

SOME FOSSIL CARNIVORES FROM THE MAKAPANGAT VALLEY

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ABSTRACT

All hitherto undescribed carnivore material from the Limeworks deposit at Makapansgat has been examined and is described. A new sub-species of *Cynictis penicillata* is defined and named *C. penicillata brachyodon*. A number of other fragments cannot be fully identified but include a jackal, probably closely related to the extant *Canis adustus*, a fox and three small felines. The status of *Machaerodus darti* Toerien is discussed and it is concluded that the specimens are not specifically distinct from *Therailurus barlowi* (Broom). The carnivore fauna of the Makapansgat deposit is compared with those of Sterkfontein and Swartkrans and the probable environments are discussed.

INTRODUCTION

Carnivores are not very richly represented in the fossils from the Limeworks Quarry on the farm Makapansgat near Potgietersrust. Toerien (1952) has described a small hyaenid, of which there are numerous specimens, and a single tooth of a large *Crocota*-like type. In a later paper (1955) he has described a machairodont represented by two fragments. The specimens described below comprise the whole of the rest of the carnivore material recovered from the deposit to date. Some of the specimens are so incomplete as to be of little intrinsic interest; it is, however, desirable that all should be recorded, so that a picture of the carnivore fauna as a whole may emerge, and not an eclectic list of the best specimens.

Cynictis penicillata brachyodon subsp. nov.
(Figs. 25, 26)

Geelmeerkat

Type.

Specimen M 282,* a skull much crushed on the left side. P⁴ and M¹ are present on both sides and are moderately worn; the other teeth are missing. The zygomatic arches and the left auditory bulla are missing.

Diagnosis.

A subspecies of *Cynictis penicillata* (G. Cuv.) of approximately the same size as the living representatives, but differing in the following particulars: the upper carnassial is shorter and wider, the paracone and metacone being small in comparison with the protocone; the auditory bulla is shorter.

* Specimen number in the collections of the Bernard Price Institute for Palaeontological Research.

