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FURTHER REMAINS OF CARNIVORA (MAMMALIA) FROM THE STERKFONTEIN HOMINID SITE

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ABSTRACT

New specimens of Carnivora from late Pliocene deposits at the Sterkfontein hominid site are described. *Proteles* is now added to the faunal list and the hyaena *Chasmaporthetes nitidula* is also identified in the Member 2 assemblage from the Silberberg Grotto. With a larger sample, Members 4 and 5 are now seen to have essentially the same large carnivore guild, a mix of extant and extinct taxa. An updated checklist of taxa is provided.

KEYWORDS: Sterkfontein, Carnivora, carnivore guild structure

INTRODUCTION

The most recent summary of the remains of Carnivora from Sterkfontein near Krugersdorp in the Transvaal was published a decade ago (Turner 1987), and dealt with material then recovered and prepared in the years since 1970. Details of that summary were incorporated in a review of the evolution of the guild of larger African Carnivora (Turner 1990). A continued programme of excavation and preparation at the site, under the day-to-day direction of R. J. Clarke, has produced further samples which are the subject of this present treatment.

The material discussed here comes from what have traditionally been referred to as Members 2, 4 and 5 of the Sterkfontein deposits. However, recent excavations suggest a revision of the stratigraphy for both Members 4 and 5 is needed (Clarke 1994; Kuman 1994; Kuman and Clarke 1996). These authors have now recognised that the southern part of what has traditionally been called Member 5 is a phase of infill that may be intermediate in time between Member 4 and Member 5 proper. They refer to this breccia as the StW 53 Infill. In addition, Member 5 has now been separated into an eastern area and a western infill. Only the Oldowan Infill within Member 5 East is considered to be uncontaminated, but higher levels may in places be subject to mixing from solution pockets (Kuman 1994). Member 5 West, on the other hand, consists of hard, cemented breccia that is uncontaminated and which is associated with an early Acheulean tool industry. In addition a Post-Member 5 Infill (in a northern part of the member) is now recognised. At least part of this latter infill may be Middle Stone Age in time.

Member 2, with some of the oldest material at the site, is contained in the underground cavern known as the Silberberg Grotto. Material from Members 4, 5 and the Post-Member 5 Infill comes from above-ground workings, and has been recorded three-dimensionally by the exavators using an alpha-numeric horizontal grid and a measure of depth. The units of measurement, inherited from original excavation at the site, are imperial, so that the horizontal grid is composed of one-yard squares and the depth is measured in feet and inches (see Kuman 1994). Listings and descriptions are given here taxonomically, with each specimen referred to by its own unique catalogue number to which is added the three dimensional grid information in the case of material from Post-Members 4, 5 and the Post-Member 5 Infill.

The fossils were studied in England with the aid of comparative material held in the Department of Human Anatomy and Cell Biology at The University of Liverpool, Liverpool City Museum and the Natural History Museum in London. Since most of the specimens are small, carriage by hand presented no problems. However, the new hyaena remains from the Silberberg Grotto, S94-13225, were encased in a large and heavy block of breccia that was still in the process of being prepared, and the need to include this important material in the study was achieved by making a high-quality resin cast of the partially prepared dentitions for dispatch to me.

Specimens described here have been returned to South Africa and will be housed in the Bernard Price Institute for Palaeontological Research at the University of the Witwatersrand, Johannesburg.

SYSTEMATIC PALAEONTOLOGY

Family Hyaenidae

Parahyaena brunnea (Thunberg, 1820) – brown hyaena

Member 5 West Infill:

Material: SF3042 (T64, 11'3"–12' 3"), anterior half of a right P^3; S94 7238 (P62, 15' 0"–16' 0"), an unerupted, isolated left P_3.

TABLE 1.

Sterkfontein Hyaenidae. Lower dentitions and mandibles L and B are length and breadth of teeth. Lp is length of protocone. Lt is length of talonid. Depths A and B are depths of mandible anterior to P2 and posterior to M1. BP/3 is breadth of mandible below P3.

Ci		P/2		P/3		P/4			M/1				P2-M1	DEPTH		B	Specimen
L	B	L	B	L	B	L	B	Lp	L	B	Lt	M/c		A	P	P/3	
Parahyaena brunnea																	
16.9	13.1	16.5	11.7	21.3	15.4	23.6	5.5	10.8	24.5	-	4.8	yes	81	40	42.9	21.2	S94-39
-	-	-	-	21.5	15.5	-	-	-	24.3	13.3	4.8	yes	-	-	-	-	S94-138
-	-	-	-	20.9	14.8	-	-	-	-	-	-	-	-	-	-	-	S94-139
Chasmaporthetes nitidula																	
-	-	-	9.3	20.8	11.2	24.6	11.8	11.9	-	-	-	-	-	-	-	-	S94-4/3/45
-	-	15.6	9.5	21.2	11.3	24.7	11.9	11.8	26.6	12.2	4.2	no	85.4	32	38.6	19.3	S94-7205
-	-	16.0	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	S94-7195
-	-	-	-	-	-	26.5	11.0	11.2	27.3	11.4	4.4	yes	-	-	-	-	S94-13224(L)
-	-	18.0	10.6	21.8	11.7	-	-	-	-	-	-	-	-	-	-	-	S94-13225(R)
Chasmaporthetes sp.																	
-	-	-	-	-	-	-	-	-	27.3	13.0	4.9	yes	-	-	-	-	S94-195

Post-Member 5 Infill:
Material: S94–137 to 142 (M61, 16' 8"–17' 8"), two semi-complete mandibles and tooth fragments from one individual; S94–25 (O62, 15' 9"–16' 9"), an isolated right P^2.

Measurements of more complete items are given in Tables 1 and 2. The teeth in the two mandible halves of SF94 137–142 bear all the normal features of a brown hyaena. The enamel is rugose and the premolars are somewhat square in occlusal outline and low-crowned while the canine is relatively high-crowned. The carnassial is short and broad, with a moderately well-developed antero-external cingulum and an elongated talonid bearing a buccally-shifted hypoconid and perhaps a small entoconid on the lingual edge of the cingulum. A metaconid is present on both left and right specimens as a small but distinct bulge at the base of the postero-internal edge of the trigonid.

The three isolated upper and lower premolars are also low crowned, rather square and have rugose enamel. They are too low crowned to be referred to *Crocuta crocuta* and not large enough to be referred to the giant hyaena, *Pachycrocuta brevirostris* (Aymard 1846).

Crocuta crocuta (Erxleben, 1777) – spotted hyaena

Member 5 East
Material: S94–165 (S51, 20' 2"–21' 2"), a proximal fragment of a left third metacarpal.

