
ANNALS OF THE TRANSVAAL MUSEUM
ANNALE VAN DIE TRANSVAAL-MUSEUM

Vol. 29

31 July 1974

No. 4

PROTELES CRISTATUS SPARRMAN FROM THE
PLEISTOCENE OF SOUTH AFRICA, WITH A NOTE
ON TOOTH REPLACEMENT IN THE AARDWOLF
(MAMMALIA: HYAENIDAE)

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(With one Plate and one Text-figure)

ABSTRACT

New fossil specimens of *Proteles cristatus* from Bolt's Farm Pit 1 are described and figured, along with a specimen from Black Earth Cave. Examination of a number of skulls of juvenile aardwolves indicates that the full dental formula of the living *Proteles* is $I_{123}^{123} C_1^1 P_{234}^{234} M_1^1$.

INTRODUCTION

The aardwolf, *Proteles cristatus* Sparrman, is a jackal-sized mammal of the family Hyaenidae. It is found today throughout much of southern and eastern Africa. Ancient Egyptian funerary reliefs from the third and second millennia B.C. suggest that the aardwolf was once present in North Africa as well (Brentjes, 1966). The skull of *Proteles* is particularly distinctive because of the reduction of its post-canine teeth to small well-spaced pegs, a development correlated with a diet consisting almost entirely of termites (Bothma, 1971). There is in this remarkable dietary specialization and dental reduction undoubtedly an evolutionary story of great interest. Unfortunately, the aardwolf has been surprisingly little studied and almost nothing is known of its evolution.

Proteles is classified by some as the sole member of the family Protelidae (Allen, 1939; Ellerman, Morrison-Scott, and Hayman, 1953; Bigalke, 1968), or with the hyaenas in the family Hyaenidae (Simpson, 1945; Walker, 1964). The recently demonstrated identity of the karyotype (Wurster & Benirschke, 1968; Wurster, 1969) and hemoglobin mobility (Seal, 1969) of *Proteles*, *Hyaena*, and *Crocuta* appears to support inclusion

of *Proteles* in the Hyaenidae. In external appearance the aardwolf resembles closely the striped hyaena (*Hyaena*), although this may be a result of mimicry and is not necessarily an indication of relationship. It is unlikely that the true relationship of *Proteles* to the hyaenas will be known until additional fossil forms are discovered.

The first published record of a fossil aardwolf was the inclusion of *Proteles* in the list of a Middle Stone Age fauna from Black Earth Cave in the northern Cape Province of South Africa (Peabody, 1954). Recently Hende (1973, 1974) described additional specimens from the much older faunas of the Kromdraai and Swartkrans australopithecine sites. Several of these specimens are particularly interesting as they appear to represent the new, more primitive species *Proteles transvaalensis* (Hende, 1974). In the present report Peabody's original specimen from Black Earth Cave is described, along with two new specimens from Bolt's Farm Pit 1 which are undoubtedly much older, although still clearly indistinguishable from the living species *P. cristatus*. The new fossil specimens are fully illustrated in the hope that this may lead to the recognition of additional specimens in other collections.

Interpretation of the dental evolution of *Proteles* requires that the homologies of the remaining cheek teeth of this genus be established, and a section on tooth replacement in *P. cristatus* has thus been added to this paper. The osteological specimens of recent *Proteles* described here are in the American Museum of Natural History [AM], New York and the Yale Peabody Museum [YPM], New Haven. The fossil specimens described here are in the University of California Museum of Paleontology [UCMP], Berkeley.

TOOTH REPLACEMENT IN *PROTELES CRISTATUS*

No attempt has been made in previous descriptions of the teeth of living *Proteles cristatus* to determine the sequence of tooth replacement or the dental homologies of the postcanine dentition. A number of juvenile specimens are now available which shed light on this matter. Tracings from x-ray photographs of these specimens are illustrated in Text-fig. 1.

The youngest available skull of a juvenile *Proteles* is AM169090 (figure 1a), which shows the complete deciduous dentition of three incisors, the canine, and three postcanine teeth. By analogy with the deciduous dentition of dogs (Tims, 1896) and other mammals (Ziegler, 1971: 51), these postcanine teeth are undoubtedly the deciduous dP_2^2 , dP_3^3 , and dP_4^4 .

