of the extinct genus Dinofelis. The new site of Motsetse has yielded in situ isolated dental remains and postcranial elements assigned to D. piveteaui. Cooper’s Cave has yielded a number of taxonomically inconclusive cranio-dental and postcranial elements from in situ deposits which we assign to Dinofelis sp. A crushed skull and associated mandible of Dinofelis from the Gladysvale Cave was recently located in the collections housed at the Geological Survey in Pretoria, South Africa. The specimen had apparently been recovered in the early 1990s during initial surveys of the site. It was partially prepared and has remained undescribed. Further preparation of the specimen revealed a complete set of the lower jaw and maxilla with dentition. The cranial base, although distorted, is also preserved. This material is here assigned to D. piveteaui and represents the first ever discovery of an associated skull and mandible of this taxon. Following the discovery of all this new material, a reassessment has been made of the taxonomic status of the genus Dinofelis in southern Africa.

Genus DINOFELIS Zdansky, 1924

The genus Dinofelis is represented at most Plio-Pleistocene sites in southern Africa. Originally described as Therailurus, this genus name was later synonymized with Dinofelis. It has been generally considered that Dinofelis has features of both machairodont cats (sabre-like canines) and felines (conical canines), with greater affinities to the former (Werdelin and Lewis, 2001). This is partly because of its body size and canine morphology which fall between both groups (Turner and Anton, 1997).

On the African continent, the earliest record of this genus is at the late Miocene site of Lothagam in Kenya and at the earliest Pliocene site of Langebaanweg in the Western Cape, South Africa (Turner, 1990a). This latter material was classified by Hendey (1974) as D. diastemata because of its similarities to European material, particularly on the size of the carnassials. However, Hendey’s argument appears to be in question (Turner, 1990b; Cooke, 1991; Werdelin and Lewis, 2001). In addition to the Langebaanweg material, the species D. barlowi and D. piveteaui originally described by Broom (1937) and Ewer (1955) are recognized in southern Africa in the Plio-Pleistocene cave deposits of the Sterkfontein Valley. The species D. darti, originally erected by Toerien (1955) for the material
derived from Member 3 at Makapansgat and subsumed by Ewer (1956) into D. barlowi, has been recently reinstated by Werdelin and Lewis (2001).

It has been generally accepted that D. barlowi was a chronologically older and a probable precursor species of D. piveteaui, the latter appearing at c. 1.6 Ma (Turner, 1990b). However, in a recent revision of the genus Dinofelis (Werdelin and Lewis, 2001) it was suggested that these two species represent different evolutionary lineages. In this scheme, D. piveteaui originated in East Africa while D. barlowi remained as a South African endemic, and D. piveteaui is considered to have migrated to the southern part of the continent c. 1.6 Ma (Werdelin and Lewis, 2001).

The various species of Dinofelis are larger and more robustly built than leopards, approximating the size of a jaguar and with powerful front limbs (Hendey, 1974; Turner and Anton, 1997). Werdelin and Lewis (2001) consider that species of Dinofelis showed an increase in size through time since its appearance in the late Miocene. However, differences in body size are known for different species of the genus. For example, postcranial remains of D. piveteaui, the last surviving species of the genus, show a decrease in body size (Werdelin and Lewis, 2001: 243). It has been suggested that Dinofelis inhabited closed environments, based on the short length of the front limbs and longer proportions of the hind limbs, in agreement with the observed morphology and behaviour of extant forest-dwelling cats (Marean, 1989; Turner and Anton, 1997, 1998). However, generalizations about the functional morphology of the genus may be best interpreted on a species by species basis (e.g., Werdelin and Lewis, 2001).

Because the holotype of D. piveteaui, the specimen KB 61 from the Kromdraai cave, South Africa, lacked the lower dentition, the newly recovered dental material described here elucidates important aspects of the mandibular and dental morphology of this species.

The context of the fossils

Motsetse

The fossil-bearing cave deposit of Motsetse, located about 16 km northeast of Sterkfontein near Krugersdorp, South Africa, was first excavated in 1999 (Berger and Lacruz, 2003) (Fig. 1). The assemblage is dominated by antelope species and also contains four carnivore genera. Primate remains consist of a single cranial fragment. No hominid remains have been recovered to date. Based on the fauna represented in the assemblage, mainly the Dinofelis material, a provisional early Pleistocene age was estimated for the excavated material (Berger and Lacruz, 2003). Two short field seasons have been conducted at Motsetse to date. During the first field season, several dental and postcranial remains of a large felid were recovered. The material (referred to as the ‘M1 set’) comprises isolated elements consisting of a left mandibular M1, P4, P3, a lower canine, and two incisors, as well as both maxillary P3. In addition, a distal humerus fragment and a proximal metatarsal ray were found. The fossils were excavated from an area of less than 25 cm² at varying depths within 4 cm of each other.

Two years later, in July 2002, an isolated P4, a P3, and two lower canines (referred to as the ‘P set’) were found in association with 14 bones of the manus and pes of a large felid. These fossils derived from a small area in decalcified sediments located 30 cm below the previous finds. Berger and Lacruz (2003) gave a preliminary description of the dental remains which they assigned to the extinct felid Dinofelis cf. piveteaui:

Taphonomic context

The isolated teeth that comprise the M1 set are considered to belong to the same individual because of close spatial proximity, similar wear stage and fossilization. For the same reasons, the isolated teeth of the P set are considered to belong to a single individual. A total of two left P4, has been recovered, as well as three lower canines from both excavation periods, implying that at least two different individuals of a large felid are represented.