Member 5 South (on boundary with StW 53 Infill)
Material: S94–112 (U59, 13' 2"–14' 4"), a broken left upper canine.

None of the items is sufficiently complete to permit measurement. The two metapodial fragments match well with comparable elements of the spotted hyaena. The canine is broken, but the absence of a triangle formed at the base of the anterior ridge points to allocation to *Crocuta crocuta*.

Post-Member 5 Infill
Material: S94–65 (O60, 19' 0"–20' 0"), a proximal half of a right second metacarpal.

Chasmaporthetes nitidula (Ewer, 1955) – "hunting" hyaena

Member 4
Material: SF94–4 (W43, 28' 10"–29' 10"), a left P_3, together with SF94–3 (W44, 28' 3"–29' 3"), a left P_4 and SF94–45 (V43, 27' 2"–28' 2"), a broken left P_2 missing most of the main crown and the anterior region. All of these latter three teeth fit into a fragment of the lingual half of a horizontal mandibular ramus, and appear to be from a single individual (Figure 1A and B, bottom). Moreover, these items appear to match the teeth of the right mandibular specimen S94–7205 listed below. The respective left and right teeth are extremely similar in size and morphology (Table 1), and have almost precisely the same wear pattern. S94–7205 (U43, 27' 0"–28' 0"), a right horizontal mandibular ramus with

TABLE 2.

Sterkfontein Hyaenidae. Upper dentition. L and B are length and breadth of teeth. Lp and Lm of paracone and metastyle

P2/		P4			Specimen
L	B	L	LP	LM	
Parahyaena brunnea					
16.2	11.8	-	-	-	S94-25
Chasmaporthetes nitidula					
20.4	-	37.8	12.3	15.7	S94-13225

P_2–M_1 in place but missing the symphyseal region and with the ascending ramus, condyle and angle broken off (Figure 1A and 1B, top). This specimen appear to belong with the left teeth and mandible fragment listed above; S94–7195 (P45, 13' 4"–14' 4"), a complete left P_2 in a fragment of mandible; S94–7198 (U43, 25' 0"–26' 0"), a fragmentary left P^2.

Member 5 West Infill

Material: S94–8061 (S64, 12'0"–13' 0"), a broken crown of a right P_4.

Most of these items have all the hallmarks of material from both Sterkfontein and Swartkrans previously referred to *Chasmaporthetes nitidula* (Turner 1987 1993; Werdelin *et al.* 1994): narrow premolar teeth, rather oval in occlusal outline and

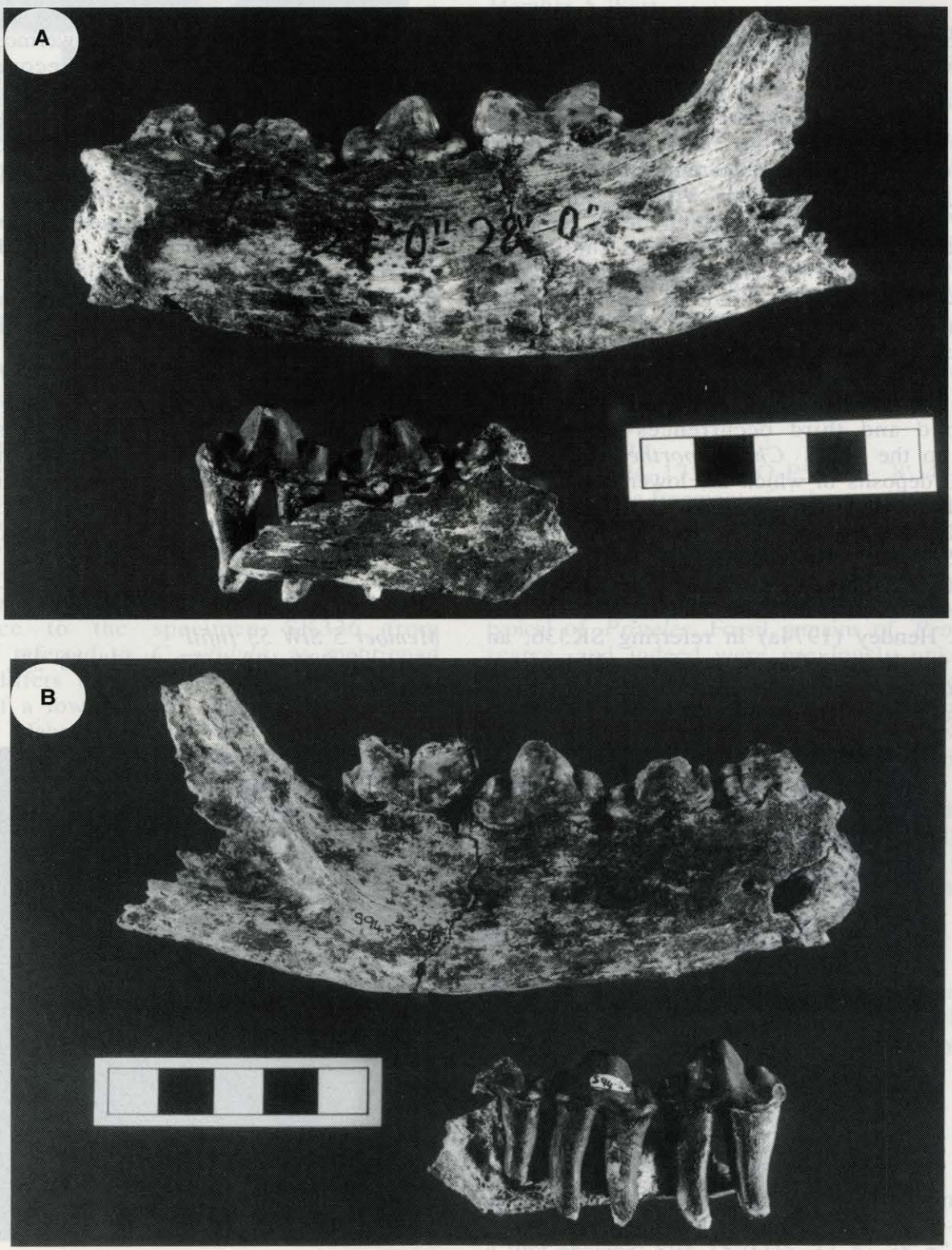

Figure 1. **A**. Lingual views of right mandible S94 – 7205 (top) and left composite mandible SF94 – 4/3/45 which both appear to be of one individual of *Chasmaporthetes nitidula*. **B**. Buccal views of the same two specimens. Scale in centimetres.

markedly hypsodont, with a *fleur-de-lis* profile to the anterior and posterior edges of the main cusp of lower specimens. However, the specimens recovered from the Member 2 deposits of the Silberberg Grotto (see below) suggest that a further evaluation of the relationships of the Transvaal material is warranted.