The permanent P^1 is the next tooth to erupt (Figure 1b); it has no deciduous precursor. As in *Hyaena* and *Crocuta*, the lower P_1 is absent in *Proteles*. Shortly after eruption of P^1 , a relatively small single-rooted lower tooth erupts behind dP_4 . As this tooth appears not to replace dP_4 , but erupts well behind it, I interpret it as M_1 . AM169446 shows a similar development of upper M^1 at a slightly later stage (figure 1c). Eruption of M_1^1 in *Proteles* at about the same time as the eruption of P^1 , and before eruption of P_2^2 , P_3^3 , and P_4^4 , is consistent with the eruption pattern in *Crocuta* (Todd & Schweikher, 1933) and in *Canis* (Nickel *et. al.*, 1960).

Deciduous dP_2^2 and dP_3^3 are clearly replaced by P_2^2 and P_3^3 , respectively. Unfortunately no specimen is yet known actually showing the replace-

ment of dP_4^4 , but considering the permanent dentition of AM 169091 (figure 1d), it is almost certain that dP_4^4 was replaced in some *Proteles*. Even if the teeth interpreted as M_1^1 in figure 1c are actually P_4^4 , the homologies of the teeth illustrated in Figure 1d are still almost certainly correct.

The sequence of eruption of the permanent cheek teeth of *Proteles* is apparently P_1 , M_1 , P_3 , then P_2 . The time of eruption of P_4 , when present, cannot be determined from the specimens available. The full dental formula of *Proteles cristatus* is the same as that of the living species of *Hyaena* and *Crocuta* (Simpson, 1966): $I_{123}^1 C_1^1 P_{234}^{1234} M_1^1$. Most mature skulls of *Proteles* have at least P_1^1 , P_2^2 , and P_3^3 present. Other teeth are variably present, and deciduous teeth, particularly dP_4^4 , are occasionally retained even in rather old skulls.

BLACK EARTH CAVE *PROTELES*

The first record of a fossil aardwolf was Peabody's (1954: 698) mention of "*Proteles*" in his faunal list of the lower level at Black Earth Cave. The specimen on which this record is based (UCMP 42735) is an edentulous left mandible illustrated in plate 4: 5,6.

The specimen includes most of the symphyseal region and the alveolus of the left lower canine, but the incisor alveoli and the very front of the mandible are not preserved. A diastema of about 14 mm separated P_2 from the canine. Three postcanine teeth are indicated by alveoli only, the teeth themselves having fallen out. By matching the spacing of the alveoli with figure 1d, the homologies were determined. The alveolus of P_2 is 3,4 mm in length. A diastema of 2,0 mm separates this tooth from the alveolus of P_3 , which measures 4,0 mm in length. A diastema of 12,7 mm separates P_3 and the next post-canine tooth, M_1 . The alveolus of M_1 is nearly circular and is only 1,8 mm in length. A small portion of the masseteric fossa of the mandible is preserved; the angle and ascending ramus are missing. In all details this mandible from Black Earth Cave is indistinguishable from mandibles of the living South African populations of *Proteles cristatus*.

BOLT'S FARM *PROTELES*

From April to July 1948, a University of California party excavated a number of lime pits at Bolt's Farm near the Krugersdorp *Australopithecus* caves (Camp, 1948). Cooke (1963) lists the fauna from the Bolt's Farm pits.

One of the Bolt's Farm pits, "Pit 1" (= Kraal Pit, UCMP locality V67256), yielded two specimens of *Proteles cristatus*, both of which were originally identified as juvenile ?felids. One of these, UCMP 89195, is the anterior portion of a right mandible preserving the right lower canine and alveoli for P_2 and P_3 (plate 4: 1,2). The mandible is broken medial to the canine, and the incisor region is not preserved. Posteriorly the mandible is broken just behind the alveolus for P_3 . The size of the canine, the diastema separating the canine and post-canine teeth, and the position of the postcanine alveoli agree very closely with mandibles of the living southern African populations of *Proteles cristatus*, being indistinguish-

able from AM 169091 from Molepolole in Botswana. X-radiographs of the fossil specimen indicate that its postcanine teeth were single-rooted, as in the living form (figure 1d). Maximum and minimum diameters at the base of the canine are, respectively, 7,3 mm and 5,4 mm. The diastema between the canine and alveolus of P_2 is 16,1 mm, and the alveoli of P_2 and P_3 are respectively 4,3 and 5,2 mm in length.