Cooper’s Cave

Cooper’s Cave deposits are located only about 1 km west of Kromdraai and were originally described by Brain (1958). The site had been poorly known until recent field work resulted in the discovery of an abundant and diverse faunal assemblage, including a few hominid specimens (Berger et al., 2003). No detailed descriptions of the stratigraphy were available prior to that of Berger et al. (2003). Based on certain key faunal indicators, the site has been provisionally assigned an age between 1.9 and 1.6 Ma (Berger et al., 2003). Craniodental and postcranial elements of Dinofelis have been recently recovered from this site. Two left mandible fragments indicate that at least two individuals are represented at this site.

Gladysvale Cave

The Gladysvale Cave is located about 13 km northeast of the main Sterkfontein caves. Several underground chambers as well as de-roofed and collapsed areas have been identified. The chronology, palaeontology and stratigraphy of these deposits are best known in the Gladysvale External Deposits dating to the Middle Pleistocene (Lacruz et al.,
Fig. 1

Map showing the location of various cave sites referred to in the text. The broad black line demarcates the Cradle of Humankind World Heritage Site.
2002). Mining for limestone and bat guano was extensive in some areas of the cave. Many fossil-rich breccia blocks resulted from the mining activities and thus cannot be stratigraphically associated in situ infills. It is unfortunate that the Dinofelis skull and mandible described below derived from one such breccia dump. The specimen was preliminarily prepared during the early 1990s and came to rest in the collections of the Geological Survey undescribed. Further preparation of this specimen has been recently carried out.

Only craniodental remains have been identified from Gladysvale. Previous identifications of Dinofelis material from this cave are intriguing in that both D. barlowi and D. piveteaui have been reported (Berger, 1993; Cooke, 1963; Savage, 1978). The only Gladysvale specimen analysed by Werdelin and Lewis (2001), a single P4, is housed at the University of California and has not been included in this study.

MATERIALS AND METHODS

Bernard Price Institute for Palaeontological Research, Johannesburg
Sterkfontein: Dinofelis barlowi: 5853 (right M1), 5855 (isolated left P3)

Transvaal Museum, Pretoria
Swartrkans: Dinofelis sp.: SK 335 (right mandible with P3 and M1)
Bolt’s Farm: Dinofelis barlowi BF: 55-22 (skull and mandible with complete dentition)
Kromdraai: D. piveteaui: KA 61 (skull with complete dentition), KA 62 (isolated P3), KA 63 (isolated M1 in fragment of mandible)
Sterkfontein: D. barlowi: TM 1579 (isolated P4), STS 131 (mandible with P3, P4, M1 and P5 with broken metastyle), 5853 (right mandible with M1), 5855 (isolated P4)
Makapansgat: Dinofelis sp.: M 607 (right mandible with P3, P4 and M1).

South African Museum, Cape Town
Langebaanweg material: Dinofelis diastemata (sensu Hendey, 1974): L 20284 (left and right mandibles with c, P3, P4, P5, and M1), L 12237 (left mandible fragment with P4 and M1), L 20685 (left mandible with c, P3, M1), L 51591 (left mandible with c, P3, P4 and M1), L 2674 (right maxillary fragment with P4 and P5), L 5757 (isolated left P3), L 24930 (incomplete isolated P4), L 47523 (maxilla with P4 and P5).

Measurements

Measurements of the teeth were taken with digital callipers to the nearest 0.1 mm and consist of standard length (L) and width (W). In addition, the following measurements were taken.

<table>
<thead>
<tr>
<th>Code</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lmp4</td>
<td>Length of the metastyle of the P4</td>
</tr>
<tr>
<td>WP4pro</td>
<td>Width of the P4 at the protocone</td>
</tr>
<tr>
<td>LM4pa</td>
<td>Length of the paraconid of the M4</td>
</tr>
<tr>
<td>LM4pro</td>
<td>Length of the protoconid of the M4</td>
</tr>
</tbody>
</table>

Suitable morphological characters of clear taxonomic utility among the Felidae are difficult to interpret in the light of the high degree of similarities displayed by the extant taxa. Fossil cats are usually represented by fragmentary specimens, adding to the difficulty in obtaining defining taxonomic characters. In the analysis presented here we have chosen the leopard as outgroup. A sample of 105 leopards (Panthera pardus) of pooled sexes representing a wide geographical range of this species derived from Kenya, Tanzania, Gabon, India, Namibia and South Africa was used for statistical comparisons. This valuable information has been kindly provided by Dr Hannah O’Regan. Statistical analysis of the fossil material is restricted by the small sample sizes. Where possible, bivariate analyses consisting of scatter plots of logarithmically transformed values are shown. Other tests used (e.g., Pearson’s correlation coefficient index) are noted in the relevant sections.

DESCRIPTION OF THE MATERIAL

The following descriptions refer only to the dental remains.

Motsetse Dinofelis

Maxillary teeth

MT 1966. This specimen is an isolated left P4 of an adult individual (Figs 2B, 9). The roots are missing but the tooth crown is well preserved. The tooth has an ectoparastyle moderately expressed. The protocone is reduced and is joined to the paracone by a faint ridge. The metastyle is long and is missing a tiny portion of enamel near the contact with the paracone. However, this has not affected the morphology or the measurements. Morphologically, the tooth is very similar to that of D. piveteaui from Kromdraai, but slightly smaller. It differs from material assigned to D. barlowi in the length of the metastyle and in the reduced size of the protocone (Table 1).

