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Cooke, H B S

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DINOFELIS BARLOWI (MAMMALIA, CARNIVORA, FELIDAE) CRANIAL MATERIAL FROM BOLT'S FARM, COLLECTED BY THE UNIVERSITY OF CALIFORNIA AFRICAN EXPEDITION

by

H.B.S. Cooke

2133 - 154th Street, White Rock B.C., Canada V4A 4S5

ABSTRACT

The collections made by the University of California African Expedition in 1947-48 at Bolt's Farm, near Sterkfontein, included some fine cranial and postcranial material of *Dinofelis barlowi*, associated with baboon skeletons and crania suggestive of a natural trap situation. The *Dinofelis* crania are described and compared with other species of this genus, generally lending support to Hemmer's view of a lineage *D. diastemata, D. barlowi, D. piveteaui*. The age of the deposit is estimated to be in the vicinity of 2 Ma.

INTRODUCTION

Bolt's farm lies due south of the celebrated ape-man site of Swartkrans and 3 km southwest of the Sterkfontein locality (fig. 1). Chance finds of fossils were made during small-scale lime quarrying operations by the farm owner, Mr W. Bolt, and by Dr Robert Broom in his reconnaissance of the area in 1936; several interesting specimens have been described, notably by Broom (1937, 1939, 1948) and Shaw (1938). In 1947 and 1948, the area was studied systematically by the Southern Section of the University of California African Expedition, under the leadership of Dr Charles Camp. A number of small patches of breccia were located and a considerable amount of fossil material was recovered by Dr Frank Peabody and, after crude preparation in the field, it was shipped back to the University of California at Berkeley for curation. At the invitation of the Director of the Museum of Paleontology, Dr R.A. Stirton, the present writer spent the period October 1957 to June 1958 at Berkeley for the purpose of developing and identifying the material but the resulting Report was not published. Peabody (1954) had completed a valuable account of the geology of the Taung deposits, including a list of the fossils then identified, but his untimely death in 1958 occurred before he had prepared any account of the material from the Transvaal deposits. However, the present writer was fortunate in having useful discussions with Dr Peabody and access to his field notes, as well as a subsequent opportunity to examine the deposits in the field . The collections were re-examined in 1975 during a lengthy stay in Berkeley and again updated in 1983 during a shorter visit. A new mustelid from Pit 10 has already been described (Cooke, 1985) and accounts of other "highlights" from the collections are in preparation, but the bulk of the material remains largely unpublished.

THE BOLT'S FARM DEPOSITS

The geological setting of the australopithecine breccias in the Sterkfontein area has been well described by Brain (1958), whose masterly analysis of the mechanisms of formation of the deposits and the characteristics imposed on the sediments by their genesis is still probably the best model available. Bolt's Farm was not specifically included in Brain's account. The cavities in which the breccias were deposited were formed in the dolomite limestones of the Chuniespoort Group of the Transvaal Sequence and have a generally northerly to northwesterly dip, varying locally as a result of minor folding. On Bolt's Farm the inclination is around 15° towards the northwest. The solution fissures on the farm are related to a joint or fracture system orientated at approximately 065° east of north, and there is a secondary fracture system at about 160°, solution having taken place most readily at the intersections of these two fracture systems.

Dr Peabody carried out a plane table survey of the Bolt's Farm area and assigned numbers to the individual collecting localities. Figure 1 is redrawn directly from his map and the names assigned to the localities are given in Appendix "A", together with the University of California Museum of Paleontology locality numbers. Topographically this area consists of the greater part of a rounded hill the crest of which is formed by a chert-rich zone in the limestones and rose some 50m above a small seasonal creek that runs northwards on the east side of the hill. Most of Peabody's sites have been destroyed in recent years by extensive quarrying and reliance must be placed on Peabody's field notes and on notes made in 1958 by the present writer.

The individual sites at Bolt's Farm were not comparable in scale to those of Swartkrans or Sterkfontein and in general consisted of residual pockets of material, the

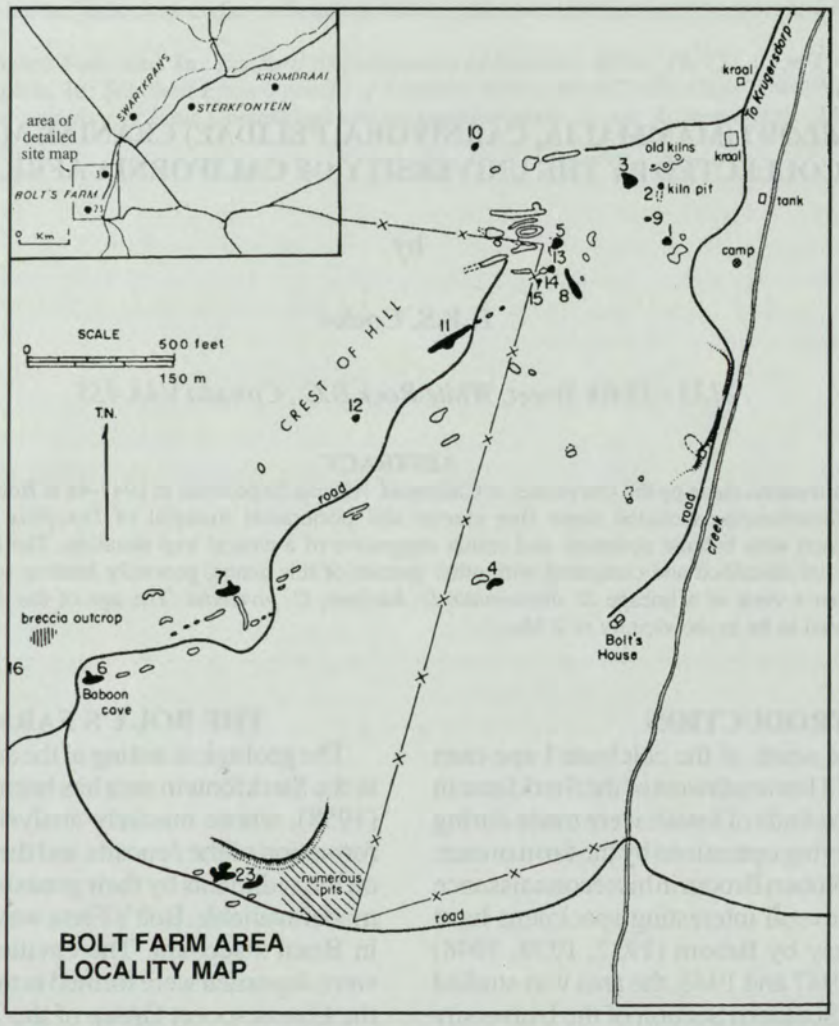

Figure 1. Plan of a portion of Bolt's Farm showing the localities worked by the University of California African Expedition in 1947-48 (from a plane-table survey by Dr. F.E. Peabody). The names and University of California locality numbers are given in Appendix A. The *Dinofelis* came from the southernmost site, Pit 23 (UCMP Loc. V-4888). Inset shows the relationship to the well-known australopithecine cave breccia localities.

relationship of which to the former walls and floors of the original cavities could not be determined. Few of the sites were rich in fossils but in the aggregate they have furnished very substantial collections of fossils and it is probable that they differ somewhat in age. The matrix in which the bones occur is usually a little darker than the typical so-called "pink" breccia from Sterkfontein and resembles rather the material from Swartkrans and Kromdraai. The colour is nearest to the "moderate brown" (5 YR 4/4) of the Rock Colour Chart of the Geological Society of America but some samples may trend in the direction of moderate or pale reddish brown (10R 4/6 and 10R 5/4). Mineralogical analyses confirm the general resemblance to the Swartkrans and Kromdraai deposits, as indicated by Brain's data (1958). In a number of cases the consolidated breccia is overlain by a "loose fill" of dark uncemented debris, often containing identifiable bones of living species and sometimes stone flakes or artefacts. Occasionally parts of the breccia have been decalcified and may resemble the "loose fill". For the record, the various sites and taxa identified from the breccias are given briefly in Appendix "A", The most interesting deposit, from which the fine *Dinofelis* material came, is Pit 23, and it is described below.