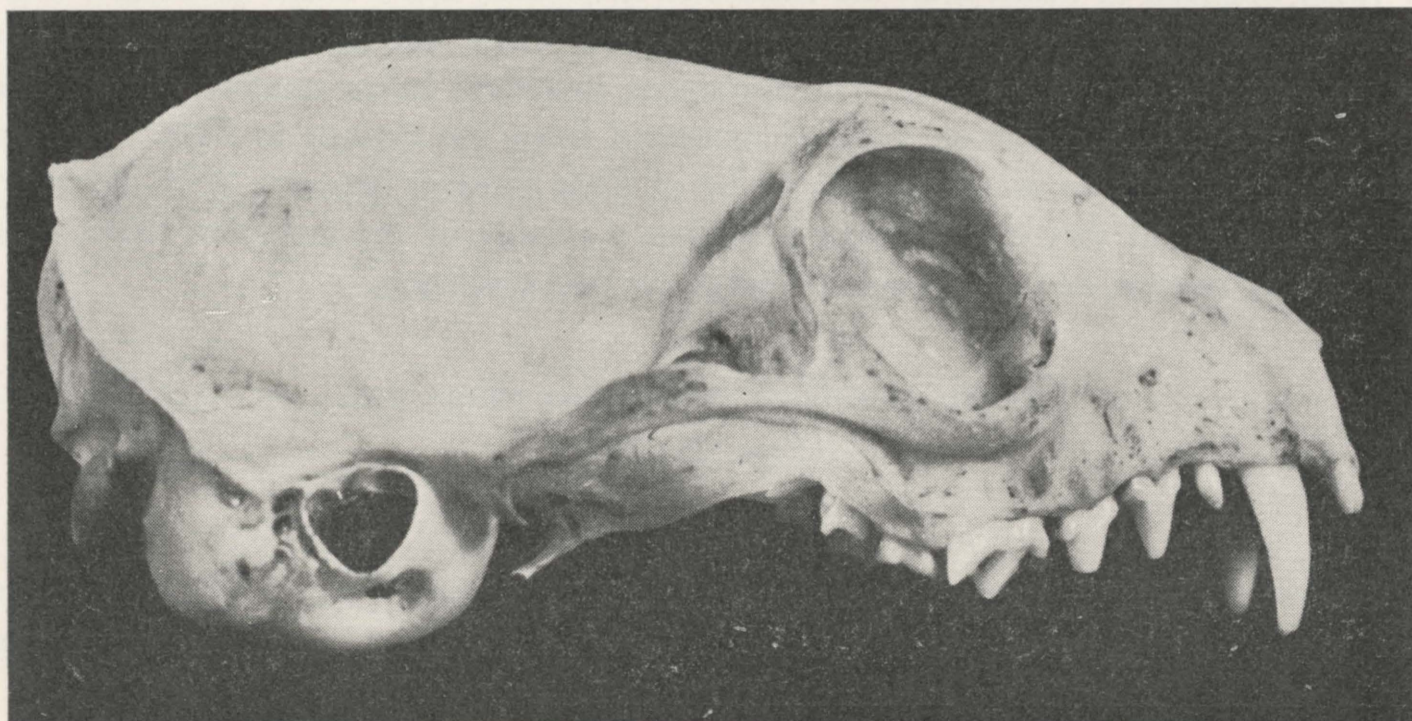
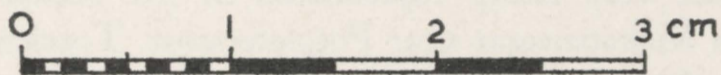
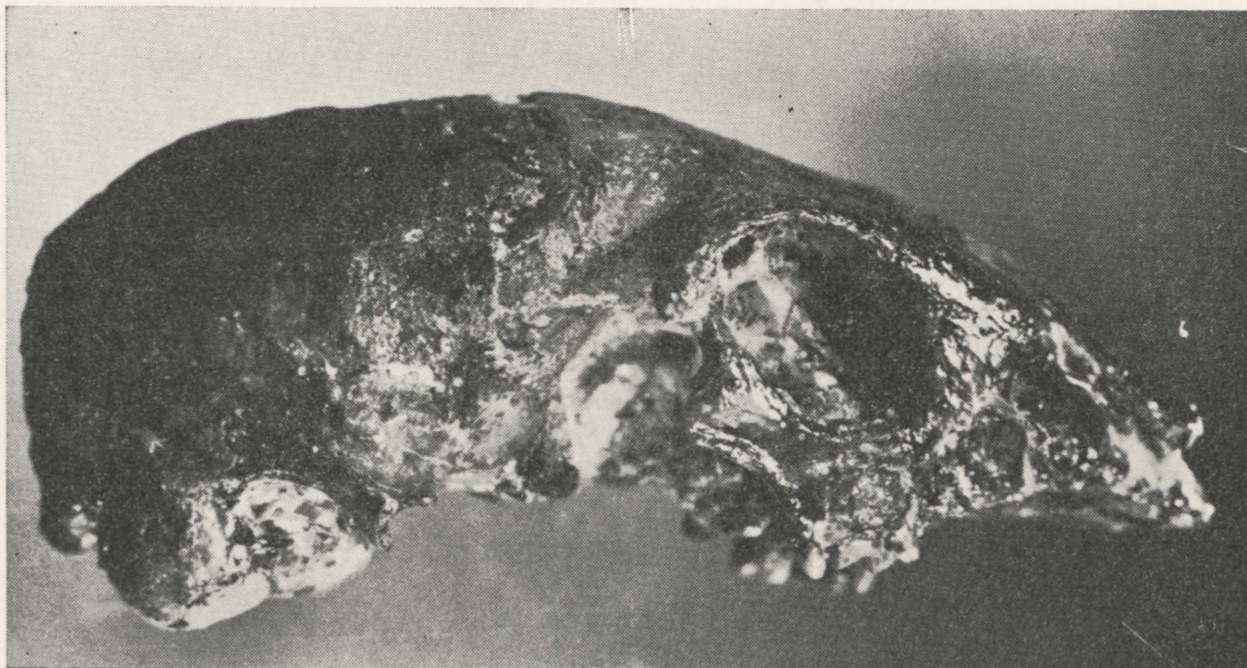


Fig. 25—*Cynictis penicillata brachyodon*, specimen M 282. Side view of skull, with skull of extant *C. penicillata* (below) for comparison.