Mt 06/07 and MT 12. These specimens are isolated P4 of the left (Fig. 2A) and right side respectively in slightly different stages of attrition. Both specimens were found during the first excavations. The specimen 06/07 was found in two parts and has been re-fitted with paraloid. There are strongly developed posterior accessory cusps on both specimens. A sharp enamel ridge forming a basin-
Table 1

Measurements of maxillary teeth of *Dinofelis* specimens derived from the various cave sites in South Africa's Sterkfontein Valley and Langebaanweg

<table>
<thead>
<tr>
<th>Site</th>
<th>Specimen</th>
<th>Taxon</th>
<th>LP3</th>
<th>WP3</th>
<th>LP4</th>
<th>WP4pro</th>
<th>LP4met</th>
</tr>
</thead>
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<tr>
<td>Motsetse</td>
<td>MT 1966</td>
<td><em>D. piveteaui</em></td>
<td></td>
<td></td>
<td>38.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>MT 06/07</td>
<td><em>D. piveteaui</em></td>
<td>19.2</td>
<td>9.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>MT 12</td>
<td><em>D. piveteaui</em></td>
<td>18.3</td>
<td>8.9</td>
<td></td>
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</tr>
<tr>
<td>Cooper's Cave</td>
<td>CD 3835</td>
<td><em>Dinofelis</em> sp.</td>
<td>17.1</td>
<td>8.2</td>
<td></td>
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<tr>
<td></td>
<td>CD 7323-c</td>
<td><em>Dinofelis</em> sp.</td>
<td>17.2</td>
<td>8.7</td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>CD 7323-a</td>
<td><em>Dinofelis</em> sp.</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Bolt's Farm</td>
<td>BF 55-22</td>
<td><em>D. barlowi</em></td>
<td>19.3e</td>
<td>10.0e</td>
<td>37.0e</td>
<td>16.5</td>
<td>14.0</td>
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<tr>
<td></td>
<td>UCMP 69506</td>
<td><em>D. barlowi</em></td>
<td>19.8</td>
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<td>33.3</td>
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<tr>
<td>Kromdraai</td>
<td>KA 61</td>
<td><em>D. piveteaui</em></td>
<td>19.9</td>
<td>9.8</td>
<td>41.0</td>
<td>13.0</td>
<td>17.8</td>
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<td>Sterkfontein</td>
<td>5855</td>
<td><em>D. barlowi</em></td>
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<td>13.7e</td>
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<tr>
<td></td>
<td>STS 131</td>
<td><em>D. diastemata</em></td>
<td>21.5</td>
<td>11.3</td>
<td>36.2</td>
<td>16.5</td>
<td>13.8</td>
</tr>
<tr>
<td>Langebaanweg</td>
<td>L 5757</td>
<td><em>D. diastemata</em></td>
<td></td>
<td></td>
<td></td>
<td>33.4e</td>
<td></td>
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<tr>
<td></td>
<td>L 24930</td>
<td><em>D. diastemata</em></td>
<td>20.4</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>L 47523</td>
<td><em>D. diastemata</em></td>
<td>20.0</td>
<td>10.9</td>
<td>33.6</td>
<td>17.5</td>
<td>12.8</td>
</tr>
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<td></td>
<td>L 2674</td>
<td><em>D. diastemata</em></td>
<td>19.5</td>
<td>8.5</td>
<td>31.0</td>
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</tr>
</tbody>
</table>

Specimens of *Dinofelis piveteaui* recovered from the Motsetse cave. A: P3 (MT 06/07); B: P4 (MT 1966); C: lower canine (MT 1971); D: P3 (MT 04); E: P4 (MT 03); F: M1 (MT 02)
like structure is present behind these cusps, similar to that of KA 61. Cooke (1991) pointed to the less prominent presence of these accessory cusps on specimens attributed to *D. barlowi*. In addition, the P₃ of BF 55-22 from Bolt’s Farm (*D. barlowi*) is stouter than that of KA 61 and the Motssetse material. MT 06/07 has an anterior accessory cusp and an enamel protuberance on the lateral side of this cusp, which is missing on MT 12, probably through wear. MT 12 shows a greater amount of wear on the tip of the main central cusp.

**Mandibular teeth**

*MT 02.* This specimen is an isolated left M₁ of an adult individual with roots and the whole crown preserved (Fig. 2F). The anterior root is larger and projects perpendicularly to the occlusal plane. The posterior root is less robust and curves posteriorly. Cementum annulus can be seen in both roots, decreasing in spacing towards the root cervix. The tooth has two main cusps, the paraconid being shorter than the protoconid (Table 2). A vestigial talonid is present at the base of the protoconid similar to M₁ of other *Dinofelis* like M 607 or STS 5853. MT 02 is smaller than the M₁ of *Homotherium*, and the P₃ and P₄ from Motssetse associated with the M₁ are morphologically different from *Homotherium* premolars in lacking the characteristic backward tilt. MT 02 is narrow mediolaterally (Table 2), giving an overall slender appearance. Marked wear facets caused by the M₁ are present on the lateral and posterior face of the protoconid. Under a light microscope they appear as parallel striations at an angle of about 45° to the cemento-enamel junction (CEJ). The wear facets on the main cusps end very close to the CEJ.