"TIT HILL PIT", NO. 23

Peabody's Pit 23 (UCMP Locality V-4888) was nicknamed "Tit Hill Pit" and is of particular interest as the breccia is unusually rich in bone, representing the remains of a relatively small number of individuals whose cranial and postcranial skeletons are preserved, although not generally in articulation. The vast amount of postcranial material was only partially developed for display purposes and not all the cercopithecoid cranial remains were extracted by the present writer in 1957/58. Cercopithecids are dominant and from the cranial remains it would appear that not fewer than 8 and not more than 15 individuals left their skeletons in the deposit. Surprisingly, they belong to three distinct genera, the two baboons *Parapapio broomi* and *Papio robinsoni*, together with the colobine *Cercopithecoides williamsi*. The best cranial material was sent to Dr Leonard Freedman, who described it in 1965, then including a fourth species *Parapapio whitei* now synonymized with *P. broomi*. Subsequently all the

cercopithecoid material was studied by Dr Eric Delson at the American Museum of Natural History, further developed and reassessed. The co-occurrence of these three primates would, according to the criteria discussed by Delson (1984), suggest an age for the deposit very close to 2.0 Myr. The other major element comprises three felid crania referred to *Dinofelis barlowi*, as well as a large number of postcranial bones, including some limb segments in partial articulation. Only the cranial elements will be considered here as the postcranial material is at present being extracted and studied by Dr Curtis W. Marean, who will describe it in due course, adding immensely to our knowledge of the genus and its functional anatomy. He has already (Marean, 1989) given an interesting discussion of the probable habits of the African sabre-toothed cats. According to Dr Marean (in litteris) there is one large carnivore astragalus that is distinct from those assigned to *Dinofelis* and similar in some respects to material referred to *Homotherium*.

The unique character of this association clearly demands some abnormal mode of occurrence. The felids are an adult male and female and a younger individual, probably male, so that it is likely that they represent a single family. Their presence is suggestive of some sort of trap into which they fell and from which they could not escape – a natural game-pit in fact. Such a trap could also account for the presence of the baboons, which include at least two infants that might have been riding on their mothers' backs. Both cat and baboon coprolites occur, showing that some animals were alive for a time at least, and yet the deposit is quite unlike a den or lair. The only other identifiable fossils are passerine bird skull and limb bone, a few fragmentary bones of a canid (probably a jackal), and an assortment of bits of small insectivores, rodents and lizards in the typical "rodent" breccia derived from owl pellets. The absence of any bovid or equine remains is in striking contrast to their normal abundance in the cave breccias and this may suggest that the opening of the inferred trap was in a rather inaccessible location such that only agile animals could be trapped. An opening within an elevated rocky outcrop might meet these requirements, but it must be admitted that these inferences are speculative.

DESCRIPTION

Dinofelis barlowi (Broom, 1937)

Meganthereon barlowi Broom, 1937, 1939
Machaerodus transvaalensis (Pars) Broom, 1939
Therailurus barlowi Ewer, 1955
Machaerodus darti Toerien, 1955
Dinofelis barlowi Hemmer, 1965

A damaged skull (Transvaal Museum 1541) and an upper canine (TM 1542) from the Sterkfontein Type Site were described by Broom in 1937 as a new species, placed in the genus *Meganthereon* as *M. barlowi*, primarily because of the size and form of the upper canine. A brief description of the upper carnassial was added two years later (Broom 1939) and in this paper another new species was described as *Machaerodus transvaalensis* on the basis of a canine from Sterkfontein, together with a left upper carnassial (TM 1579).

In 1955, Ewer described a new species, on the basis of a good cranium from Kromdraai (TM Ka 61) with the cheek teeth, basicranium and zygomatic arches almost perfectly preserved but lacking most of the frontals and the saggital crest; there were also two mandibular fragments (TM Ka 62, 63). Ewer referred this material to the European Pliocene genus *Therailurus* and named the Kromdraai form *T.piveteaui* in honour of the founder of that genus. At the same time she described a much crushed and broken skull with some associated mandibular fragments (TM STS 131) and the tip of an upper canine (TM STS 132) found at the Sterkfontein Type site, assigning it to Broom's species *barlowi* but placing this in the genus *Therailurus*. She also withdrew from *Machaerodus transvaalensis* the upper carnassial Broom had included with the type canine and referred this tooth to *Therailurus barlowi*. While Ewer's paper was still in the press, Toerien (1955) described a mandibular ramus and the anterior portions of a snout and mandible from the Makapansgat Limeworks, naming it *Machaerodus darti*, although mentioning the similarity of the canine to that of *"Meganthereon barlowi"*. In 1956 Ewer indicated that *darti* should be regarded as a synonym of *Therailurus barlowi*.

A decade later Hemmer (1965) reviewed the genotypical species of *Therailurus, T. diastemata* and concluded that it belonged to the same genus as the northern Chinese *Dinofelis abeli* Zdansky 1924, which genus therefore had priority. Hemmer suggested that *Dinofelis diastemata, D. barlowi* and *D. piveteaui* formed a connected succession while *D. abeli* was more isolated morphologically. Subsequently he proposed (Hemmer 1973) that *"Felis" cristata* Falconer and Cautley 1836 from the Pinjor stage of the Siwaliks in India and *"Panthera" palaeoonca* from the Blancan of Texas should also be regarded as species of *Dinofelis* and he endeavoured to show some degree of temporal relationship in the relative increase in lengths of the carnassials as expressed in the ratios P^4/P^3 and M_1/P_4.

Material: Bolt's Farm, Pit 23 (UCMP Loc. V-4888): Cranium and mandible, TM BF 55-22, 23 (cast UC 113720); smaller, damaged cranium, UC 69506, and associated mandibular rami; crushed remains of cranium and mandible, UC 64443; numerous associated postcranial bones, UC 69525-69530, 80286-80288, 80309-80310, 88754-88802.

The best cranium and its associated mandible have been given to the Transvaal Museum, Pretoria (TM BF 55-22,23) and casts are retained at the Museum of Paleontology in Berkeley. It is convenient to designate this skull as "A" and it is believed to have been an adult male. The second skull, "B", is also well preserved, but smaller and is considered to have been an adult female (UC 69506); the

two halves of its mandible are incomplete. The third skull, "C", is extremely crushed and distorted, the lower jaw having been driven partly into the cranium and twisted sideways (UC 64443). It is thought that this skull belonged to a full-grown, but still youthful, male animal as it appears to be almost as large as skull "A"; exact measurements are not possible.

The Cranium: Skull "A" is very well preserved, the main damage being corrosion of the right side of the braincase in the frontal region, damage to the jugal, to the squamosal and to the tympanic areas. There is no obvious distortion or crushing and it has been possible to restore the missing parts with considerable accuracy. The zygomatic arches are lost and their original contour is a little uncertain. The extreme tip of the premaxilla is missing and the incisors are broken or lost, except for RI^3. Both canines are present, although the tip of the right one is damaged. On the left side P^3, $P^4$and M^1 are reasonably well preserved, but on the right side all are damaged, P^4 only slightly so. The cranium is shown in lateral aspect in Figure 2A and a palatal view is given in Figure 2B. Measurements are set out in Table 1.

TABLE 1
Measurements on crania of Transvaal *Dinofelis*

	BOLT'S FARM PIT 23			
	'A'	'B'	Type	Ratio
	TM/BF 55-22	UC 69506	TM/Ka61	Piv/'B'
Skull height (sagittal crestabove foramen magnum)	60 e	58 e	71	1,22
Occiput height	54 e	52 e	61 e	1,17
Condylobasal length	246	230 e	223 e	0,97
Basilar length	227	206 e	198 e	0,96
Bizygomatic breadth	184 e	168	186 e	1,10
Length of zygomatic opening	55	49	44	0,90
Cranial width	82	-	-	-
Width of nasal opening	39	-	39 e	-
Width of nasal bones at anterior end	41 e	-	40 e	-
Bulla length/breadth	42/26,5	44/27	42/26	0,95/0,96
Palate length ($I\text{-}P^4/P^4$ line)	105	96	96 e	1,00
Width across incisor row ($I^3\text{-}I^3$)	43,5	39,5	45	1,14
Width of palate behind canines	69	61	66	1,08
Width of palate across outside $P^4\text{-}P^4$.	116	104	117	1,13

e= estimated measurement

Skull "B" is 8-9% smaller than skull "A", as will be noted from the comparable palatal views in Figure 2c and the measurements in Table 1. The left zygomatic arch is broken but that on the right side is intact. The tip of the premaxilla is broken away and only the socket of the RI^3 is preserved. Both canines are marked by matrix-filled alveoli but a pair of detached canines was found in the block and it is possible that they belong to the skull. The first molars are lost. LP^3 and LP^4 are intact but those of the right side are damaged. The nasal and frontal areas are well preserved but the back of the parietal and the lambdoidal ridge are broken.