Member 2 (Silberberg Grotto)
Material: S94–13225, a block of breccia containing broken and crushed mandibular, cranial and dental remains of what appears to be a single individual. The resin cast provided sufficient detail of the dentition for identification and some measurements, details of which are given in Tables 1 and 2. Visible items consist of a left horizontal ramus with P_3, P_4 and M_1, a right horizontal ramus with P_2, P_3 and P_4 together with the anterior portion of M_1, a right maxilllary fragment with a trace of the canine alveolus, P^2, P^3, and P4, and a fragment of a left maxilla with a broken P^3. Some of these items are shown in Figure 2.

The teeth are generally similar to those from Member 4 referred to above. However, the material now available from the site provides only the second and third occurrences of material assigned to the genus *Chasmaporthetes* from the Transvaal deposits in which the lower carnassial is clearly associated with the rest of the dentition. Previously, the only other associated carnassial was that of SK14005 from Member 1 at Swartkrans referred to *C. nitidula* by Brain (1981) following unpublished discussion with Hendey. Brain also followed Hendey (1974a) in referring SK336, an isolated tooth in a fragment of mandible from Swartkrans, to *C. nitidula*. Neither of those carnassials bears a metaconid (SK14005 is illustrated by Hendey, 1978: Fig 10, SK 336 by Ewer 1955, Plate 3, Figure 1, where it was incorrectly assigned to the Nimravidae), and this is also true of the new Member 4 specimen S94–7205. Against that fact, we now have evidence of the clear presence of that cusp together with an essentially simple talonid bearing a trenchant hypoconid in the new Member 2 specimen. The new specimen from Member 2 also provides the first evidence for the presence of two species of the genus *Chasmaporthetes* in the lowermost levels at Sterkfontein, since previously recovered items from there have included only the type specimen of *Chasmaporthetes silberbergi* (Broom 1948).

In general, the absence of a metaconid and a carnassial talonid with a simple, trenchant hypoconid have been taken as characteristic of the genus *Chasmaporthetes* (Kurtén and Werdelin 1988). However, in a recent evaluation of the rich hyaenid material from the earliest Pliocene deposits at Langebaanweg in the Cape Province (Werdelin *et al.* 1994), we pointed out that the type specimen of the material that we have now referred to *Chasmaporthetes australis* (Hendey 1974), PQ-L14199, does have a metaconid on both left and right carnassials. The presence of this primitive feature on the specimen from the lowermost levels of Sterkfontein points to an interesting link with the earlier material from Langebaanweg, although it is not clear at this stage that the two are conspecific.

Chasmaporthetes sp. indet.

Member 5 StW 53 Infill
Material: S94–195 (V57, 9' 11"–10' 3"), an isolated left M_1.

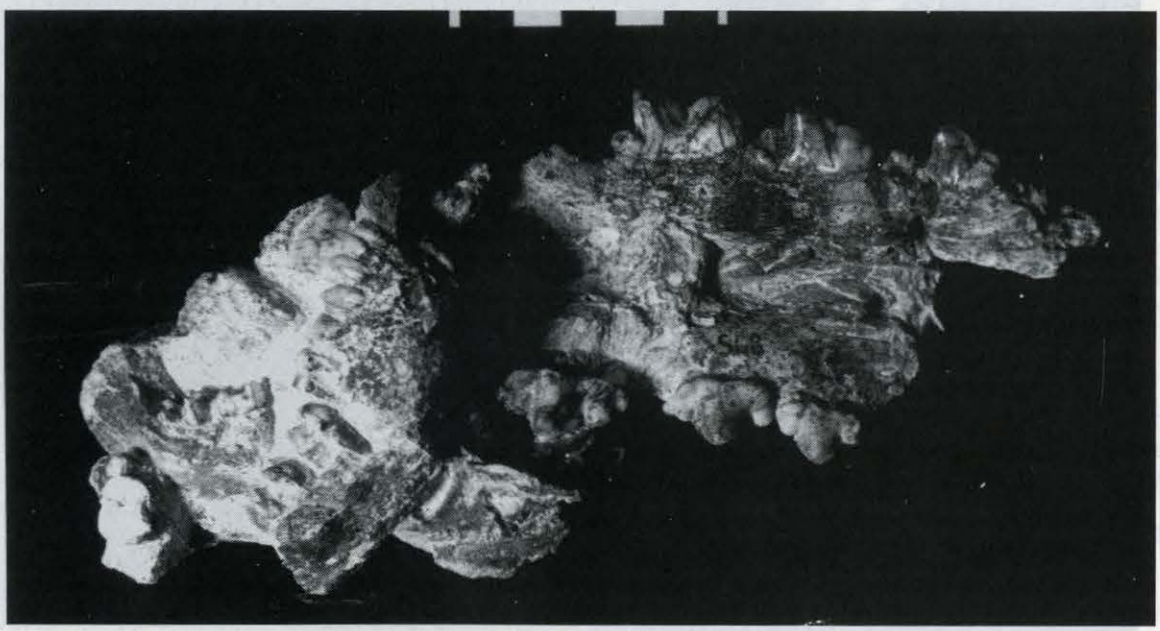

Figure 2. Remains of a single individual of *Chasmaporthetes nitidula*, S94 – 13225. To the right may be seen the left (top) and right mandibles. The block of mixed material at the left of the specimen contains various portions of the upper dentition mixed with jaw fragments of a primate. Scale in centimetres.

Figure 3. Lingual view of the left M_1 S94 - 195, *Chasmaporthetes* sp. indet. The small metaconid may be seen below the fractured area at the rear of the protoconid. Scale in centimetres.

This specimen is rather interesting. Dimensions are given in Table 1 and the tooth is illustrated in Figure 3. The tooth is superficially quite cat-like, with almost equal development of the paracone and protocone and a bulging occlusal outline, although it is clearly hyaenid on the basis of its well-developed talonid. This region of the tooth bears a strong hypoconid, almost centrally placed, with no evidence of an entoconid. The tooth differs in these features from *Hyaena hyaena* and *Parahyaena brunnea* and differs entirely from the carnassial morphology of *Pachycrocuta brevirostris* and *Crocuta crocuta*. Overall, it shows a strong resemblance to the specimen SK336 from Swartkrans referred to *C. nitidula* as mentioned above. It differs from the latter, however, in the presence of a low yet well-developed metaconid, backwardly placed to sit on the buccal margin of the talonid rather than closely set against the rear of the protoconid. In this feature it is similar to the carnassial of the new hyaenid from Member 2