*MT 03 and MT 1988.* These specimens are isolated P₃s with complete crowns and partially preserved roots. MT 03 (Fig. 2E) was found in association with the M₁ and MT 1988 with the P₄. MT 03 is slightly larger than MT 1988 (Table 2), although morphologically they are identical. Cooke (1991) suggested that the P₃ of *D. barlowi* and *D. piveteaui* are morphologically quite similar. The distal end of the talonid is raised forming a pronounced ridge. A common feature observed in both specimens from Motssetse, which is also present but less prominent in the Kromdraai specimen KA 62 of *D. piveteaui* (an isolated right P₃), is the presence of a small cuspsulid at the base of the anterior cusp on the lateral side of the tooth. The holotype of *D. piveteaui* (KA 61) shows a similar feature on the P₃ described by Ewer (1955). MT 03 has marked wear facets on the lateral side of the talonid which have carved a shallow groove on this cusp, and the tip of the anterior cusp is broken. There is a high degree of variability in the length and breadth of P₃ of *Dinofelis* (Table 2).

*MT 04.* This specimen is a left P₃ preserving the crown and posterior root (Fig. 2D). The tooth is damaged on the lingual side due to a small break, although the breadth of the tooth could be estimated. The anterior cusp is smaller than the posterior cusp, which forms a sharp basin-like structure broken in the medial aspect. The main cusp is located towards the anterior portion of the tooth, thus giving an asymmetric appearance.

*MT 01, MT 1967, MT 1971 and MT 1969.* With the exception of MT 1969, a fragment of the tip of an upper canine, the rest of the teeth are isolated mandibular canines. MT 1971 (Fig. 2C) and 1967 belong to the same individual as the P₃ and represent complete right and left canines with the roots preserved. MT 01 is a left canine slightly larger than the other two. None of the specimens have serrated edges. All of this material is too mediolaterally compressed to belong to *D. barlowi* (Turner, 1997).

*MT 1968 and MT 05.* These two specimens are isolated incisors probably of the lower (MT 1968) and upper dentition (MT 05). Prominent tubercules are present in both sides of the lingual aspect of MT 05 and only one in MT 1968. The latter tooth is pointed, although the lack of incisors in the Bolt’s Farm material and of lower incisors in KA 61 precludes making any further comparisons.

**Dinofelis from Cooper’s Cave**

Cooper’s Cave specimens are derived from decalcified sediments and many contain manganese incrustations, which in some places precludes the use of light-microscopic work.

**Maxillary teeth**

*CD 16765.* A right pre-maxillary fragment with incomplete I₁, I₃ and I₄. The I₁ is obliquely broken and both cusps of the other two incisors are too damaged for us to be confident about its morphology. However, it can be pointed out that the I₃ is narrow mediolaterally. The teeth are encased in a fragment of the pre-maxillary bone preserved from the midline suture. A palatal groove is present. The pre-maxilla preserves the floor of the nasal area.

*CD 16769.* An upper canine fragment lacking half of the crown. The specimen was broken near the cervix of the crown but it could be refitted with the corresponding portion of the preserved root. The root on the lingual side measures c. 20.8 mm in length and the preserved crown measures c. 18.4 mm in the same area. The width of the crown near the cervix is somewhat intermediate between the canines on KA 61 and the Bolt’s Farm specimen (BF-55-22). The antero-posterior length is 21.5 mm. No serrations are present in this tooth.

*CD 3835.* An isolated right crown of P₃ lacking the roots (Fig. 3). This specimen is very gracile and
### Table 2
Measurements of mandibular teeth of *Dinofelis* specimens derived from the various caves in South Africa’s Sterkfontein Valley.

<table>
<thead>
<tr>
<th>Site</th>
<th>Specimen No</th>
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<th>Wc</th>
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<th>Wp4</th>
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<th>Wm1</th>
<th>Lm1pa</th>
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<td>Motsetse</td>
<td>M1 set</td>
<td><em>D. pivotaeui</em></td>
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<td>11.5e</td>
<td>14.2</td>
<td>6.8</td>
<td>22.5</td>
<td>10.0</td>
<td>30.2</td>
<td>12.4</td>
<td>11.8</td>
<td>14.3</td>
</tr>
<tr>
<td></td>
<td>P4 set</td>
<td><em>D. pivotaeui</em></td>
<td>15.6</td>
<td>11.1</td>
<td></td>
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<td>21.3</td>
<td>10.4</td>
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<tr>
<td>Bolt’s Farm</td>
<td>BF 55-23</td>
<td><em>D. barlowi</em></td>
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<td>SK 335</td>
<td><em>Dinofelis</em> sp.</td>
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<td>Kromdraai</td>
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<td><em>D. pivotaeui</em></td>
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<td>KA 62</td>
<td><em>D. pivotaeui</em></td>
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<td>Sterkfontein</td>
<td>STS 131</td>
<td><em>D. barlowi</em></td>
<td>16.1</td>
<td>8.7</td>
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<td>S94-9</td>
<td><em>D. barlowi</em></td>
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<td></td>
<td>5853</td>
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<td>9e</td>
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<td>Makapansgat</td>
<td>M 607</td>
<td><em>Dinofelis</em> sp.</td>
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<td>7.2</td>
<td>21.1</td>
<td>9.7</td>
<td>25.5</td>
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<td>Langebaanweg</td>
<td>L 20284</td>
<td><em>D. diastemata</em></td>
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<td>11.1</td>
<td>14.4</td>
<td>7.5</td>
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<td>10.0</td>
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<td>8.1</td>
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This legend refers to the M1 List of measurements of *Dinofelis* mandibular teeth from South Africa. The Kromdraai specimen KA 63 has suffered what appears a recent break and part of the anterior area of the paraconid is missing, so we are using Cooke’s (1991) measurement of the length. In addition, the width of the tooth was erroneously measured as 16.9 by Cooke (1991) and Werdelin and Lewis (2001) questioned the validity of this measurement. Our measurement indicates a width of 12.9.