Skull "C" is badly crushed, although the back of the palate and the basicranial region, including the auditory bullae and occipital condyles, are moderately intact. The mandible is apparently complete but was driven obliquely upwards and the left ramus, from canine to M_1, can be seen against the maxilla while, on the other side, the right P^3 and P^4 are exposed against the middle of the right ramus.

It seems reasonable to regard any differences between "A" and "B" as due to sexual dimorphism but, as size alone tends to be deceptive, Figure 3A has been prepared to compare the palatal aspects by enlarging "B" to the same condylobasal length as "A". The fit is surprisingly close, with only minor differences in the sutures which are probably within the range of individual variation. "A" does seem to be slightly broader and the restoration of the zygoma in "A"may well be an underestimate. "A" appears to have the cheek teeth slightly farther forward and they lie a little closer to the wall of the maxilla. There are some differences in the auditory bullae, that in 'A' being antero-posteriorly more compressed, somewhat like that of the tiger. The bullae are not greatly inflated and are largely hidden in profile view by the large mastoid processes and paraoccipital process. Both processes are relatively smaller in "B" than in "A".

The charcteristics of the skull in *Dinofelis piveteaui* have been well described by Ewer (1955) and major features of four species were compared in tabular form by Hemmer (1965). However, the cranium of *D. barlowi* has been known hitherto only by very poorly preserved material and it seems useful to comment on features shown by the Bolt's Farm crania. The braincase is inflated and the interorbital constriction may be slightly narrower than the postorbital constriction, whereas in the living large cats the converse is usually true. The postorbital process is short and blunt with the tip curving downwards. The occiput is narrow and resembles that of the leopard more than that of either lion or tiger. The mastoid process is large and lies closer to the post-glenoid than to the large paraoccipital process; the latter wraps around the bulla to about the same extent as in the lion. The enlarged mastoid process extends forwards under the external auditory meatus. The styliform process is weakly developed. The stylomastoid process is fairly well back and is unusually large and well separated from the medial vertical wall of the mastoid process. The bullae are relatively short and the glenoid process has the appearance of being "pushed back" towards the mastoid process, giving a sharp curvature to the root of the zygoma, unlike the gentle sweep in the leopard. The glenoid fossae are almost perpendicular to the axis of the skull and lie well above the occlusal plane. The articular surfaces of the glenoid are short and the zygoma curves forward rather abruptly (see Figure 2B). The anterior border of the premaxilla is wide and broadly rounded, being less rounded than in the leopard and not as

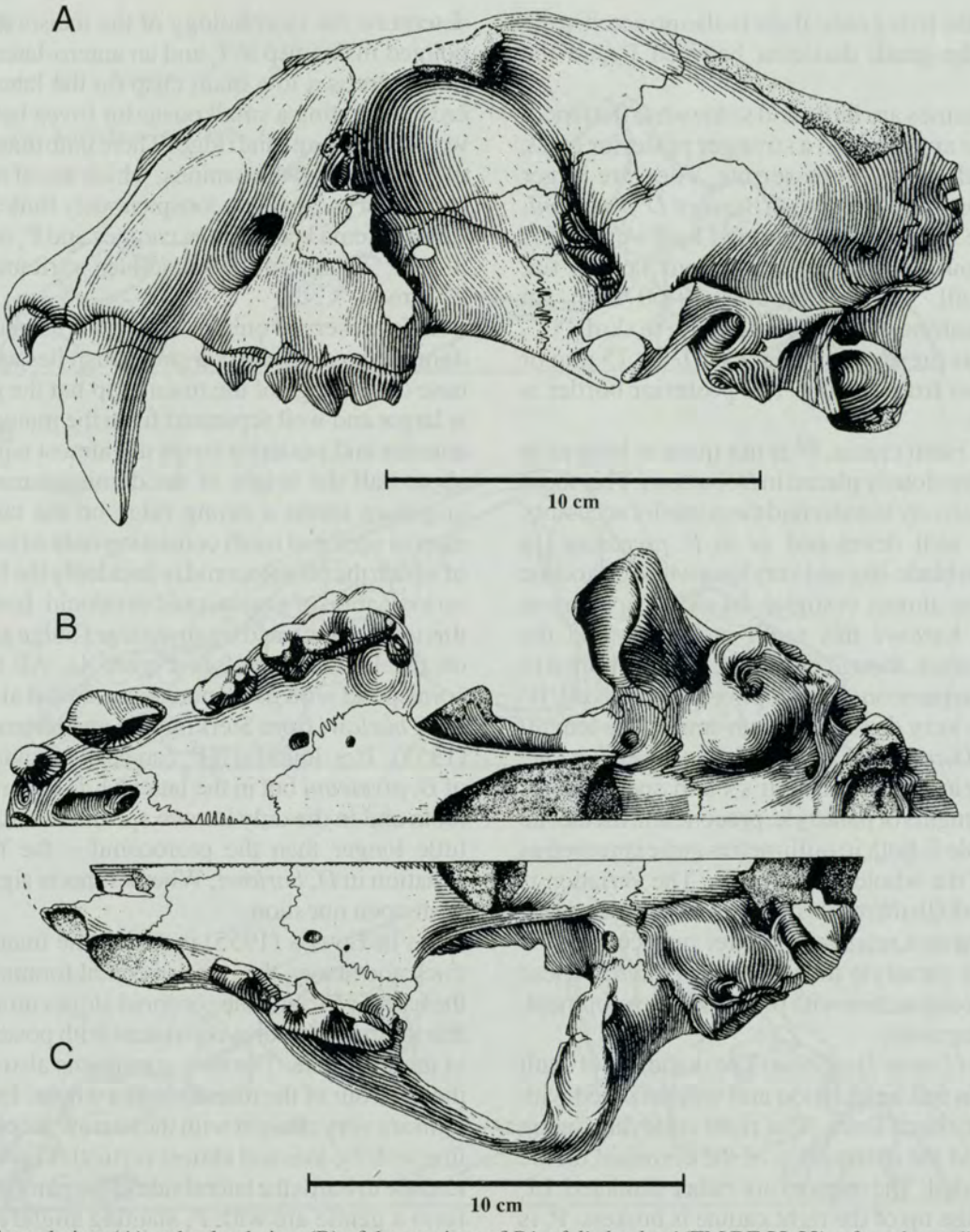

Figure 2. Left lateral view (A) and palatal view (B) of the cranium of *Dinofelis barlowi* (TM BF 55-22) referred to as "skull 'A'". Palatal view of "skull 'B'" is given in C, aligned on the back of the palatine to show differences in size. (One-half natural size)

"squared off" as in the lion and tiger. Immediately behind the canines the palate is constricted and then widens lion and tiger. Immediately behind the canines the palate is constricted and then widens rapidly so that P^3 is set at a slight angle to P^4 (see Figure 2C). Behind M^1, the border of the palate is perpendicular to the axis of the skull, then curves abruptly towards the back to flank a rather wide palatine notch. This notch is rounded in a single smooth curve, unlike the rather rectangular shape seen in lion and tiger or the double curve usually found in the leopard. The mid-line of the palatine extends only a little way behind the back of the maxilla at M^1 - M^1, unlike the prolonged palatine found in leopard, lion and tiger. Both the precanine and postcanine diastemas are short. Although the large canines require an expanded area of the maxilla to house their roots, the snout is not very much wider than in the leopard (about 75mm compared with 60 - 65 mm) and the nasal aperture is almost exactly the same size as in the leopard.

Upper dentition: The upper incisors are all badly damaged, with the exception of the left I^3 in skull "A". This has a simple pointed main cusp with a moderately well developed posterior wear fossette; the tooth is gently curved. It is slightly longer and narrower than in *D. piveteaui* (see Table 2). The width across the incisors is 43.5 mm. The central incisors were clearly smaller than I^3. As in the true sabre-toothed cats, the incisors were set in a very gentle curve, unlike the almost straight

arrangement in the living cats; there is also no notch in the premaxilla in the small diastema between I^3 and the canine.