The second specimen from Bolt's Farm, UCMP 89194, includes the anterior portion of the left maxilla with the left canine, P^1 , and P^2 intact, together with a part of the left premaxilla preserving alveoli for the second and third incisors (Plate 4: 3,4). Again, this fragment compares very closely with specimens of the living South African *Proteles*. The upper canine of UCMP 89194 is not fully erupted, and it seems unlikely that this specimen and the lower jaw UCMP 89195 were parts of the same individual. The upper postcanine teeth are respectively 2,3 mm and 3,6 mm in length, which appears to be well within the range of variation of living populations of *proteles cristatus*.

DISCUSSION

It is clear from the descriptions given above that the fossil specimens of *Protelis cristatus* described here from Black Earth Cave and Bolt's Farm Pit 1 are virtually identical to corresponding parts of the living aardwolf. On the basis of Peabody's (1954) work, the age of the Black Earth Cave specimen would appear to fall within Cooke's (1967) Florisbad-Vlakkraal Faunal Span, and it is probably not more than 50,000 years old. The specimens from Bolt's Farm Pit 1 are undoubtedly much older. Most of the Bolt's Farm fauna falls within the Swartkrans Faunal Span (Cooke, 1967), which is tentatively correlated with the lower part of Olduvai Bed II (Cooke, 1968). Lower Bed II at Olduvai is dated at approximately 1,0 million years (Maglio, 1970). It is possible that the Pit 1 fauna is an old as Olduvai Bed I (Cooke, pers. comm.), or almost 2 million years old.

Specimens of *Proteles* are now known from three of the Krugersdorp Pleistocene localities. Those from Bolt's Farm Pit 1 described here and from the decalcified breccia at Swartkrans (Hendey, 1974) represent the living species *P. cristatus*. Other specimens from Swartkrans and Kromdraai B are significantly larger than the living aardwolf, and appear to represent the more primitive species *Proteles transvaalensis* (Hendey, 1974).

On this evidence Bolt's Farm Pit and the Swartkrans decalcified breccia are almost certainly later in time than the main Swartkrans and Kromdraai B localities. The specialized adaptation of *Proteles* makes it unlikely that more than one evolutionary lineage existed in Africa. Thus the discovery of additional specimens of *Proteles* from other sites, particularly the well-dated East African localities, should assist greatly in correlating the East and South African Pleistocene faunas.

Populations of *Proteles cristatus* virtually indistinguishable from the living form have been a part of the South African mammal fauna for at least the past 1 million years. This, and the evidence provided by *P. transvaalensis*, indicates a probable Pliocene or earlier date for divergence of *Proteles* from the ancestral hyaenid stock.

ACKNOWLEDGEMENTS

I wish to thank Dr H.B.S. Cooke, Dalhousie University, for information on the Bolt's Farm Pit 1 locality and for reading the original manuscript; and Drs J.T. Gregory, University of California Museum of Paleontology, and S. Anderson, American Museum of Natural History, for permission to borrow the specimens described here. The original manuscript was submitted before I was aware of the Kromdraai and Swartkrans specimens, and I am grateful to Dr Q.B. Hendey, South African Museum, for his comments and for providing his manuscript on *P. transvaalensis*. I also thank Grant E. Meyer, Yale Peabody Museum, for his assistance.

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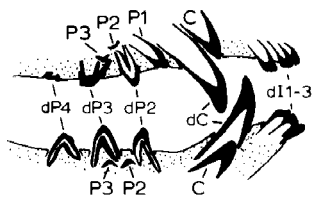
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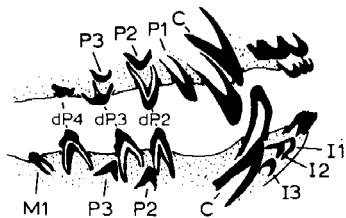
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A.M. 169090
MOLEPOLOLE



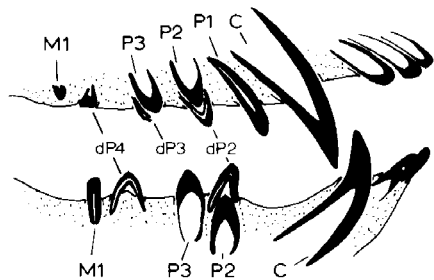
A

Y.R.M. 4019
"SOUTH AFRICA"