The Motsetse specimens referred as the ‘m1 set’ consists of p3 (MT 04), p4 (MT 03) and m1 (MT 02) and canine (MT01).

The Motsetse specimens referred as the ‘P4 set’ consist of p4 (MT 1988) and canine (MT67).
small (17.1 mm in length), being the smallest of all recorded specimens. It is most similar to, but smaller than, MT 12 and far smaller than KA 61, BF 55-22 and STS 131. The cusps of CD 3835 are very sharp and pointed. This specimen differs from the cheetah in the greater breadth of the tooth and in the possession of a strongly developed posterior ridge.

**CD 7323-c.** An isolated right P3 lacking the roots. There is a small anterior accessory cusp showing three enamel protuberances on the lateral side. There is a posterior basin-like area behind the posterior cusp. It is similar in morphology to P3 of both KA 61 and BF-55-22 albeit smaller.

**CD 7323-a & b.** An incomplete P3 broken along the paracone and missing a portion of this cusp, preventing refitting of the preserved anterior and posterior tooth regions. The metastyre is preserved but the lingual aspect of the crown near the cervix is missing, exposing the dentine. Only the distal half of the paracone is present, joined to the metastyle. A portion of the root is preserved between these two cusps. The parastyle is preserved but incomplete, lacking the posterior region that would have joined to the paracone. A moderate ectoparastyle is present. The break, which runs occluso-cervically splitting the parastyle, obscures the possible presence of the protocone. These two specimens were collected in close proximity to CD 7323-c.

**Mandibular remains**

**CD 18836.** A right mandible fragment with M1 and P3 (Fig. 4). The ascending ramus is missing but part of the masseteric fossa is preserved. The fossa is relatively deep. The distal region of this specimen has not been preserved posterior to the mandibular foramen. The inferior border appears less straight than in BF 55-22 or M 607. The mandible is broken along the inferior aspect. It has a remarkably gracile appearance, with shallow mandibular depth. As in CD 18836, the inferior border of the mandible is less straight than in BF 55-22 or M 607. The position of the mandibular foramen is located more distally than in these specimens and KA 63. It is noticeable that the M1 was a very long tooth. Although the crown is not preserved, the cervical enamel can still be seen, which enables us to estimate its length (29.3 mm). The mandible shows some resemblance to that of a very large leopard, although our estimated length of the M1 is substantially larger than the largest leopard in our comparative sample of 100 individuals (length M1 = 23.2 mm) and far larger than the mean for this species (Table 2). It also differs from Megantereon or Homotherium in the length of this tooth.

**Dinofelis from Gladysvale**

**GV-skull.** The crushed Dinofelis skull from Gladysvale had not been previously given an accession number and thus we will provisionally refer to this specimen as GV-DS-1 (DS-Dinofelis skull). The skull consists of the mandible, maxilla, face, and part of the basicranium. This individual died with the mandible in occlusion (Figs 6–8). The specimen has suffered severe distortion post-mortem which has resulted in the flattening of the skull. The specimen was originally found in the mid-1990s, with the right side down. The left side was cleaned after recovery, exposing part of the dentition, which was damaged. The right side has remained embedded in matrix until further preparation with acetic acid during 2005.

**Mandible**

The left side of the mandible preserves the canine root, P3, P4 and the M1, which is hidden by fragments of the upper carnassial. The corpus is preserved to about the gonial region. The P3 preserves a single root and has lost most of the enamel on the disto-buccal half, exposing the dentine. However, what is left of the crown indicates that the tooth had three cusps and a pronounced distal ridge similar to the Motsetse specimen MT 04. The P4 preserves the roots and most of the enamel crown. Three cusps can be identified in this tooth, which also has a strong distal ridge like MT 03 and MT 1988.

The right side of the mandible preserves the ramus and most of the coronoid process. The anterior and inferior portion of the body from the canine to the M1 is not preserved. The P3, P4 and M1 are present but are hidden by the occluding maxillary teeth. No morphological or metrical information could be obtained.

**Maxilla**

The maxilla and face are crushed and thus we focused on the dental remains. The left side does not preserve complete tooth crowns; however, the right side preserves half of the canine crown, and a
The P3 is damaged, only preserving the roots and the most cervical enamel.

It is unfortunate that the lingual aspect of the P4 is encased in hard matrix, which precludes identification of the protocone cusp despite several attempts to expose this surface. However, the fragile state of the skull prevents us from continuing further preparation. The tooth, however, is long and narrow, with a long metastyle. It is mesio-distally longer than MT 1966. There is a pronounced ectoparastyle. The tips of both anterior cusps are broken.

**TAXONOMY OF THE DESCRIBED MATERIAL**

Distinguishing taxonomic features of the dentition of *Dinofelis* are most evident in the relative length of the metastyle blade of the P3 and the width of the
protocone cusp of this tooth (Ewer, 1955; Cooke 1991). The overall appearance of the premolars in *D. piveteaui* appears to be less pantherine–like.

Motsetse

The morphology of the Motsetse P$^4$ conforms to that of *D. piveteaui* based on the size of the protocone and the length of the metastyle (Table 1 and Fig. 9) and therefore it, together with the other associated material, is assigned to this taxon.