The upper canines are large and somewhat flattened, with a moderate anterior and a stronger posterior crest, neither of which seems to be serrate. They are larger antero-posteriorly and wider than those of *D. piveteaui*. In the latter the canine was estimated by Ewer (1955) to be only about 40-45 mm long from jaw to tip, whereas in skull "A" it measures 59-60 mm. An isolated upper canine, possibly belonging to skull "C", is 40 mm long as preserved but lacks at least 15 mm or probably 20 mm from the tip. The posterior border is almost straight.

In the Bolt's Farm crania, P^3 is not quite as long as in the specimens previously placed in *D. barlowi*. This tooth in skull 'B' is relatively broader and the posterior accessory cusp is not as well developed as in *D. piveteaui*. In *D. piveteaui* P^4 is blade-like and very long with a protocone so weak as to be almost vestigial. In all the specimens referred to *D. barlowi* this tooth is shorter and the protocone is distinct, though not large, and it is joined to the summit of the paracone by a sloping ridge. In skull 'B' the protocone is very distinct, though small. The length/breadth ratio in *D. piveteaui* is about 3.1 and in *D. barlowi* from Sterkfontein and in the Bolt's Farm specimens is about 2.2. The lengths of parastyle, pracone and metacone are given in Table 3, both in millimetres and expressed as a percentage of the whole length of P^4. The variation is fairly large, although there does seem to be a tendency for *D. barlowi* to have a relatively shorter metacone and a relatively larger parastyle than in *D. piveteaui*. These trends, taken in conjunction with protocone development, are probably diagnostic.

Mandible and Lower Dentition: The mandible of skull 'A' was found in full articulation and was detached with great skill by Richard Estes. The right condylar region was missing, and the extreme tip of the coronoid on the left side is corroded. The incisors are rather damaged, LI_1 being lost, and the tip of the right canine is broken. P_3 is broken but P_4 and M_1 are present on both sides, the right ones somewhat damaged. The jaw is illustrated in Figure 4. The mandible believed to belong to skull 'B' is much damaged on the left side but retains the canine, P_4 and M_1; the right ramus is well preserved, though lacking incisors and with the canine damaged, but P_4 and M_1 are almost intact. The badly crushed skull displays the lower aspect of the mandible and it proved possible to expose the teeth of the left side, which included P_3, and these teeth are illustrated in Figure 4C. The dimensions are given in Table 4.

The size and general form of the jaw resemble a large leopard but the symphysis is wider, shorter and flatter, tending towards the form of the tiger symphysis. The incisors are about the same size as those of the lion and are also arranged in a similar very gentle curve – almost a straight line. They are placed well above the occlusal plane of the cheek teeth. Damage makes it difficult to determine the morphology of the incisors, but there is a pointed main cusp in I_3 and an antero-lateral wear facet. In I_2 there is a low main cusp on the lateral side of the crown, creating a small posterior fovea between it and a weak postero-medial ridge. There is no diastema between the incisors and the canines, which are of moderate size, gently curved and not conspicuously flattened or ridged. The diastema between the canines and P_3 is about 25 mm in "A", 22 mm in the mandibles attributed to "B" and 21 mm in "C".

P_3 is preserved only in "C" and is a small tooth with a dominant central cusp; a small cusp lies anteriorly at the base of the ridge of the main cusp but the posterior cusp is larger and well separated from the main one. In P_4 the anterior and posterior cusps are almost equal in size and about half the height of the dominant main cusp. The cingulum forms a strong ridge on the talonid. M_1 is a narrow sectorial tooth consisting only of two main cusps of which the prototoconid is decidedly the larger. There is no indication of a metaconid or talonid. In mandible "A", this tooth is widened by an outward bulge at the cingulum on the lingual side (see Figure 4). All these features correspond with those noted in material already referred to *D. barlowi* from Sterkfontein and Kromdraai by Ewer (1955). It is doubtful if P_4 can be distinguished from that of *D. piveteaui* but in the latter M_1 is apparently a stouter tooth and in the only known specimen the paraconid is a little longer than the protoconid – the reverse of the situation in *D. barlowi*. Whether this is significant or not is an open question.

As in Ewer's (1955) material, the mandible is rather thick and heavy, the inferior dental foramen lies close to the back of M_1, and the coronoid slopes up sharply behind this tooth, all features consistent with posterior reduction in the mandible. The new specimens also serve to show the contour of the mandible as a whole. In plan view the rami are very straight with the narrow ascending ramus in line with the axis and almost vertical (Fig. 4A). The cheek teeth lie towards the lateral side of the ramus but themselves form a gentle arc with P_3 slanting slightly inwards. The mental foramen is below the front of P_3. In profile the inferior border is almost flat from the base of the rather flattened symphysis to a point below M_1, then rises gently before curving down to a robust angular process (Fig. 4B). The angular process extends well behind the condyle, whereas the back of the coronoid process is directly above the back of the condyle. The ascending ramus rises fairly steeply behind M_1 and the distance from the back of M_1 to the condyle is only 36-37% of the length of the jaw from the front of the incisor sockets to the condyle, which is shorter than in the leopard or lion and more like the tiger. The coronoid process is also relatively short.

Ewer's (1955) reconstruction of the back of the ramus in the left mandible Ka 63 from Kromdraai, referred to *D. piveteaui*, shows a very small angular process lying in front of the condyle and this may well be incorrect, unless there is a significant departure from the situation in *D. barlowi*.

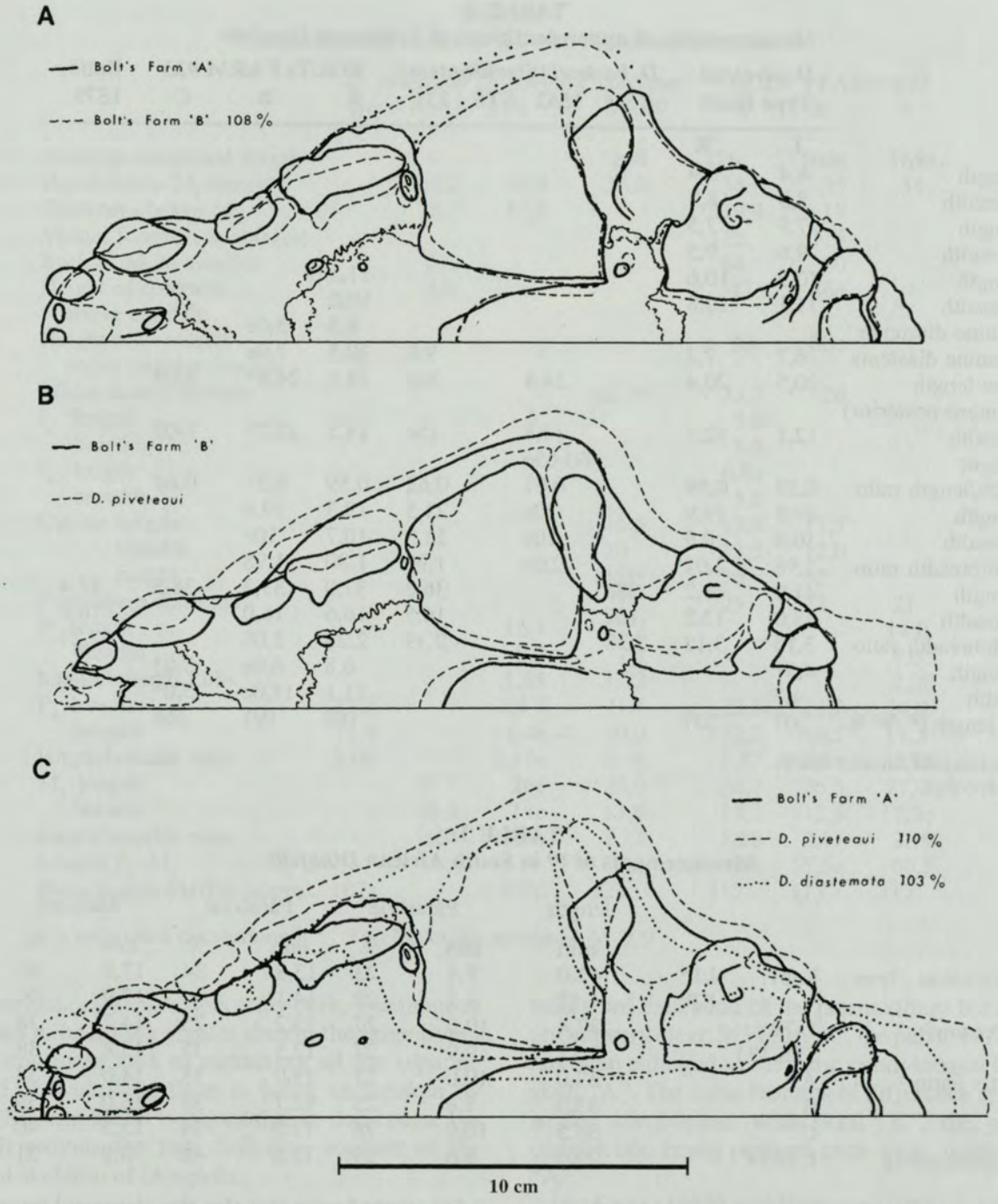

Figure 3. Comparative outlines of palatal aspect of different specimens of *Dinofelis*. A compares the two Bolt's Farm skulls 'A' and 'B' with 'B' enlarged to the same condylobasal length as 'A'. B compares skull 'B' with the similar-sized type cranium of *Dinofelis piveteau* and with a specimen of the European *D. diastemata*, both enlarged to the same condylobasilar length as 'A'.