Description.

The skull is that of a small herpestine and in general conformation closely resembles that of the living *C. penicillata*. The postorbital processes on the frontals and jugals are well developed. Unfortunately the damage to the skull makes it impossible to be certain whether they actually met to form a complete postorbital bar or not. The posterior region of the skull is not elongated and the front of the auditory bulla lies on a level with the post-glenoid process. In extant *Cynictis penicillata* the anterior chamber of the bulla is considerably longer than the posterior, but in the fossil the anterior chamber is of about the same length as the posterior. As a result, in proportion to the length of the skull, the total length of the bulla is less in the fossil than in extant specimens.

Although the anterior premolars are not preserved, the alveoli show that P^1 was present and P^3 had a well developed internal root.

P^4 is rather different in its conformation from the corresponding tooth in extant specimens of *C. penicillata*. The protocone is large and forwardly sloping, and the width of the tooth, measured across the protocone, falls within the range of the living specimens. The paracone and metacone are weakly developed, and the length of the tooth, measured along the jaw margin, is considerably below the limit for extant specimens.

M^1 is a triangular tooth of the usual form. Its length is slightly above the mean for extant specimens, but well within the range. Since P^4 is short the relative proportions of the two teeth differ in the fossil and extant subspecies: relative to the length of the upper carnassial the first molar is considerably longer in the former than in the latter.

M^2 is not preserved in the fossil, but the alveoli show that it was present, 3-rooted, and considerably smaller than M^1 .

Remarks and comparisons.

The characters in which the fossil specimen differs from extant *Cynictis penicillata* have been noted above. In table I values are given for a series of 15-20 extant specimens from the Kaffrarian Museum collection, for comparison. It will be seen that the only measurements in which the fossil falls outside the range of the extant specimens are the length of P^4 and the length of the auditory bulla. The significance of the difference may be tested by expressing the divergence of the value for the fossil from the mean of the extant specimens as a function of the standard deviation of the latter. Table II shows the results of this procedure. d/σ is the difference between the fossil and the mean for the extant specimens divided by the standard deviation: from this is derived P , the probability of a member of the living group diverging from the mean by as much as the fossil does. In both the length of P^4 and the length of the bulla the fossil differs significantly from the extant specimens. The length: breadth ratio of P^4 , the length of M^1 relative to



Fig. 26—*Cynictis penicillata brachyodon*, specimen M. 282. Palatal view, with extant *C. penicillata* (on right) for comparison

P⁴ and the length of the bulla relative to the basilar length have been treated in the same way, and the results are also given in Table II. In all these ratios the fossil differs significantly from the extant specimens.

In the relative shortness of P⁴ and of the auditory bulla the fossil resembles *Paracynictis selousi* de Winton, but differs from that species in its smaller size, lesser extension of the palate behind M¹ and absence of a separation between the postglenoid process and the anterior wall of the bulla.

Broom (1939) has described the snout of a herpestid from Kromdraai. He considered that this might belong to the same species as the lower jaw which he had previously (1937) described as *Crossarchus transvaalensis* from Bolt's Farm. This species differs from *Cynictis penicillata brachyodon* in the much greater length of P⁴ and the 2-rooted M².

A lower jaw of a species of *Cynictis* has been described from the Swartkrans deposit (Ewer 1956 b). The specimen does not show any characters which justify more than subspecific separation from the extant species. It was therefore referred to *Cynictis penicillata*. Although regarded as subspecifically distinct from the extant *C. penicillata* the paucity of the material made it impossible to provide any adequate diagnosis, and no subspecific name was bestowed on the specimen. It seems probable that it belongs to *C. penicillata brachyodon*: the rather short lower carnassial accords well with the identification, but further evidence is necessary before the association of the Makapan skull with the Swartkrans mandible can be taken as established.

Measurements.

In this and the descriptions which follow, all measurements are given in millimeters.