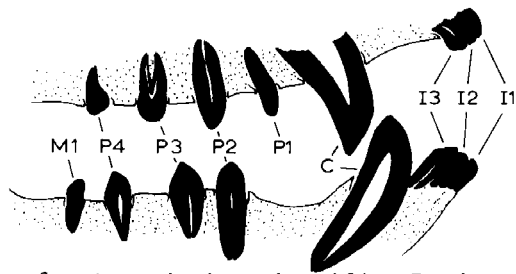
B

A.M. 169446
CITRUSDAL



C

A.M. 169091
MOLEPOLOLE



D

Fig. 1 A-D. Four stages of tooth eruption in southern African *Proteles cristatus*, traced from x-ray photographs, all natural size.

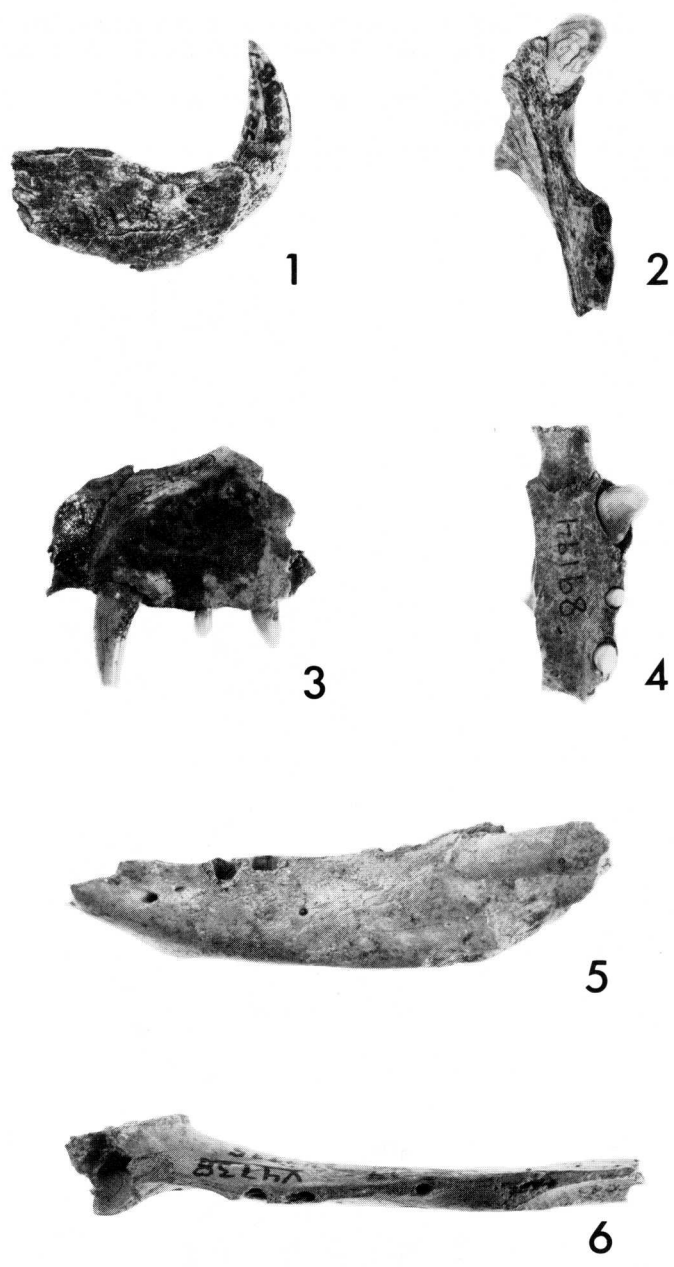


PLATE 4

Fossil aardwolves from Bolt's Farm and Black Earth Cave, South Africa, in the collections of the University of California Museum of Paleontology, Berkeley; all approximately natural size. Fig. 1: UCMP 89195 from Bolt's Farm Pit, 1 right mandible fragment, lateral view. 2. same as figure 1, occlusal view. 3. UCMP 89194 from Bolt's Farm Pit 1, left maxilla fragment, lateral view. 4. same as figure 3, occlusal view. 5. UCMP 42735 from Black Earth Cave, left mandible, lateral view. 6. same as figure 5, occlusal view.