Ewer (1955), in her consideration of *D. piveteaui* attempted to estimate the height of the coronoid above the condyle of the lower jaw by assuming that it followed the normal feline pattern of being 70 - 80% of the zygomatic opening. In skull "A" the zygomatic opening is 55 mm, 80% of which would be 44 mm. However the height of the coronoid as preserved is 42 mm and it is reliably estimated to have been close to 47 mm (or 85% of the opening). For skull "B" the zygomatic opening is 49 mm, yet restoration indicates that the height of the coronoid was close to 46 mm, or more than 90% of the size of the zygomatic opening. This suggests that Ewer's interesting formula does not work well for *Dinofelis*.

Wear on the teeth: Although the canines in skull "A" are damaged, they show signs of wear on the antero-lingual surface, which is matched by very weak facets on the lower canines. However, the main wear on the lower canines, both in "A" and in "B ", is on the lingual face, away from any possible interaction with the upper teeth. This is presumably the result of rasping bones. There is also a wear facet on the antero-internal face resulting from the contact with I^3. P^3 shows no wear on the external face

TABLE 2
Measurements of upper dentitions of Transvaal *Dinofelis*

	D. piveteau Type Ka61		*D. barlowi* (Sterkfontein) 1541	1542	STS 131	BOLTs FARM #23 A	B	C	Bolts 1579
	L	R							
1^1 length	6,4	6,4							
breadth	8,5	8,7							
1^2 length	7,9	7,5							
breadth	9,6	9,5							
1^3 length	10,3	10,6				11,5			
breadth	11,1	10,8				10,0			
Precanine diastema						8,5	5,0e		
Postcanine diastema	6,7	7,2			9,0	10,5	7,0e		
Canine length	20,5	20,4		24,4	24e	24,5	24,8*	23,0	
(Antero-posterior)									
breadth	12,1	12,1		14,8	15e	14,5	12,7*	14,0	
height				60-65e					
breadth/length ratio	0,59	0,59		0,61	0,62	0,59	0,51	0,64	
P^3 length	19,8	19,9		20e	21,5	19,3	19,8		
breadth	10,0	9,9		10e	11,3	10,7	10e		
length/breadth ratio	1,98	2,01		2,0e	1,90	1,80	1,98		
P length	41,0	41,2	38e		36,2	37,0	33,3	38,5	37,4
breadth	13,0	13,2	16e		16,5	16,6	16,0		16,8
length/breadth ratio	3,15	3,12	2,38		2,19	2,23	2,08		2,23
M^1 length	4,5*					6,8	6,0e	3,0*	
breadth	4,7					11,1	11,0e	5,0*	
ratio length P^4 /P^3 %	207	207				168	191	168	

e = estimated measurement
* = alveolus

TABLE 3
Measurements of P^4 in South African *Dinofelis*

			length	Parastyle		Paracone		Metcone	
			mm	mm	%	mm	%	mm	%
D. piveteau type	Ka61	LP^4	41,0	9,4	23	13,8	34	17,8	43
		RP^4	4,12	9,2	22	14,1	34	17,9	44
D. barlowi	1579		37,4	10,0	27	13,2	25	14,2	38
	STS 131		36,2	9,9	27	12,5	35	13,8	38
Bolt's Farm	A		37,0	10,0	27	13,0	35	14,0	38
	B		33,3	7,6	23	12,7	38	13,0	39
	C		38,5	10,0	26	13,0	34	15,5	40
Langebaanweg	L 2674		29,0	8,6	29	11,5	40	8,9	31

but there is wear on most of the lingual side and the tips of the main and anterior cones are flattened obliquely. Relatively slight wear is apparent on the external surface of P_4, the tip of which just touches the heel of P_3, leaving a faint groove. P^4 has a facet or shallow groove truncating the back part of the ridge from the small protocone to the paracone, with matching wear on the antero-internal corner of paraconid of M_1. The whole of the back part of P^4 is polished on its lingual side, as is the outer surface of M_1 but there are no extra facets like those described by Ewer (1955A) in *D. piveteaui*. M_1 has dentine exposed at its tip, although it does not occlude with M_1.

Postcranial skeleton: Most of the individual skeletal elements are represented in the collections and included several blocks with articulated or partially-articulated bones. One large block (UC 88774) shows the distal end of the right femur and also the damaged remains of the lower half of the left tibia and fibula, in articulation with the astragalus and calcaneum. Another block (UC 88773) contains an almost complete left front foot with the carpal bones and metacarpals articulated but the phalanges somewhat scattered. A third large block (UC 88775) exposes much of the left scapula with the articular half hidden beneath a right hip bone, while the proximal ends of a right tibia and fibula emerge from beneath the scapula. The lower half of a baboon pelvis lies across the feline pelvis. Many additional blocks contain other parts so that the total collection includes most of the elements of the skeleton. There appear to be three size groups, the largest representing an animal not fully adult, as is shown by the state of the epiphyses. The second individual is only marginally smaller but fully grown and the third is

TABLE 4
Measurements on lower jaws of Transvaal *Dinofelis*

	D. piveteaui		*D. barlowi*	Makapan	BOLT'S FARM #23		
	Ka62	Ka63	STS 131	M 607	A	B	C
Condylo-symphsial length				154	176	160e	165e
Depth below M_1 (inner)		35,2	32,0	33,0	36	35	34
Thickness below M_1		18,7	17,5		19,4	17	
Mental foramen to condyle					122	115	
Back of M_1 to condyle		61e			64	60	
Height of coronoid above condyle		43e			47e	46e	
Height of coronoid above angular process					90e	83e	
Width across incisors				(27)*	33,7	26	
I_2 length					5,0		
breadth					5,5		
I_3 length					6,8e		
breadth					5,5		
Canine length				16,5	18,9	17,5	
breadth				10	13,5	12,0	
height				(35)*	30	32	
Postcanine diastema				21	25	22	21
P_3 length			16,1	12,2			14,0
breadth			8,7	7,1			7,0
length/breadth ratio			1,85	1,72			2,00
P_4 length	23,7		24,7	21,4	22,8	22,5	24,0
breadth	11,4		11,4e	10,0	12,2	10,5	11,5
length/breadth ratio	2,08		2,17e	2,14	1,87	2,14	2,08
M_1 length		27,7	26e	25,9	26,7	26,5	27,0
breadth		16,9	14e	11,6	14,2	12,5	12,3e
length/breadth ratio		1,64	1,85e	2,23	1,88	2,11	2,19
Length P_3 -M_1				57,5	60e	57,5e	60,5
Ratio length M1/P4 (approx. 107)			105e	121	117	117	112

e = estimated measurement *on Makapan specimen M 209

an adult but distinctly more delicately built. The range in size appears to be a little greater than in the large living cats. The enormous task of extracting all the separate bones and of evaluating them is being undertaken by Dr Curtis Marean and it is hoped that in due course his report will provide the first definitive account of the postcranial skeleton of *Dinofelis*.

DISCUSSION

The type specimen of *D. piveteaui* is very similar in size to skull "B" and the palatal aspects are very alike, as will be seen in Figure 3B. The zygomatic breadth is a little greater in *D. piveteaui*, the ratio of zygomatic width to basilar length being 94% in *D. piveteaui* compared with 82% in both the Bolt's Farm crania. The mandibular fossa is longer in *D. piveteaui* and extends to the edge of the zygomatic opening. The palate itself is wider in *D. piveteaui* and not much constricted at the postcanine diastema, as it is in skull'B'. The back of the palatine lies a little farther forward in *D. piveteaui*, level with M^1 but otherwise the palatine bones are very similar in shape. It is suspected that the left and right maxillae do not meet on the mid-line of the palate but are separated by a narrow backward extension of the premaxillary but the sutures are not very clear. In Figure 3C, the palate of *D. piveteaui* has been enlarged to the same condylobasal length as in skull "A". The same features of difference are shown as in the comparison with skull "B", the post-canine constriction being perhaps even more marked in skull "A".