Table I

	Fossil M 282	Extant <i>Cynictis penicillata</i>		
		Mean & S.E.	Range	Number of specimens
P ⁴ length	4.7	6.3 ± 0.11	5.4 — 7.0	19
breadth	4.6	5.0 ± 0.12	4.0 — 5.7	19
M ¹ length	3.7	3.5 ± 0.07	2.8 — 4.0	19
breadth	6.8	6.9 ± 0.11	6.0 — 7.7	19
Basilar length	58.0	62.0 ± 0.86	55.3 — 67.8	18
Width across condyles	16.0	16.1 ± 0.16	15.2 — 17.4	16
Width across bullae	ca. 29.0	28.0 ± 0.31	25.8—30.3	17
Length of bulla	14.2	17.0 ± 0.16	15.8 — 18.5	15

Table II

	Fossil M 282	Extant Mean	Extant S.D.	<i>Cynictis penicillata</i> d/ σ	P.
P ⁴ length	4.7	6.3	0.48	3.35	<.001
P ⁴ length: breadth	1.02	1.27	0.08	3.24	<.003 >.001
P ⁴ length: M ¹ length	1.27	1.81	0.122	4.06	<.0004
Bulla length	14.2	17.0	0.62	4.47	<.0004
Bulla length: basilar length	0.245	0.272	0.009	3.01	ca. .003

INCOMPLETELY IDENTIFIED SPECIMENS

*Canis cf. adustus.**Witkwasjakals.*

Specimen M 285, a fragment of a mandibular ramus with the anterior end of M₁, P₄ and P₃ and the roots of P₂, P₁ and the canine.

The measurements of the teeth of this specimen are given in table III, compared with those of a series of specimens of the extant *C. adustus* Sundevall and *C. mesomelas* Schreber. Values for the fossil subspecies of the latter described from the Sterkfontein, Swartkrans and Kromdraai deposits (Ewer 1956 a) are also included. The lengths of P₃ and P₄ are within the range of both living species, but the estimated length of P₂ is rather small. The tooth is smaller in *C. adustus* than in *C. mesomelas*, and moreover it is larger in the fossil subspecies than in the living group of the latter so that the resemblance of specimen M 285 is closer to *C. adustus* than to *C. mesomelas*.

Two other fossil jackals are known from the Transvaal deposits; *C. brevirostris* from Sterkfontein and *C. terblanchei* from Coopers. Specimen M 285 is distinguished from *C. brevirostris* by the fact that the premolars do not show the close crowding together characteristic of that species. In *C. terblanchei* P₂ is longer than in *C. adustus*, so that it seems that the species to which the specimen belongs is most closely related to *C. adustus*, but no definite identification can be made.

Table III

	M 285	<i>C. adustus</i>		<i>C. mesomelas</i>			
		mean	range	mean	range	mean	range
P ₂ length	ca. 7.0	7.6	7.2 — 8.2	8.0	7.2 — 9.0	9.0	8.0 — 10.1
P ₃ length	8.9	8.6	8.0 — 9.0	8.8	7.1 — 10.0	9.8	9.0 — 12.3
breadth	3.2	3.4	2.8 — 4.4	3.5	3.0 — 4.0	3.9	3.5 — 4.5
P ₄ length	10.0	9.8	9.3 — 10.6	10.3	9.2 — 11.5	11.2	10.2 — 12.6
breadth	4.2	4.2	3.7 — 4.7	4.3	3.6 — 4.8	4.8	4.4 — 5.6
P ₁ - P ₄ length	ca. 33	35.0	31.7 — 36.4	34.8	31.5 — 37.1	35.0	32.5 — 38.6

The values for *C. adustus* are based on 10 and those for the living *C. mesomelas* on 14 specimens. For the fossil *C. mesomelas* the numbers range from 5 to 8 different dimensions.

Vulpes sp.

Silvery jackals

Specimen M 296, posterior part of the cranium of a small fox, broken off at the level of the post-orbital constriction. Since no teeth are preserved this specimen cannot be identified further, and it is not even possible to say whether it is or is not different from the extant *Vulpes chama* Smith.

Felidae.

Herbivore / Serval cat.

Specimen M 295, a fragment of the maxilla of a feline preserving P³ only. The tooth is larger than in the extant *Leptailurus serval*, but distinctly smaller than in the living leopard: it is thus of about the same size as that of the living *Caracal caracal* Schreber. The specimen differs from the extant members of the species in that there is an alveolus for P², whereas this tooth is usually absent in the living caracal.