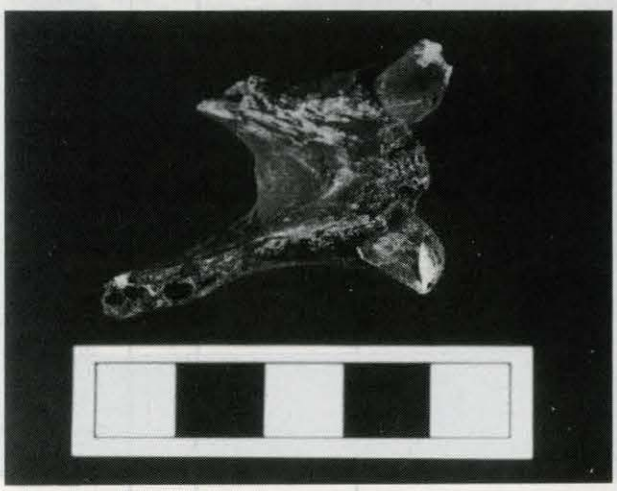

Figure 4. Occlusal view of the mandible S94 – 199 of *Proteles* sp. Scale in centimetres.

referred to *C. nitidula*, although it differs from it in being considerably more robust. It is quite possible that the tooth will prove to belong to *Chasmaporthetes silberbergi*, but in the absence of evidence for that identification I have decided to restrict allocation to the genus level.

Proteles Geoffroy, 1824–aardwolf

Member 5 West

Material: S94 –199 (N64, 10' 8"– 11' 8"), anterior left and right mandibles with fully fused symphysis, both broken canines in place, incisal alveolar region heavily damaged, alveoli of right P_3 and P_4 present with long post canine diastema; S94–7234 (P62, 15' 0"–16' 0"), a right anterior maxilla and premaxilla with alveoli of the incisors and canine and roots of the first two postcanine teeth; S94–7231 (N61, 14' 11"–15' 11"), a right anterior mandible ramus with the broken canine in place; S94–68 and 71 (M61, 15' 8"–16' 8"), a mandibular symphysis fragment and right canine that fits. The mandible has partial alveoli for both canines, roots of the left incisors and right I_1 in damaged alveoli, a broken right I_2 and a worn but complete right I_3.

Member 5 East

Material: S94–175 (N-O-P55–56, 8' 4"–12' 6", blasted area), a fragment of right mandible with roots of P_3 and P_4 and root of M_2.

Specimen S94–199 is shown in Figure 4, and illustrates the long symphysis, extended postcanine diastema and heavily reduced postcanine dentition typical of *Proteles*. Fossil remains of *Proteles* are scarce, and indeed were previously unknown at Sterkfontein despite previous references that appear to have been based on cataloguing errors rather than misidentification (Turner 1987: 345). Hendey (1973, 1974a) described material from Kromdraai B and Swartkrans, and referred specimens from the latter locality to both the extant species, *Proteles cristatus* (Sparrman 1783), and to a new species *Proteles transvaalensis* Hendey, 1974. I described further material from Swartkrans (Turner 1993) and noted that while one of Hendey's specimens from Swartkrans clearly warranted taxonomic distinction, the rest differed from the extant species largely on size. That is also true of the new material from Sterkfontein described here, and I therefore confine my referral to the genus level.

Hyaenidae indet.

Member 4

Material: SF94–46 (W44, 22' 3"–23' 3"), an anterior fragment of a left P^4; S94–102 (O48, 20' 6"– 21' 6"), a first phalanx; S94–15 (Q45, 37' 6"–38' 6"), a third phalanx; SF3176 (T49, 11' 8"–12' 8"), left fourth metacarpal; S94–174 (W45-46 Southwall Slump,

Member 4), right third metatarsal missing the distal end; S94–196a and b (Q46, 14'9"–15' 9") third and second phalanges; S94–108 (Q46, 15' 9"–16' 9") a left astragalus; S94–83 (Q45, 36' 6"–37' 6"), a broken right astragalus; S94–84 (Q45, 36' 6"–37' 6"), a second phalanx; SF94–116 (N46, O-P45), second phalanx; S94–8 (T43, 14' 10"–15' 10"), posterior fragment of a right P^4; S94–13226 (Q49, 14' 4"–15' 4"), a right upper canine.

Member 5 West Infill
Material: S94–7232 (M64, 12' 8"–13' 8"), a left deciduous third molar; S94–184a and b (O61, 10' 0"–11' 5"), buccal fragment of right P^3; S94–190 (Q61, 11' 9"–12' 9"), an anterior right mandible fragment with P_2; S94–188 (Q61, 11' 9"–12' 9"), crown fragment of a lower right canine; S94–189 (Q61, 11' 9"–12' 9"), a fragmentary left I_3; S94–194 (Q60, 15' 5"–16' 5"), an isolated left I_2.

Member 5 East
Material: S94–152 (R52, 29' 8"–30' 8"), an anterior fragment of a left P_3.

Near Contact with Member 4
Material: S94–164 (S51, 20' 2"–21' 2"), a distal articulation of a metapodial.

Oldowan Infill
Material: S94–121 (R56, 28' 4"–29' 4"), a posterior portion of a right P^4; S94–34 (R56, 29' 4"–30' 4",), an isolated left I^1; S94–64 (P54, 30' 1"–31' 1"), a posterior fragment of a right P^4; S94–92 (P53-54, 32' 10"–36 ' 10"), a right astragalus.

StW 53 Infill
Material: S94–120 (V60, 11' 7"–12' 7"), a right third metatarsal missing the distal end.

Post Member 5 Infill
Material: S94–148 (M60, 19'2"–20'2"), a left I^1.SF 4013 (T62, 18'1"–19'1") an isolated right P^1; SF134 (T64, 9'5"–10'5"), an anterior half of a right M_1; S94–8081 (N63, 13'7"–14'7:), the tip of an unworn right permanent lower canine; S94–8032 (N63, 13'7"–14'7"), a left deciduous lower canine; S94–78 (M61, 14'8"–15'8"), a first phalanx

Family Felidae
Subfamily Machairodontinae

Dinofelis barlowi (Broom, 1937) – "false" sabretoothed cat

Member 4
Material: S94–56a and b (O31, 10' 3"–11' 3"), a left mandibular ramus and partially complete dentition; S94–9 (T43, 14' 10"–15' 10"), a right M_1 in fragment of mandible; SF3871 (T60, 18' 2"–19' 2"), a fragment of an isolated left upper canine.

Measurements are given in Table 3. The horizontal ramus of the mandible SF94–56 a and b has been broken and repaired beneath the P_4, while the ascending ramus is contained within a skin of cemented breccia and would probably fragment if further preparation were to be attempted. Nevertheless, sufficient detail of the mandibular and dental morphology is available to make identification possible (Figure 5).