The lower teeth from Motsetse differ from those of extinct hyaenas of the genus *Chasmaporthetes*, with which they could perhaps be confused, in the smaller size of P$^3$ and the anterior portion of the P$^4$,
which is narrower medio–laterally and has a higher and less antero–posteriorly extended central cusp in the Motsetse specimen. The Motsetse M1 does not have an extended, hyaena–like talonid, but is more similar to other Dinofelis material.

Several aspects of the morphology and size of the M1 set indicate that it belongs to the genus Dinofelis: the canines are somewhat flattened and lack the serrated edges that are typical features of the extinct genus Homotherium (Turner, 1987); the
canines are larger than those of leopard (*Panthera pardus*) and smaller than those of lion (*P. leo*); the M₁ is much narrower than in lion and larger than in any leopard, but smaller than in *Homotherium*, and the morphologies of the P₂, P₃, and both P₄s are those of a primitive felid because of the number and morphology of the accessory cusps. However, the material differs from the corresponding dental elements in *D. barlowi* in being less wide and comparatively less like pantherine cats. The length of the Motsetse M₁ (Table 2) is one of the greatest recorded for this genus (Fig. 10), and matches the likely morphology of the lower carnassial implied by the upper carnassial in *D. piveteaui*, while the morphology of the P₄ is identical to the isolated specimen KA 62 from Kromdraai previously referred to that species by Ewer (1955) on the basis of an apparent association with the type specimen. The M₁ set is accordingly assigned to the species *D. piveteaui*.

Cooper’s Cave

The Cooper’s Cave *Dinofelis* material so far recovered is very fragmentary and unfortunately does not preserve a complete P₄. The length of the metastyle on the broken P₄ (CD 7323–a) is greater than in the known specimens of *D. barlowi* and the Langebaanweg material, and smaller than in the Motsetse and Kromdraai specimens. The length/breadth of the M₁ (CD 18836) is smaller than in the known *D. piveteaui* material from South Africa (Fig. 10). The two isolated maxillary P₃s, one of which was recovered near the broken P₄, are indeed smaller than all other *Dinofelis* P₃ so far recovered from South Africa, but are similar to *D. piveteaui* premolars in the blade–like appearance and the sharpness of the cusps. The P₃ is slender and in this respect is quite similar to other premolars of *D. piveteaui*. The overall features seen in the premolar morphology, including the length of the metastyle, indicate a greater affinity to *D. piveteaui*. However, given the metrical variation in lower premolars referred to *Dinofelis* (Figs 11, 12), more complete material is needed to carry out a more detailed analysis. Therefore we provisionally assign the Cooper’s Cave material to *Dinofelis* sp. pending further discoveries at this site. The provisional age of the Cooper’s site is broadly contemporaneous with Kromdraai (Berger et al., 2003), from where the type specimen of *D. piveteaui* was recovered (Ewer, 1955). Sexual dimorphism is poorly known in the genus but could explain the size differences between for example the Kromdraai and the Cooper’s Cave material.

Gladysvale Cave

The skull and associated mandible GV–S–1 are classified as *D. piveteaui* on the basis of the long metastyle on the P₄ and the morphology of the P₃, which is most similar to the *D. piveteaui* specimen MT 04 from Motsetse.

**REVISION OF THE TAXONOMY OF SOUTHERN AFRICAN DINOFELIS**

The variation known for the *Dinofelis* material in the southern African region has been difficult to interpret because the samples are small. The most recent appraisal of the taxonomic affinities of each specimen has been that of Werdelin and Lewis (2001), and this will form the basis for our discussion.

The taxonomy of the Langebaanweg material

Hendey (1974), who originally classified the
Langebaanweg Dinofelis material as *D. diastemata*, suggested (p. 178) that the most obvious feature that separates *D. diastemata* from *D. barlowi* or *D. piveteaui* is the size of the carnassials, which are shortest in *D. diastemata*. The samples of the two latter species available to Hendey were small. Recent research has brought to light new fossil material of *D. barlowi* and *D. piveteaui* from the Sterkfontein and surrounding caves and thus variation of the carnassial size can be better interpreted. In addition, the recovery of newer material from Langebaanweg prompted Turner (1990b) to suggest that the size differences between *D. diastemata* and *D. barlowi* originally observed by Hendey (1974) could be in part attributed to sexual dimorphism, and that the Langebaanweg material ‘may therefore probably be referred to *D. barlowi*’.

Cooke (1991) and Werdelin and Lewis (2001) provisionally maintained Hendey’s specific status albeit with some reservations. Indeed Cooke (1991: 19) specifically commented on the morphological similarities between *D. barlowi* and *D. diastemata*, calling the attribution of the Langebaanweg material to *D. diastemata* into question. We interpret Cooke’s statements to suggest the Langebaanweg material conforms to a potential ancestor of *D. barlowi* rather than being conspecific with the European *D. diastemata*. A similar argument was proposed by Werdelin and Lewis (2001), who did not consider the Langebaanweg material to be conspecific with *D. barlowi* but also recognized that it does not conform to the morphology seen in the European *D. diastemata* samples. Werdelin and Lewis (2001) pointed out that upper P3 is relatively long in relation to P4 in the Langebaanweg samples, and that these differences are not seen in other species of *Dinofelis*. It is therefore unclear what the specific designation of the Langebaanweg material should be.