As Ewer (1955) and Hemmer (1965) have noted, the frontal and occipital regions in *Dinofelis* lie at about the same height above the palatal plane, unlike the situation in most other large cats. The braincase is large and inflated, with a distinct post orbital constriction. The height of the braincase at the frontal/parietal border relative to the condylobasal length is about the same in both the type of *D.piveteaui* and in skull 'A' but the profiles are rather different (Figure 5), especially in the occipital and tympanic regions. The occiput is actually higher in *D. piveteaui* than it is in the physically larger skull "A" and the braincase thus has a relatively longer and flatter, more leopard-like profile. *D.piveteaui* displays a considerable backward extension of the lambdoid crest which overhangs the condyles by about 3 cm, compared with about half this amount in skull 'A', even if a generous

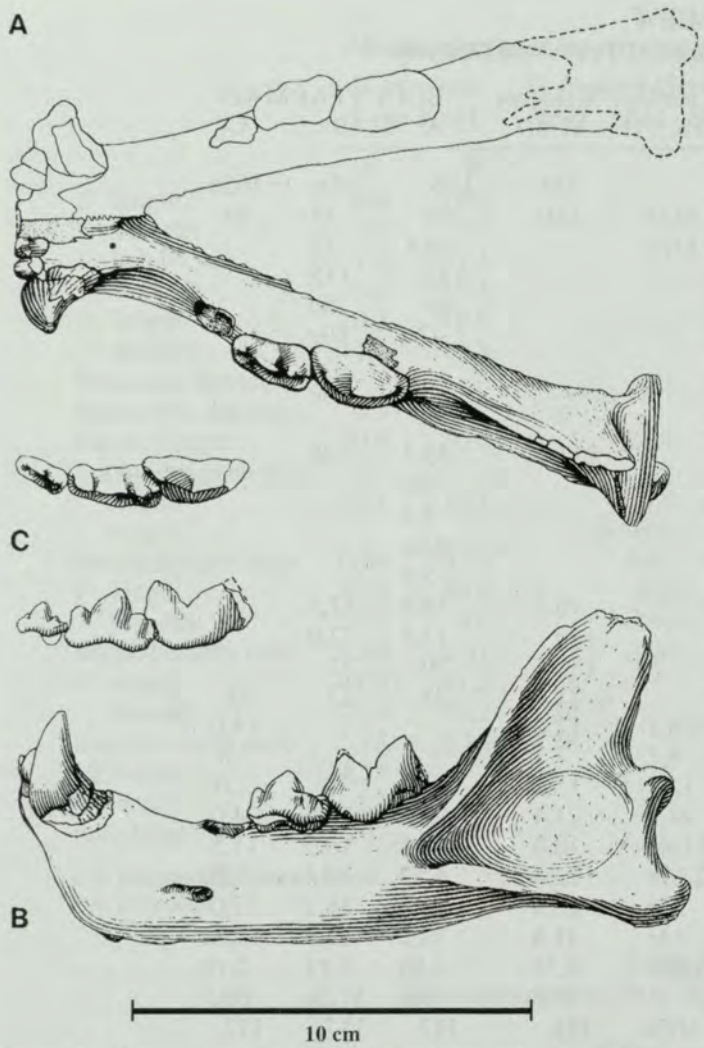

Figure 4. Dorsal view (A) and left lateral view (B) of mandible of Bolt's Farm 'A'. C shows occlusal and outer lateral views of left cheek teeth of specimen 'C'. (One half natural size).

allowance is made for possible losses in the fossil. In all three of the Bolt's Farm crania the auditory bullae are less inflated than in *D. piveteaui* and are antero-posteriorly compressed, more like the tiger than the lion or leopard. The mastoid process is large and in profile the bullae are almost hidden, whereas in *D. piveteaui* the bullae project well below the mastoid process and paraoccipital process (Figure 5). With reference to a theoretical plane from the tips of the premaxillae to the base of the occipital condyles (which might loosely be called the "basal plane") the bases of the crowns of P^3 and P^4 in the Bolt's Farm crania lie effectively *on* the plane (as in the leopard, for example) whereas in *D. piveteaui* they tilt forwards at an angle of about 8 - 9°, bringing P^3 well below the reference plane. Thus the front of the palate appears to be elevated above the "basal plane" and the canine is slightly tilted forwards rather than lying vertical. By comparison, the front of P^3 in *D. diastemata* is only slightly below the reference plane but P^4 is well below it so that the bases of the P^3 and P^4 in *D. diastemata* have a backward tilt of almost 10° from the reference plane (Figure 5). If confirmed by other material, this could be a useful diagnostic feature and is consistent with Hemmer's (1965, 1973) concept of a lineage from *D. diastemata* through *D. barlowi* to *D. piveteaui*. In the true sabre-toothed cats, the cheek teeth lie well below this reference plane.

Hitherto, the mandible has been poorly known. *D. piveteau* is represented only be a piece of the left mandible broken in front of M_1 and again through the ascenind ramus so that the back part was missing (Ka63). It was illustrated by Ewer (1955), Figure 6) with a reconstruction that does not agree very well with the mandibles of "A" or "B" from Bolt's Farm, probably underestimating the unusual enlargement of the angular process. There is also part of a right mandible from Swartkraans (SK335) which Ewer (1955) declined to identify specifically but which probably belongs to *D. piveteaui* as the rather damaged P_4 and M_1 are very similar to Ka63 and Ka64. The only other mandible is that from Makapansgat (M607) described by Toerien (1955) as *Machaerodus darti* but regarded as referable to *Dinofelis barlowi* by Ewer (1956), partly on the grounds of its general resemblance to the lower jaw of the European *D. diastemata*. In size the Makapansgat jaw is closely comparable with that of the specimen "B" from Bolt's Farm and the profiles of the two are compared in Figure 6B, aligned approximately along the bases of the cheek teeth and the condylar process. The angular process is damaged and its original size cannot be determined but it was probably not as large as in 'B'. The height of the corpus below M_1 is less in the Makapansgat jaw than in "B" but the contour of the inferior border is otherwise similar. The symphsis is not flattened, nor as high, so the base of the canine appears to be roughly on the same plane as the cheek teeth, instead of well above it as in the Bolt's Farm specimens and in European *D. diastemata*. There may be some damage or distortion of the symphsial area but this is not obvious. A rather damaged snout (M 209) figured by Toerien (1955) has a canine a little higher than in the Bolt's Farm specimens but is otherwise very similar. The portion of the symphysis resembles that of the mandible but is distorted and cannot be used to determine the original form. The Makapansgat partial premaxilla and maxilla retain almost half of each of the upper canines, which are indistinguishable from those of the Sterkfontein and Bolt's Farm specimens, leaving little doubt that it belongs to a *Dinofelis*. The incisors are smaller than in other specimens but damage makes exact measurements difficult. The lower cheek teeth are marginally smaller than in material from Bolt's Farm and Sterkfontein but the M_1 has the typical elongation of the protoconid as compared with the paraconid; there is a vestigial talonid in M_1 not seen in the other material but regarded as unimportant by Ewer (1956). The apparent difference in the symphysis makes assignment to *D. barlowi* a little uncertain, although not unreasonable.