The overall features of the specimen are very similar to those seen in the material of *D. barlowi*

TABLE 3.
Sterkfontein Felidae. Lower dentitions and mandibles.
L and B are length and breadth of teeth, C - cd is distance from anterior edge of canine to centre of condyle; HRC is height of coronoid process; Depth A and B are depth of mandible anterior to P3 and posterior to M1; BP/4 is breadth of mandible below P4.

Ci		p/3		p/4			M/1		C-cd	HPC	P3-M-1	DEPTH		B	Specimen
L	B	L	B	L	B	Lp	L	B				A	B	P/4	
Dinofelis barlowi															
15.5	10.1	-	-	-	-	-	26.5	13.5	148	75	64	29.5	36.5	18.0	S9s4-56a/b
-	-	-	-	-	-	-	26.9	11.7	-	-	-	-	-	-	S94-56
Panthera leo															
-	-	-	-	25.3	13.8	13.5	-	-	-	-	-	-	-	-	S94-131/132
-	-	-	-	-	-	-	29.1	15.2	-	-	-	-	-	-	S94-7233
-	-	15.0	8.4	-	-	-	-	-	-	-	-	-	-	-	SF 2858
-	-	20.9	11.5	29.4	15.5	14.8	-	-	-	-	-	-	-	-	S94-7228/9
-	-	-	-	-	-	-	30.0	16.0	-	-	-	-	-	-	S94-7224
Panthera pardus															
-	-	-	-	-	-	18.2	9.2								S94-28

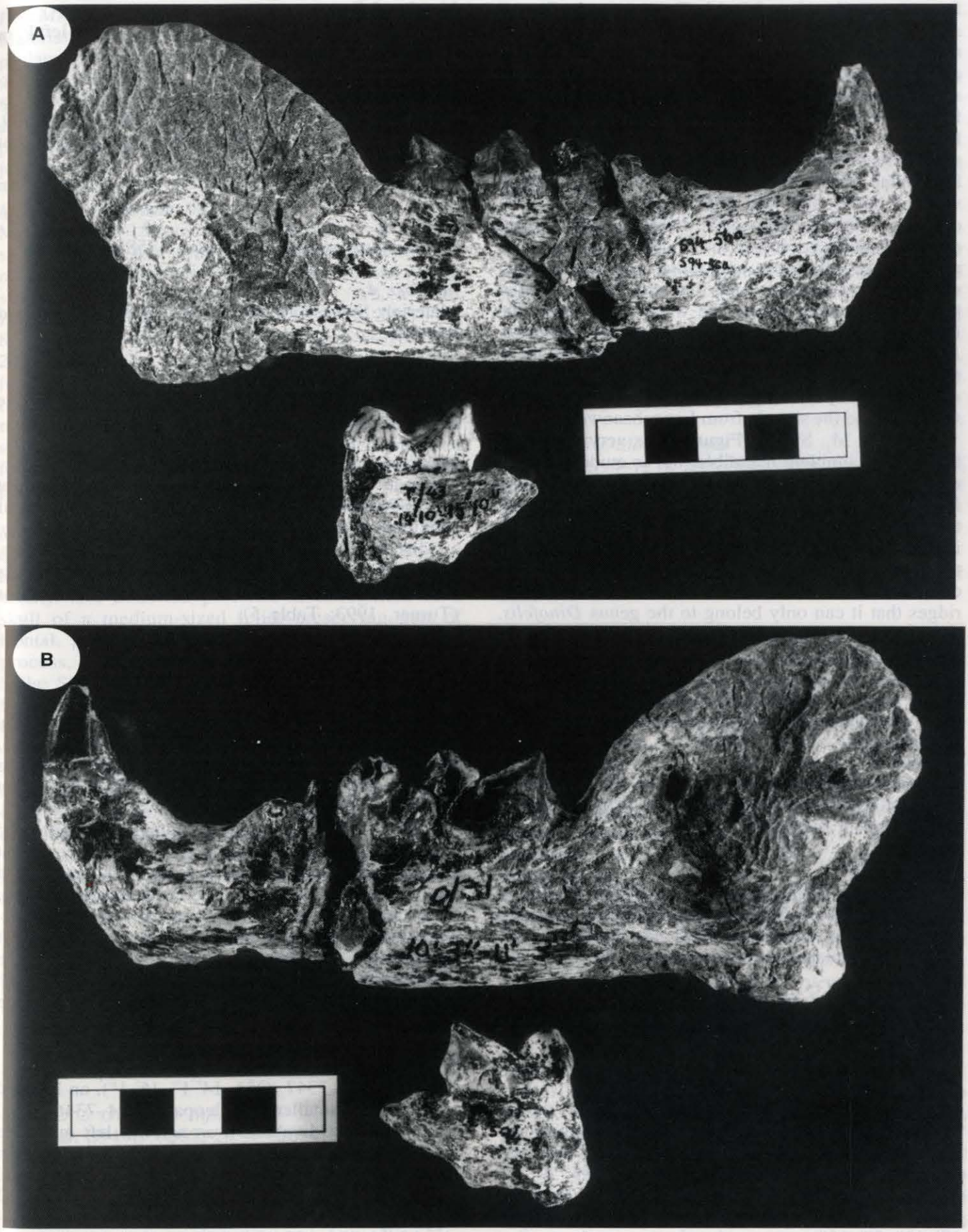

Figure 5. **A**. Lingual views of left mandible S94 – 56 a and b (top) and right M_1 S94 – 9 of two individuals of *Dinofelis barlowi*. **B**. Buccal views of the same two specimens. Scale in centimetres.

from the nearby site of Bolt's Farm recently figured and described in some detail by Cooke (1991), to the mandible from Makapansgat Member 3 also discussed by Cooke and to some of the Langebaanweg specimens (Hendey 1974b). Among the most notable features of the new jaw, many of which may be seen in Figure 5, are the very square and almost vertical symphyseal region, the relatively straight and shallow horizontal ramus, the narrow and steeply ascending vertical ramus and the large angular process. The canine is small and somewhat flattened, while the P_4, despite damage, is very narrow and high crowned. The carnassial is also long and rather narrow, with an elongated protoconid, and the rear border of the protoconid is very sharp. The whole tooth gives the impression of being large relative to the mandible. At the base of the protoconid is what appears to be the merest trace of a vestigial talonid, a feature noted by Cooke (1991: p. 19) in both the Makapansgat specimen and the sample from Langebaanweg.

The right M_1, S94–9 (Figure 5), is very similar to that in the complete mandible, but is evidently from an older and somewhat larger individual. The fragmentary upper canine, SF3871, preserves only the junction of the crown enamel with the root, but it is evident from the flattened cross section of the tooth in conjunction with its size and the absence of crenulations on the unworn anterior and posterior ridges that it can only belong to the genus *Dinofelis*. The tooth is not flat enough to be referred to *Dinofelis piveteaui*.