Roar cat.

Measurements: P³ length 13.3; breadth of main cusp 5.1.

Specimen M 292 is an anterior mandibular fragment, with damaged canine; M 266 is a fragment with M₁ and damaged P₄. Both specimens belong to a felid of about the size of the extant *Leptailurus serval*. They may possibly belong to *Leptailurus spelaeus*, described by Broom (1937, 1939) from Bolt's Farm.

Specimen M 267 is a mandibular fragment with M₁, P₄ and P₃. The specimen belongs to a felid closely similar to the extant *Felis cafra* Desmarest, but the material does not permit any definite identification.

THE MAKAPANGSAT SABRE-TOOTH

The sabre-tooth material from Makapansgat comprises a mandibular ramus and the anterior portion of a snout and mandible. These are described by Toerien (1955). The mandible is peculiar in that the coronoid process is very well developed, and the lower canine is not as much reduced as is usual in machairodonts. Toerien notes the similarity of the upper canine to that of *Megantereon barlowi* Broom, but, since the Makapansgat material clearly does not belong to the genus *Megantereon* he does not suggest that the two may belong to a single species. Although of the opinion that the specimens probably represent a new genus, in default of more extensive material Toerien concludes that "it is preferable to refer the specimens to an existing genus, of which *Machaerodus* appears to be the most suitable". It was accordingly named *Machaerodus darti*.

Since Toerien's paper was written new machairodont material from Sterkfontein, Swartkrans and Kromdraai has been described (Ewer 1955b). This includes a very complete skull from Kromdraai belonging to a species in which the typical machairodontine specialisations are relatively slightly developed. The specimen shows many similarities to *Therailurus diastemata* (Astre) and has been referred to the genus *Therailurus*. Re-examination of the original material of "*Megantereon*" *barlowi*, together with some new specimens from Sterkfontein, shows that this species is very similar to the Kromdraai *Therailurus* and that its reference to the genus *Megantereon* cannot be correct. It is therefore transferred to the genus *Therailurus*. This at once raises the question of whether *Machaerodus darti* may not be identical with *Therailurus barlowi*. The upper canines are so closely similar, and the unspecialised character of the lower jaw so reminiscent of the mandible of *Therailurus diastemata* described by Piveteau (1948) that there can be little doubt that "*Machaerodus*" *darti* belongs to the genus *Therailurus*. Unfortunately there is no well preserved mandible of *T. barlowi* from Sterkfontein, but one much damaged specimen includes M₁, P₄ and P₃. The teeth are rather larger than those of the Makapansgat mandible, but the difference is no greater than the range of variation shown in the living leopard. In general construction the teeth are very similar except that in the Makapansgat mandible M₁ has a vestigial talonid which is not present in the Sterkfontein specimen. A vestigial character is often highly variable, and this difference alone can hardly be taken as warranting specific separation. In view of the remarkable similarity of the upper canines it seems justifiable to conclude that the two belong to a single species, while recognising that further material may indicate a difference at the subspecific level. *Machaerodus darti* Toerien thus becomes a synonym of *Therailurus barlowi* (Broom).

DISCUSSION

A comparison of all the known mammal remains has shown (Ewer 1956c) that many of the Makapansgat species occur also at Sterkfontein or at Swartkrans, and

the deposits were presumably formed at periods which were not widely separated. A comparison of the carnivore faunas of the deposits may therefore be of some interest, and may possibly throw some light on the ecological difference between Makapansgat and the other two deposits.

Table IV shows the distribution of carnivores in the three deposits. The main difference between Makapansgat and the other two deposits lies in the poor representation in the former of large carnivores. The Makapansgat hyaenid is a relatively small species, resembling the living striped hyaena; apart from the two specimens of a moderately large machairodont and the single large hyaenid tooth, the rest of the carnivores are all small species. Sterkfontein and Swartkrans include large hyaenids, leopards and lion-like animals as well as sabre-tooths.

Table IV

x indicates the presence of a single specimen, xx remains belonging to 2 or 3 individuals, xxx numerous specimens.