The case of the species *D. darti*
Toerien (1955) assigned *Dinofelis* material from Makapansgat Member 3 originally placed in the genus *Machaeorodus* by himself to the new species *D. darti*. This taxon is best represented by the holotype, a right mandible (M 607) lacking the anterior teeth and part of the ramus. Ewer (1956) revised this material and concluded that in the light of newer samples of *Dinofelis* from the Sterkfontein Valley sites (described in Ewer, 1955) *D. darti* should be subsumed within the *D. barlowi* hypodigm (Ewer, 1956: 64). A feature on M 607 noted by Toerien (1955) and Ewer (1956) was the presence of a
vestigial talonid on the M₁ not seen in other *Dinofelis* specimens. However, Ewer (1956) considered that this was a vestigial trait variably expressed and thus of little taxonomic significance. Reed (1996) classified the Makapansgat specimen as *Dinofelis* sp., principally on the basis of the M₁ talonid and the narrow width of this tooth. To clarify these points, it must be noted that a talonid similar to M 607 is expressed in *D. piveteaui* from Motsetse (MT 02) and *D. barlowi* from Sterkfontein (Sts 5853). Therefore, in agreement with Ewer (1956), we discount the taxonomic significance of this trait. Additionally, although the width of the M₁ on M 607 is smaller than in other samples of *D. barlowi*, the differences are very slight (Fig. 11).

More recently Werdelin and Lewis (2001) reinstated Toerien’s original specific designation for the Makapansgat material. Werdelin and Lewis (2001: 237) based this re-classification on differences in the length of the P₃, although these authors also mentioned an ‘ensemble of features’ seen in this specimen. This variation clearly derives from the small size of the P₃ length in M 607. Therefore, while metrical variation of the P₃ and M₁ in M 607 falls within the range of variation in other *Dinofelis* species (easily within *D. barlowi*, also see Figs 10 and 12), the ratios involving the P₃ length will show differences by virtue of the size of this tooth alone. Although the M 607 P₃ is admittedly a small tooth, its morphology is similar to that of other *D. barlowi* specimens (i.e., STS 131) in the lack of a prominent anterior cusp. *Dinofelis piveteaui*, by contrast, shows strongly developed anterior cusp(s). *Dinofelis barlowi*, on the other hand, shows a more blade-like appearance (i.e., MT 04 and GV-DS-1). Ewer (1956) argued that the variation observed between the *D. barlowi* material and M 607 was no greater than the variation observed in modern leopards, and the overall robustness of the mandible and the morphology of the masseteric fossa and ramus are similar to other specimens of *D. barlowi* (i.e., ST 5853). To test this, the coefficient of variation (CV) was calculated for P₃ length in modern leopards and *Dinofelis*. The CV value for our sample of *P. pardus* is 10.9 while the CV value of all southern African fossil *Dinofelis*, corrected for small sample sizes following Sokal and Rohlf (1981), is 11.1, indicating no significant differences. Figure 11 shows logarithmic plots of the length and breadth of P₃ of *P. pardus* and of the known *Dinofelis* material from southern Africa. M 607 falls at the extreme of the variation seen in fossil specimens due to its short length and relative width. However, these differ-
ences are comparable to the variation observed in our wide sample of leopards.

To summarize this section on M 607, the expression of non-metric traits in this specimen can be described as follows:

- The talonid morphology on the M607 M1 has been reported in other *Dinofelis* M1.
- As in other *D. barlowi* specimens, the P3 on M 607 does not have a prominent anterior cusp.
- Less blade-like appearance of both premolars of M 607.

These traits indicate that M 607 is most similar in morphology to other *D. barlowi* specimens. Additionally, the metrical variation displayed by the length of P3 with regards to other *Dinofelis* specimens is similar to the range of variation in modern leopard. We therefore find no strong evidence in the size of a single tooth to support the attribution of M 607 to a new species of *Dinofelis*. We would propose a more conservative interpretation, and in agreement with Reed (1996), we suggest that M 607 be attributed to *Dinofelis* sp. pending further discoveries at the site.

**DISCUSSION**

The new *Dinofelis* dental remains from Cooper’s, Motsetse, and Gladysvale caves add important information to the variation of material assigned to the species *D. piveteaui* in particular, and also within the genus. The Motsetse M1 is a very long and narrow tooth (Figs 2F, 10), the protoconid being the largest cusp. The only previous M1 specimen assigned to *D. piveteaui* in South Africa is KA 63, which has suffered an unfortunate recent break on the anterior region of the paraconid that precludes us from taking direct measurements. Cooke (1991: 14) indicated that the protoconid is shorter in *D. piveteaui* than in *D. barlowi*. If the taxonomic attribution of the Motsetse specimen is correct, it may indicate that the protoconid is in fact the largest cusp on the M1 of *D. piveteaui*.

The Motsetse lower carnassial appears to indicate a temporal trend in that the lower carnassials of *Dinofelis* increased in length but not in width. This feature is shown in Fig. 10, which presents logarithmic plots of length and breadth of *Dinofelis* from southern Africa. Ewer (1955) reported 16.9 mm as the width of the referred Kromdraai *D. piveteaui* M1, KA 63. Werdelin and Lewis (2001) questioned the validity of this measurement as it appeared too broad (their Fig. 36, p. 206). Our measurement of the Kromdraai specimen (Table 2) supports the claims of Werdelin and Lewis (2001).