Subfamily Felinae

Panthera leo (Linnaeus, 1758) – lion

Member 4
Material: S94–7200 (L42, 19' 0"–20' 4"), a proximal right radius; S94–2 (U43, 20' 2"–21' 2"), a crown of a right upper deciduous canine.

Member 5 West
Material: S94–7228 and S94–7229 (N62, 17' 0"–18' 0"), an isolated left P_3 and an isolated left P_4, possibly from the same individual; SF94–186 (Q60, 10' 8"–11' 8"), an isolated right fragmentary P^3.

Post Member 5 Infil/MSA Area
Material: S94–7224 (N59, 20' 0"–21' 0"), an isolated left M_1.

Oldowan Infill
Material: SF94–128 and 131–135 (R57, 27' 4"–28' 4"), a left mandibular horizontal ramus with P_4 and fragments of M_1; S94–149 and 150 (R57, 28' 4"–29' 4"), two fragments of a left P^4; S94–23 (R53, 29' 2"–30' 2"), a fragment of canine root; S94–13 (R55, 31' 4"–32' 4"l), a lower right first incisor; SF4151 (T50, 19' 10"–20' 10"), a posterior fragment of a canine crown; S94-2408 (Q57, 23'8"–24'8"), a large, slightly broken right scapholunare.

Member 5 East
Material: SF2858 (S51, 19' 7"–20' 2"), a worn left P_3 in a fragment of mandible.

Post Member 5 Infill
Material: S94–7233 (N59, 10' 0"–11' 0" and N59, 12' 0"–13' 0"), a left M_1, broken posteriorally but rejoined.

Some measurements of lion teeth are given in Table 3.

Panthera pardus (Linnaeus, 1758) – leopard

Member 4
Material: S94–28 (P46, 13' 8"–14' 8"), an isolated left M_1.

Post-Member 5 Infill
Material: S94–103 (M61, 17' 8"–18' 8"), the posterior half of a smaller felid P^3.

Member 2 (Silberberg Grotto)
Material: **S94–7208**, an anterior fragment of a right M_1; **S94–8060/8058** and **S94–8059**, two right proximal fifth metatarsals.

This material is too fragmentary for assessment, although the isolated first molar (Table 3) falls within the range of sizes recorded from Swartkrans (Turner, 1993: Table 5).

Felidae indet.

Member 4
Material: S 94–7197 (O46, deep pit, ca. 30'–42'), a first phalanx of a small felid; S94–115 (N46, O-P45, blasted area), a distal end of a fifth metacarpal of a medium-sized felid; S94–117 (N46, O-P45), a root of canine of a medium-sized felid; S94–89 (S47, 26'–10"–27' 8"), the proximal end of a large left third metacarpal; S94–7202 (P47, 12' 2"–13' 2"), a first phalanx of an anterior first digit (dew claw) of a medium-sized felid between leopard and lion in size; S94–7201 (P47, 10' 2"–11' 2"), a left I^2 of a medium-sized felid; S94–61 (U49, 23' 0"–24' 0"), a large left fifth metacarpal; S94–12 (T43, 22' 11"–23' 11"), a distal right radius fragment of a large felid; SF4456 (U46, 23' 4"–24' 9"), a left first metacarpal of a large felid.

Member 5 East
Material: S94–7347 (Q51, 14' 1"–15' 1"), an isolated right canine, smaller than leopard; S94–7346 (Q55, 17' 1"–18' 1", Member 5), an anterior left mandible with roots of the canine and premolars, smaller than leopard; S94–111 (U59, 13' 2"–14' 4"), a proximal left second metacarpal of small leopard size; S94 62 (T53, 17' 2"–18' 8"), a first phalanx of a medium-sized felid; S94–177 (N-O-P55-56, 8' 4"–12' 6" blasted area), a first phalanx of a small felid.

Post Member 5 Infill
Material: S94–181a and b (P60, 9' 5"–10' 5"), a first phalanx of a large felid; S94–144 (M63, 15' 9"–16' 9"), a second phalanx of a large felid; S94–183 (O60, 8' 3"–9' 3"), a left navicular of a large felid; S94–30 and 31/29 (O60, 18' 0"–19' 0"), left and right proximal radius fragments of smaller medium-sized juvenile felids.

Member 5 Oldowan Infill
Material: S94–154 and 156 (Q56, 28' 2"–29' 2"), a small proximal left second metatarsal and a distal left metapodial fragment that may be of the same specimen; S94–109 (Q57, 28' 8"–29' 8"), a shaft fragment of a large radius; S94–110 (Q57, 28' 8"–29' 8"), a medium-sized distal metapodial; S94–16 (S55, 23' 8"–24' 8"), a first phalanx of a medium-sized felid; S94–125 and 122 (Q55, 26' 4"–27' 4"), a complete first phalanx and a distal first phalanx of a medium-sized felid; S94 127 (R57, 27' 4"–28' 4"), a shaft of a right third metacarpal of a medium-sized felid; S94–93 (P53–54, 32' 10"–36' 10"), a second phalanx of a medium-sized felid.

Member 2, Silberberg Grotto
S94–37, a left navicular of a medium to large felid; SF5937, a right zygoma of a large felid; SF5936, a broken and distorted posterior left fragment of a skull of a medium-sized felid, preserving part of frontal, parietal, squamosal with part of zygomatic process, occipital, basicranium and left auditory bulla; S94–7212, a right first metacarpal of a large felid; S94–7213, the first phalanx of a right anterior first digit of a large felid; S94–7209, the distal end of a second phalanx of a medium-sized felid; S94–7214, the shaft of a first phalanx of a moderately large felid; S94–7215, the distal end of a metapodial of a moderate sized felid; S94 7210, the proximal end of a first phalanx of a large felid.

SF5937 is rather short to belong to a pantherine felid such as *P. leo*, and may therefore belong to a machairodont

Family Viverridae

A small number of teeth and a single edentulous mandible can be referred to this family, although identification beyond that is based largely on size.

Subfamily Herpestinae

Herpestes Illiger, 1811 – mongoose

Member 5 Oldowan Infill
Material: S94-49 (Q52, 29' 4"–30' 4"), a right upper canine.

Post Member 5 Infill
Material: SF1152 (P59, 13' 1"–14' 1"), a right upper canine.

Suricatta Desmarest, 1804 – mongoose

Member 5 West Infill
Material: S94–193 (Q61, 15' 5"–16' 5"), an edentulous left mandible, broken at the front.

Member 5 Oldowan Infill
Material: S94 –108 (R54, 22' 2"–23' 2"), a right upper canine.