	Makapansgat	Sterkfontein	Swartkrans
HYAENIDAE			
<i>Leecyaena</i>			x
<i>Lycyaena</i>		xx	xxx
<i>Hyaena</i>	xxx	x	xx
<i>Crocota</i>	x		xx
MACHAIRODONTINAE			
<i>Therailurus</i>	xx	xx	x
<i>Megantereon</i>		x	x
FELINAE			
Leopard		x	xxx
"Lion"			xx
Small felines	xx		
CANIDAE			
Jackal, <i>mesomelas</i> type		xxx	xxx
Jackal, <i>adustus</i> type	x		
Fox	x		x
VIVERRIDAE			
<i>Cynictis</i>	x		x

Differences in the carnivore faunas of cave deposits may reflect either differences in the character of the surrounding country, or differences in the structure of the caves themselves which render them suitable or unsuitable as carnivore lairs. The northern Transvaal is today near the southern limit for a number of typically central African species. It may therefore be its more northerly situation which determines that, unlike the other deposits, Makapansgat has a hyaenid resembling the extant striped hyaenas, whose range today does not extend as far south as the Union of South Africa; and the jackal at Makapansgat resembles the side-striped species whose range is more northerly than that of the black-backed jackal.

Some of the differences in the carnivore faunas may also reflect differences in the abundance of thick bush cover at Makapansgat and at the other deposits. The lion prefers relatively open country, and is less common in thick bush, whereas for small felids like the Wild Cat and the Caracal the reverse is true. The Black-backed jackal also is common in more open country and the Side-striped in thicker cover. These facts would suggest that thick cover may have been more abundant at Makapansgat than at the other deposits. The absence of leopard at Makapansgat, however, remains puzzling, since this species has no aversion to thick cover. Two explanations are possible. Firstly, the Makapansgat cave may have been of a type unattractive to leopards, although fragments of hyaenas and Sabre-tooths are found in it. This does not seem very plausible. The second possibility is related to the times at which the deposits were laid down. It has been suggested (Ewer 1956 c) that Sterkfontein and Makapansgat are almost of an age, with the former probably a trifle the earlier, while Swartkrans comes somewhat later. Now leopard remains are very common at Swartkrans, whereas at Sterkfontein they are represented by only a single tooth. It is therefore possible that leopards were extremely rare in South Africa at the times when the Makapansgat and Sterkfontein deposits were laid down, but had established themselves a little later when the Swartkrans deposit was being formed. If this can be substantiated the presence or absence of leopard may become of considerable importance in dating. Some support for this idea is afforded by a consideration of the distribution of the *Lycyaenas*. *Lycyaena* is a genus in which the specialisations for bone crushing, characteristic of hyaenids, did not develop as rapidly as they did in other more progressive lineages. Most of the *Lycyaenas* had become extinct by the end of the Pliocene, presumably as a result of competition with their more efficient relatives. Those species which survive into the Pleistocene are the one Villafranchian European species, *Lycyaena lunensis* del Campana and the species found at Sterkfontein and Swartkrans. These show certain peculiarities which have been interpreted (Ewer 1955 a) as reflections of a secondary adaptation to a purely predatory habit — in fact an attempt to survive by avoiding competition with the advanced hyaenids. The attempt was not successful, for the *Lycyaenas* do not survive into the middle Pleistocene, and the reason seems obvious. Having failed originally as scavengers in competition with the advanced hyaenids, the *Lycyaenas*, as predators, found themselves in competition with the leopards. The much larger

canine teeth and the powerful claws of the leopard leave little doubt as to the outcome. The *Lycyaenas* and leopards occur together at Swartkrans: after that there are no more *Lycyaenas*, but the leopards have survived until today.

ACKNOWLEDGEMENTS

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- p. 69 First line after introduction, for "constitute" read "constitue"; six lines from bottom, for "Congrés" read "Congrès".
- p. 70 Second line, for "Congrés" read "Congrès".
- p. 71 Second line, for "*M. antiquees*" read "*M. antiquus*"; third line fifth paragraph, for "fore" read "forme"; fifth line from bottom, for "Figures" read "Figure".
- p. 74 Second last line of long paragraph, for "simplication" read "simplification".
- p. 75 Last line third paragraph, for "antérieur" read "antérieur".