Langebaanweg, in the southwestern Cape Province has furnished some material from "E" quarry, including several fragments and a few loose teeth, but also the two halves of a well preserved mandible (L20284) with the canines and cheek teeth on both sides, although the backs

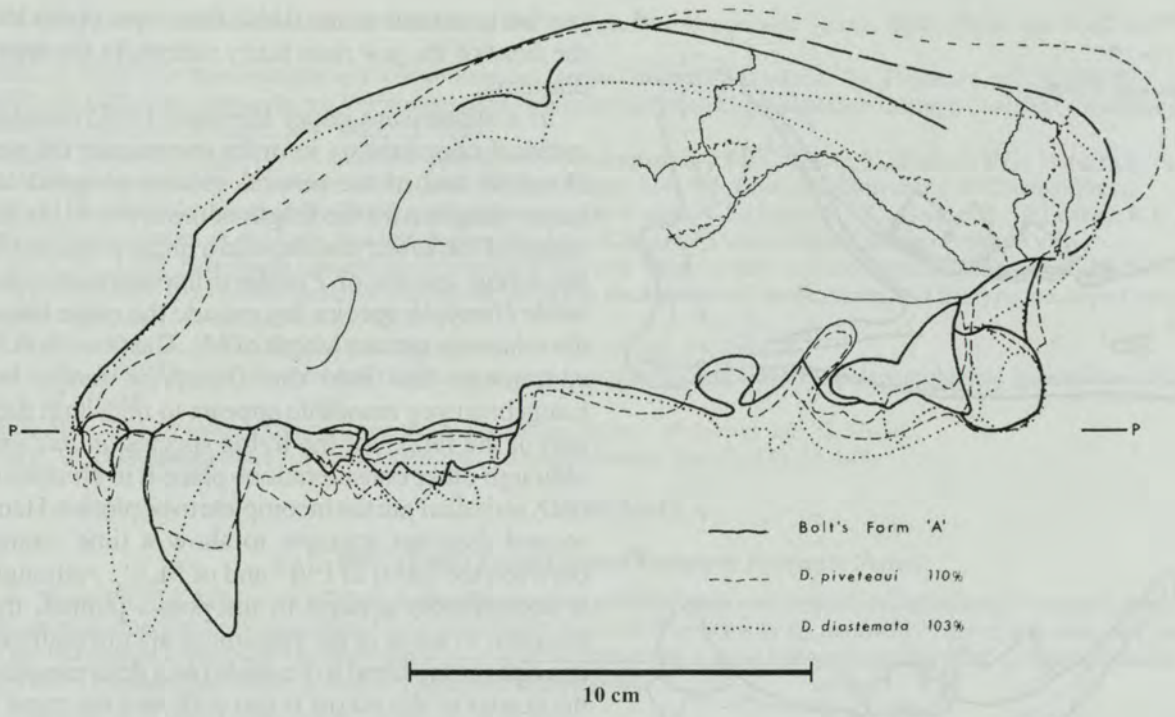

Figure 5 Comparative outlines of crania of *Dinofelis* specimens orientated on a plane (P-P) from the tip of the prexmaxilla to the base of the occipital condyle, enlarged to the same condylobasal length. (Bolt's Farm specimen 'A' is one half natural size).

of the ascending rami are lost. It was described by Hendey (1974) who placed it in *Dinofelis* and regarded it as not separable from the European *D. diastemata*. The upper canines are very similar both in size and morphology to those of *D. barlowi* and *D. piveteaui*. The only known P^3 is narrower than in the Transvaal material and the well worn P^4 is smaller, with the paracone significantly longer than the metacone (see Table 3); there are much abraded remains of what was originally a fairly prominent protocone lying between the parastyle and paracone, apparently better developed than in *D. barlowi*. The lower cheek teeth are morphologically very similar to those of *D. barlowi* but P_4 is a little narrower and M_1 is shorter as well as slightly narrower with the paraconid blade little more than half of the length of the protoconid (6,5 and 12,3 mm); there is a vestigial talonid, as in the Makapansgat jaw. The profile of the jaw is shown in Figure 6A in comparison with Bolt's Farm mandibles. The similarity is clear but the differences appear to warrant the specific separation of the Langebaanweg material from *D. barlowi*, for which it nevertheless provides a very reasonable ancestor. The reference of this material to the European *D. diastemata*, however, is less certain as the European species has a shallower corpus. the incisors carried on a slightly protruding shelf, and the M^1 with the paraconid not as small compared with the protoconid as it is in the Langebaanweg material.

Dinofelis is now also known from East Africa, although only preliminary accounts have been published. M.G. Leakey (1976) records a good mandible (KNM-ER 1549) from below the KBS tuff which matches very well with the South African material of *D. barlowi*, although the postcanine diastema is a little shorter; this may possibly be due to age as the canines are not yet fully erupted. There is also an undescribed, somewhat damaged cranium (KNM-ER 2612) from Koobi Fora which matches quite well with skull "B" from Bolt's Farm (Leakey *in litteris*). The Ileret beds, higher in the sequence have provided a partial mandible (KMN-ER 666) with the teeth damaged but the reduction in size of the incisors and of P_3, together with the short diastema suggest affinity with *D. piveteaui* (Leakey 1976). An expedition from Yale University, led by David Pilbeam, recovered a good cranium at Kanam East (KNM-KE 21), together with some postcranial material and this is referred by M.G. Leakey (*in litteris*) to *D. piveteaui* but is slightly smaller than the Kromdraai type cranium. The Omo area has also yielded material from the Usno Formation and from various levels in the Shungura Formation which appear to belong to *Dinofelis*, some of it resembling *D. barlowi* (Howell and Petter 1976). Thus the range of the genus in Africa is fairly extensive and detailed accounts of the East African material are awaited with interest.

In 1965, Hemmer listed the major characteristics for four species of *Dinofelis* – *D. abeli*, *D. diastemata*, *D. piveteaui* and *D. barlowi*. The Bolt's Farm material serves to confirm the comments made by Hemmer, but also allows some additions to the following items for which data were not available for *D. barlowi*: The nasals are similar to those of *piveteaui*. In both *D. abeli* and *D. diastemata* the mastoid process is nearer to the paraoccipital process than to the post-glenoid process whereas both in *D. piveteaui* and *D. barlowi* the reverse is the case; in all four the mastoid is large, possibly larger

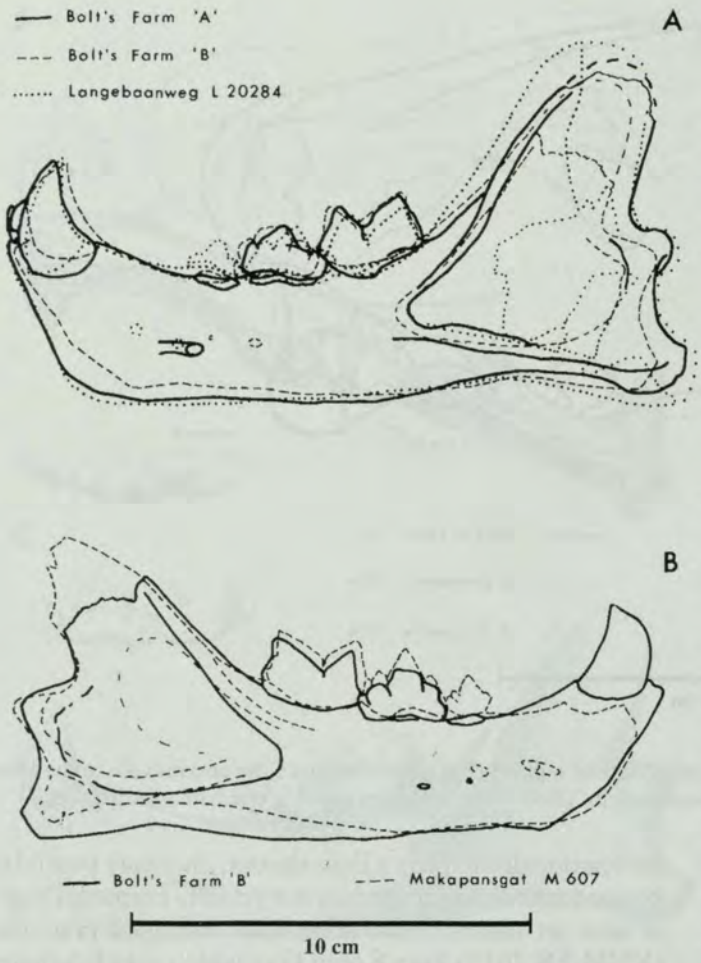

Figure 6 Comparative outlines of (A) of mandibles of Bolt's Farm 'A', Bolt's Farm 'B' and Langebaanweg L 20284 (A); and (B) of Bolt's Farm 'B' and Makapansgat M607 to show similarites and differences. (All one half natural size).

in *D. barlowi* than in *D. piveteaui*. The palatine notch is broad and rounded at the front, as in *D. piveteaui* and *D. diastemata* whereas in *D. abeli* it is a little less rounded and narrower. The upper incisor row is gently rounded, as in the other species. Otherwise Hemmer's diagnoses are fully supported by the new material although one might add the strong development of the angular process in the lower jaw of *D. barlowi*. Hemmer states that the mandibular border in the diastema does not rise particularly; this is apparently the case in the Makapansgat jaw but is not true of the Bolt's Farm specimens in which the front of the jaw rises fairly sharply in the area of the diastema.