StW 53 Infill
Material: S94–7223 (V60, 14' 0"–15' 0"), an upper right canine and second premolar in a fragment of maxilla.

Mungos Geoffroy & Cuvier, 1795 – mongoose

Member 5 West Infill
Material: S94–7230 (N62, 16' 0"–17' 0"), a right M_1.

Member 5 Oldowan Infill
Material: S94–7216 and 7217 (R56, 32' 4"–33' 4"), an upper right canine and a lower molar fragment; S94–39 (Q55, 25' 4"–26' 4"), a right upper canine.

Member 5 East
Material: S94–96 (Q51, 20' 4"–21' 4"), a right upper canine.

Family Canidae

The canid sample is largely fragmentary. It consists for the most part of material of jackal size (*Canis adustus*, Sundevall 1846 and *C. mesomelas*, Schreber 1778), but specific allocation is difficult. Only one specimen stands out as being from a larger animal.

cf *Lycaon pictus* (Temminck, 1820) – hunting dog
Member 5 East Infill
Material: S94–7220 (Q53, 18'8 "–19' 2"), an isolated right P_4.

With a length of 15.7 mm and a breadth of 7.5 mm this specimen is far larger than any specimen of *C. adustus* or *C. mesomelus* in my comparative measurement sample of twelve individuals of each species, and similar in size to *L. pictus*.

Canis sp. indet. – jackals

Member 4
Material: S94–163 (W44-45 blasted area), a fragment of right P^4; S94–6 (W45, 28' 11"–29' 11"), an isolated right M_2; S94–7196 (R49, 25' 11"–26' 11"), an isolated lower left incisor; S94–66 (W44, 24' 3"–25' 3"), a posterior portion of a left horizontal mandibular ramus with M_2 in place and the alveolus of M_3; S94–22 (O42, 16' 9"–17' 9"), an isolated left P^4; SF4481 (U49, 22' 4"–23' 0"), rear fragment of a right P_4; SF4604 (U51, 11' 0"–12' 0"), a posterior fragment of a

right P^4; S 94–50 (Q48, 14' 2"–15' 2"), a proximal left fourth metatarsal; SF1611 (R42, 8' 2"–9' 2", Member 4), a proximal right radius.

Member 5 West Infill
Material: S94–7345 (P62, 15' 0"–16' 0"), the proximal end of a right second metatarsal; S94–7236 (O62, 16' 9"–17' 9"), the anterior half of a right M_1; S94–8062 (S65, 12' 0"–13' 0"), the posterior portion of a premolar; S94–8063 (Q63, 13' 0"–14' 0"), an isolated left M^1; SF3133 (T63, 10' 5"–11' 5"), an isolated left lower canine.

Post Member 5 Infill
Material: S94–7235 (M64, 8' 8"–9' 8"), a distal metapodial fragment; S94 51 and 52 (O59, 10' 6"–11' 6"), an isolated right P_2 or P_3 and a right mandible of a small canid with matrix-filled alveoli; S94 17-20 (P60, 16' 6"–17' 6"), a right M^1, a fragmentary right P^4, a left I^3 and a left M_1; S94–192 (Q59, 18' 0"–19' 0"), an isolated right P^2; S94–143 (P60, 17' 6"–18' 6"), an isolated left M_2; SF603 (M63, 12' 9"–13' 9"), a posterior fragment of a right P^4; S94–105 and 106 (16' 0"–17' 0"), a proximal left radius and a left lower canine; S94 –187 (O61, 10' 5"–11' 9"), a proximal right humerus fragment; S94–73–77, 79 and 80 (M61, 14' 8"–15' 8"), a series of specimens. 73, a posterior juvenile skull; 74, a proximal left second metatarsal; 75, a proximal left second metacarpal; 76, a right maxillary fragment with the root of P^4, alveolus of M^1 and M^2 in place; 77, a broken right astragalus, 79, a distal left femur; 80, a distal right femur; S94 –67 (M61, 15' 8"–16' 8"), a fragment of right maxilla and premaxilla with alveoli of canine, P^1 and P^2.

Member 5 Oldowan Infill
Material: S94–7218 (R57, 26' 4"–27' 4"), a right astragalus; S94–14 (S52, 24' 5"–25' 5"), an isolated P_3 or P_4; S94–53 (R55, 26' 4"–27' 4"), an isolated right P^2; S94 168 and 169 (Q56, 29' 2"–30' 2"), a proximal left radius and a probable fragment of canid radius; S94–155 (Q56, 28' 2"–29 ' 2"), a proximal right fourth metatarsal; S94–97 (R56, 26' 4"–27' 4"), an isolated left I^2; S94–114 (R56, 30' 4"–31' 4"), a left isolated P_1.

StW 53 Infill
Material: S94–172 (V57, 10' 3"–11' 0"), right horizontal mandibular ramus with P_2–M_2 in place and a probable alveolus for M_3.

Member 5 East
Material: S94–42 (Q50, 15' 11"–16' 11"), a third phalanx; S94–180a and b (N-O-P/55-56, 8' 4" 12' 6" blasted area), an isolated broken right M_1; S94–7221 (P57, 12' 9"–13' 9"), a right horizontal mandibular ramus with alveoli of all teeth from the canine to the anterior half of M_1; S94–7222 (P57, 12' 9"–13' 9"), a right posterior fragment of horizontal mandibular ramus with roots of M_2 and the alveolus of M_3; S94–185 (O58, 15' 11"–16' 11"), a distal right humerus; S94–41 (P57, 13' 5"–14' 5"), a fragment of a left P^4; S94–48 (Q54, 20' 0"–21' 0"), a fragment of a left M^1; S94 99 and 100 (Q55, 19' 4"–20' 4"), an isolated right M_3 and a third phalanx; S94–26 (P54, 21' 1"–22'1"), a posterior fragment of a left P_4.

ANNOTATED CHECKLIST OF CARNIVORA IN STERKFONTEIN DEPOSITS

This list provides an up-to-date summary of taxa by Member, and incorporates all previous taxonomic work.

Member 2

Family Felidae: *Acinonyx jubatus; Felis caracal; Panthera pardus; Dinofelis barlowi, Megantereon cultridens.*

Family Hyaenidae: *Chasmaporthetes silberbergi; Chasmaporthetes nitidula.*

Member 4

Family Felidae: *Panthera leo; Panthera pardus; Dinofelis barlowi; Megantereon cultridens, Homotherium latidens* [African specimens of *Homotherium* have been variously referred to Eurasian taxa, as summarised elsewhere (Turner 1990). There are arguments for sinking the Eurasian species *H. crenatidens*, to which I have previously referred Sterkfontein and other African specimens, into *H. latidens* (Turner in press)].