The Motsetse P4 specimens possess a cuspulid on the medial side of the tooth, which is also present...
in material assigned to *D. piveteaui* from Kromdraai (KA 62). The presence of this feature on the three best preserved P4 specimens assigned to *D. piveteaui* (albeit with variable prominence), may prove to be of some taxonomic relevance with further discoveries.

The morphological characters present on Motsetse and Gladysvale P4, reduction of the protocone and increased length of the metastyle, support the interpretation of Cooke (1991) of the variation in the values of the ratios between these two traits in *Dinofelis* species. Cooke (1991) defined *D. piveteaui* and *D. barlowi* with a ratio between protocone/metastyle of 2.2 for the Sterkfontein *D. barlowi* and 3.1 for *D. piveteaui*. Marean (1989) and Werdelin and Lewis (2001) interpreted this morphological change in the dentition of *D. piveteaui* as a convergence towards the typical ancestral morphology of the machairodont cats, since *Megantereon* and *Homotherium* display such a pattern. However, recent analysis of remains of *Machairodus*, the likely ancestral genus to *Homotherium*, from the later Miocene site of Batallones in Spain (Antón *et al.*, 2004) suggest that this was not the case, since the post-canine dentition of *Machairodus* is essentially pantherine.

Pearson’s correlation coefficient was performed on data for P4 presented in Table 1. Results indicate that there is a strong correlation between the reduction of the protocone and the enlargement of the metastyle ($r = 0.95$). This interpretation is supported by Fig. 13 which shows an inverse correlation between the log-transformed values of both features, indicating that the increase in size of the metastyle is accompanied by a decrease in width of the P4 at the protocone.

There are other functional aspects of the masticatory apparatus that can be considered. For example, the distal portion of the P4 metastyle in modern lions and leopards is not in direct contact with the M1 protoconid during full occlusion. They do come into contact during the occluding motion as the metastyle and the parastyle create a shearing platform with the cusps of the lower carnassial. The vestigial M1 usually makes contact with the distal and lateral part of the M1, and it is common to see wear facets in this region of the M1. Thus, an extension of the P4 metastyle, which increases the total length of this tooth, means that the vestigial M1 is pushed to a more posterior position in the maxilla (unless a more general reorganization of facial structures takes place) and becomes non-functional unless there is a similar increase in the M1 length. Therefore, it is to be expected that *D. piveteaui*
would show a relative increase on the M1, and thus the morphology of the lower carnassial seen in Fig. 2F is precisely what might be predicted from the known morphology of the upper carnassial in the type specimen of *D. piveteaui*.

**CONCLUSIONS**

Species definition in the fossil record is one of the most challenging tasks in palaeontology. In the case of feline cats, assessments are hampered by small and fragmentary sample sizes, and there are few characters that discriminate between similar-sized species such as lions and tigers. The present study of the recently discovered *Dinofelis* material from the South African caves has indicated that assessments of the P3/M1 complex are taxonomically useful. Using this functional complex, at least two populations of *Dinofelis* can be recognized in southern Africa based on the presently available samples. These are *D. barlowi*, which comprises specimens from Langebaanweg, Sterkfontein, Makapansgat and Bolt’s Farm, and *D. piveteaui* from Motsetse and Kromdraai. This distinction also reflects a chronological separation. However, in view of the small size of the Cooper’s Cave mandible and the small size of the dentition, alternative working hypotheses cannot be discounted. For example, the Cooper’s Cave material may represent females of *D. piveteaui*, with males being represented at Gladysvale, Kromdraai and Motsetse, or there may be more taxonomic complexity in the South African Plio-Pleistocene cave sites of the Sterkfontein Valley, with the presence of at least one more group of *Dinofelis*, than the two groups described above.

The extinction period of most of the Pliocene and Plio-Pleistocene larger cats and hyaenas has been broadly established at c. 1.5 Ma (Turner and Anton, 1998), although, as has been pointed out by Marean (1989), the fossil record in East Africa after that period is poorly known. The most recent last appearance date proposed for *D. piveteaui* is estimated to be c. 1.0 Ma at Kanam East, based on palaeomagnetic data (Ditchfield et al., 1999), but this remains to be confirmed. Turner (1990a) indicated the possibility that some of the extinct large African carnivores would have dwelt longer in the southern part of the continent than in eastern Africa based on a delay of the onset of grassland expansion, and indeed there are records of *Megantereon* at the site of Elandsfontein, in the Western Cape, which have been dated to c. 700–400 ky (Klein & Cruz-Uribe, 1991). However, it is noteworthy that there are elements in this faunal assemblage that may indicate a certain amount of mixing (G. Avery, pers. comm.). For example, the species *Metridiochoerus andrewsi* recorded at this site has its last appearance date in East Africa at c. 1.7 Ma (White, 1995). As the present records stand, the last recorded presence of *Megantereon* in East Africa is dated to c. 1.4 Ma in the Okote Member of Lake Turkana, although, as Turner & Anton (1998) have pointed out, newer discoveries may change the timing of extinction patterns of the larger African carnivores.

**ACKNOWLEDGEMENTS**

We are indebted to Dr Hannah O’Regan for allowing us to use leopard data obtained by her. Margaret Avery, Graham Avery and Deano Stynder of the South African Museum in Cape Town are thanked for their assistance with the Langebaanweg collection. F. Thackeray and Stephany Potze of the Transvaal Museum kindly allowed access to the collections of the Transvaal Museum and S. Potze prepared the Gladysvale skull. The Palaeo-Anthropological Scientific Trust (PAST) is thanked for generously funding this research project.

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