In a subsequent paper Hemmer (1975) made some metrical comparisons in order to evaluate the status of *Dinofelis* and of the several species assigned to it. A scatter diagram for the length of the lower M_1 against the length of the lower jaw showed a linear relationship with the living species of *Panthera* appropriately clustered while *Dinofelis* species lay outside the range because of the relatively greater length of M_1. The three Bolt's Farm specimens fall into the *Dinofelis* range but the Langebaanweg mandible appears to lie within the upper part of the range for the living species *on this criterion* although other considerations place it in *Dinofelis*. Data of *D. piveteaui* are too incomplete to be plotted. Hemmer's second diagram attempts to show a time relationship between the ratios of P^4/P^3 and of M_3/P_4. Although there is undoubtedly a trend in the points plotted, the ages assigned to some of the specimens are not really reliable enough for the trend to be useful as a determinative tool; the scatter of the points is too wide and the trend for the lower jaw is too flat to be useful for discrimination. Nevertheless, this comparison endorses Hemmer's earlier (1965) inference on morphological grounds for an evolutionary sequence from *D. diastemata* through *D. barlowi* to *D. piveteaui*. Hendey's (1974) tentative phylogeny invoking phylogeny invoking a separation between the European and African *D. diastemata* seems to fit the data very well.

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REFERENCES

BRAIN, C.K. 1958. The Transvaal Ape-Man-Bearing cave deposits. *Mem. Transv. Mus.*, **11,** 1-131.

BROOM, R. 1937. On some new Pleistocene mammals from limestone caves of the Transvaal. *S. Afr. J. Sci.*, **33,** 760-768.

BROOM, R. 1939. A preliminary account of the Pleistocene carnivores of the Transvaal caves. *Ann. Transv. Mus.*, **19,** 331-338.

BROOM, R., 1948. Some South African Pliocene and Pleistocene mammals. *Ann. S. Afr. Mus.*, **31**(1), 1-38.

COOKE, H.B.S. 1985. *Ictonyx bolti*, a new mustelid from cave breccias at Bolt's Farm, Sterkfontein area, South Africa. *S. Afr. J. Sci.*, **81,** 618-619.

DELSON, E. 1984. Cercopithecoid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forsch. Inst. Senckenberg*, **69,** 199-218.

EWER, R.F. 1955. The fossil carnivores of the Transvaal caves. Machairodontinae. *Proc. Zool. Soc. Lond.*, **125,** 587-615.

EWER, R.F. 1956. Some fossil carnivores of the Makapansgat valley. *Palaeont. afr.* **4,** 57-67.

FREEDMAN, L. 1965. Fossil and subfossil Primates from the limestone deposits at Taung, Bolt's Farm and Witkrans, South Africa. Palaeont. afr., **9,** 19-48.
HEMMER, H. 1965. Zur Nomenklatur und Verbreitung des Genus *Dinofelis* Zdansky, 1924. *Palaeont. afr.*, **9,** 785-89.
HEMMER, H. 1973. Neue Befunde zur Verbreitung und Evolution der pliozän-pleistozänen Gattung *Dinofelis* (Mammalia, Carnivora, Felidae). *N. Jb. Geol. Paläont. Mh.* **1973,** 157-169.
HOWELL, F.C. & G. PETTER, 1976. Carnivora from Omo Group formations. **In:** Coppens, Y., Howell, F.C., Isaac, G.L. & Leakey, R.F. Eds, *Earliest Man and Environments in the Lake Rudolph Basin,* 314-331. Chicago, University of Chicago Press.
LEAKEY, M.G., 1976. Carnivora of the East Rudolf succession. **In:** Coppens, Y., Howell, F.C., Isaac, G.L. & Leakey, R.F. Eds, *Earliest Man and Environments in the Lake Rudolph Basin*, 302-313. Chicago, University of Chicago Press.
MAREAN, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. *J. Hum. Evol.*, **18,** 559-582.
PEABODY, F.E. 1954. Travertines and cave deposits of the Kaap Escarpment of South Africa and the type locality of *Australopithecus africanus* Dart. *Bull. Geol. Soc. Amer.*, **65,** 671-706.
PIVETEAU, J., 1948. Un Felidé du Pliocène duRousillon. *Ann. Paléont.*, **34,** 99-124.
SHAW, J.C.M., 1938. Growth changes and variations in wart-hog third molars and their palaeontological importance. *Trans. Roy. Soc. S. Afr.*, **27,** 51-94.
TOERIEN, M.J. 1955. A sabre tooth cat from the Makapansgat valley. *Palaeont. afr.*, **3,** 43-46.
ZDANSKY, O. 1924. Jungtertiäre Carnivoren Chinas. *Palaeont. Sinica, Ser. C,* **2** (1), 1-149.

APPENDIX A

Bolt's Farm Localities and Principal Elements Found

Pit 1 "Kraal Pit" (UCMP Loc. V-67256). Loose fill containing several jaws and teeth of springbuck and bontebok, many bovid bones and teeth, an equine hoof bone, a mandible of long eared fox (*Otocyon*), fragments of the aardwolf *Proteles* and some bird and lagomorph bones. This is a typical assemblage. Modest quantity of breccia containing a good baboon foot and other skeletal elements, some feline phalanges and a damaged left femur tentatively assigned to *Dinofelis*.

Pit 2 Kiln (Loc V-67257) "Rodent" brecia" only.

Pit 3 "Kaffir Beer Cave" (Loc. V-67258) Loose fill with various living taxa, two crude stone-age cores in chert and quartzite. Breccia with much "rodent" breccia and seventy other specimens including a good, though crushed, cranium of *Procavia transvaalensis,* an almost complete, laterally compressed, skull of *Phacochoerus modestus* (= *antiquus*, to be described elsewhere) and several specimens of *Antidorcas recki.*

Pit 4. "Garage Ravine Cave" (Loc. V-67259). Scanty breccia but including a partial cranium of a large felid and the crushed mandible of a large extinct horse, probably *Equus capensis.*

Pit 5 "Smith Cave" (Loc. V-67260). Very little material.

Pit 6 "Baboon Cave" (Loc. V-67261). Thirty specimens, including a good partial skull of *Procavia transvaalensis*, a crushed cranium of *Antidorcas recki* and good partial crania of *Papio robinsoni* and *Cercopithecoides williamsi* (the latter included by Freedman, 1965). There is also a right proximal femur probably of *Dinofelis.*

Pit 7. "Elephant Cave" (Loc. V-67262). Modest amount of "rodent" breccia and the only macrofossil is a damaged proboscidean molar (to be described elsewhere).

Pit 8 Two fragmentary fossils and some "rodent" breccia.

Pit 9 No specimens.

Pit 10 "Grey Bird Pit" (Loc. V-67263). Abnormal deposit of reddish brown to dark brown breccia containing magnanous lime and dull grey bones of birds and lizards, as well as a few teeth and bones of bovids, and two baboon fragments. The best specimen is a skull of a mustelid, described (Cooke, 1985) as a new species.

Pits 11, 12, 13 Very scanty and scrappy material.

Pit 14 "Bench Mark Pit" (Loc. V-67264). Plentiful "rodent" breccia and some cranial and dental fragments of a suid resembling *Potamochoeroides shawi* but differing in some respects from the type material.

Pit 15 Very scrappy material.

Pit 16 "Equine Pit" (Loc. V-67265). Somewhat dark manganous breccia yielding 20 equine teeth and bones and rather more bovid fragments, as well as one bird skull.

Pit numbers 17 to 22 were not mapped as they yielded no worthwhile material.

Pit 23 - see text

Pits 24 and 25 lay just to the southwest of the mapped area on the property of the S.A. Mining Trust. Pit 24 yielded some rodent breccia, a fragment of an indeterminate baboon cranium and a piece of a small carnivore.

Pit 25 "Gazelle Pit" (Loc. V-67267) furnished an antelopine mandible and part of a humerus, a tooth referred to *Equus* cf *capensis* and a partial mandible and other fragments referred to a variant of *Canis mesomelas.*

Old Dumps (Loc. V-67270) near the kilns yielded twenty scrappy specimens but the exception is a good right upper first molar of *Hipparion libycum.*