Family Hyaenidae: *Chasmaporthetes silberbergi; Chasmaporthetes nitidula; Crocuta crocuta, Parahyaena brunnea* [The brown hyaena was previously referred to the genus *Hyaena*, but it is now evident that it shares only primitive features with the striped hyaena, *Hyaena hyaena*, and should be placed in a separate genus (Werdelin and Solounias 1991).]; *Pachycrocuta brevirostris.*

Family Viverridae: *Herpestes* sp.

Family Canidae: *Canis mesomelas.*

Member 5

Family Felidae: *Homotherium latidens; Megantereon cultridens, Dinofelis barlowi, Panthera leo.*

Family Hyaenidae: *Chasmaporthetes nitidula; Crocuta crocuta; Parahyaena brunnea; Pachycrocuta brevirostris, Proteles* sp. [*Chasmaporthetes silberbergi* was previously recorded from Member 5 (Turner, 1987), based on specimens SF 450, SF 452 and SF 378. K. Kuman (in litt.) now suggests that the locality of the first two is now considered to fall within Member 4, while the latter specimen comes from an area on the boundary between the two members and might better be considered as falling within Member 4. Since no other specimens are clearly recorded as having come from Member 5 I am therefore deleting this earlier record.]

Family Viverridae: *Herpestes* sp.; *Suricatta* sp.; *Mungos* sp.

Family Canidae: *Canis* cf. *C. mesomelas*; *Canis* sp. (large); cf. *Lycaon pictus*.

Post-Member 5 Infill

Family Felidae: *Pantera leo; Panthera pardus*

Family Hyaenidae: *Parahyaena brunnea; Crocuta crocuta; Proteles* sp.

Family Verridae: *Herpestes sp.*

DISCUSSION

Although *Proteles* is now clearly recorded from this site, perhaps the most significant feature of the new material is the fact that the number of species from the Silberberg Grotto has now been augmented by the inclusion of *C. nitidula*. The number of carnivore species known from all levels at Sterkfontein is now high, reinforcing the likelihood that predator activity in the vicinity of the site during formation of the deposits was considerable. Such activity is likely to have been at least in part responsible for the accumulation of vertebrate remains there, as Brain (1981) has suggested for various levels of the Sterkfontein Valley sites, although natural trapping of animals is also strongly indicated at both Bolt's Farm (Cooke 1991) and Kromdraai B (Vrba 1981) and, as McKee (1991) has pointed out, may have been more of a factor in accumulation in Member 4 at Sterkfontein than previously thought.

However, as with many of the African fossil assemblages of the Plio-Pleistocene, the number of specimens and of individuals attributable to each species is generally low and the possibilities for palaeoecological reconstruction accordingly limited beyond more general points based, for example, on guild structure. Using such an approach, McKee (1991: Table 1) has suggested that apparent differences between the carnivore guilds of Members 4 and 5 might have had a significant bearing on the palaeoecology of the locality, although as may be seen from the latest checklist given here that difference has now been eroded and the two guilds are essentially similar. The hyaena *Chasmaporthetes silberbergi* has now been removed from the listing for Member 5, as discussed above, but the species is recorded from Swartkrans in deposits broadly contemporary with deposition of that member.

Remains of larger pantherine felids suggest the presence of reasonably large lions (Table 3). These cats, together with the machairodont *Homotherium latidens*, would have been the largest predators in the region, but as I have previously stressed (Turner 1984, 1993), the extent of sexual size dimorphism in the Felidae is a potential source of confusion in any efforts to assess matters related to the size of fossil cats. The size variation represented by the two lion lower third premolars S94–7228 and SF 2858 from Member 5 (Table 3), for example, is quite easily accommodated within the pattern and limits of sexual difference seen in modern lions (Turner unpublished data). Although worn, the smaller specimen is quite clearly lion rather than, say, the fourth premolar of a leopard because although such teeth may be of similar size the cusp morphology of the two is quite distinct. This seemingly trivial conclusion about sexual variation is in turn important because it indicates that the animals represented by the larger cheek teeth in the sample are likely to have been simply normal males rather than larger females of a population with a greatly enhanced average body size. This is borne out by comparisons of the seemingly large scapholunare S94–2408 with a proximal articulation width of 49.4mm; Dawkins and Sandford (1872) describe and illustrate lion material from Upper Pleistocene cave deposits in England, and list two specimens with equivalent widths of 58.4mm and 53.3mm respectively. Nevertheless, the distal humerus previously described from Member 4 (Turner 1986: Figure 5, Table 5) still represents one of the biggest lions seen by me, and it is clear that the Transvaal lions were at times impressively large.

A substantial proportion of specimens of hyaenas, cats and dogs have been recovered from the Member 5 West Infill, a part of the deposits thought to be least mixed (Kuman in litt.; Kuman and Clarke 1996). This concentration could be taken to suggest some preferential denning in the vicinity, although which species were denning and which collecting the bones of others remains an open question. It is interesting to note that the sparse fossil record of *Proteles* has been so significantly increased with material from this part of the deposit and from the Post-Member 5 Infill, and may suggest that this species was at least one of the residents of the site at some point based on aspects of behaviour of the living aardwolf (Rautenbach 1982).

The guild of larger carnivores present is typical of much of the latter half of the Pliocene and earliest Pleistocene of eastern and southern Africa (Turner 1990, Werdelin & Turner 1996). It shows a considerable mix of the modern and still extant taxa such as lion, leopard, cheetah, spotted and brown hyaenas, together with archaic taxa such as the machairodont cats, the so-called hunting hyaenas of the genus *Chasmaporthetes* and the aptly-named giant hyaena *P. brevirostris* (Turner and Antón 1996). The genus *Canis*, represented by the jackals, seems to enter Africa some time between 3.0 and 2.5 myr, although the earliest record is extremely spotty. Only after around 1.5 myr does this guild change to leave the modern range of species. The only guide to the age of deposits that can therefore be derived from the Carnivora concerns latest appearances and extinctions.

Taxa in the Member 5 West Infill, believed to be one of the later parts of Member 5, include *C.nitidula*,

Proteles sp., *Panthera leo* and numerous specimens of small *Canis*. Previous suggestions (Turner 1990) that *C. nitidula* may have been present as late as 1.0 myr were based on its appearance in Member 3 at Swartkrans (Turner 1993), but there is now thought to be no compelling evidence for placing Member 3 there significantly later than Member 1 at around 1.8–1.5 myrs (Brain 1993). Accordingly, the Member 5 West Infill carnivore guild assemblage is not incompatible with an age of around 2.0–1.5 myr as suggested by the archaeology (Kuman 1994) and, more generally, by other components of the fauna (Delson 1988; Vrba 1985).

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