

First evidence for a species of raccoon dog, *Nyctereutes* Temminck, 1838, in South African Plio-Pleistocene deposits

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ABSTRACT — Material from Plio-Pleistocene age deposits in South Africa, previously described as a species of extinct jackal, is here referred to the genus *Nyctereutes*. Although widely known from Eurasian deposits of this age, this is the first record of *Nyctereutes* in Africa. Today *Nyctereutes* is represented by a single species, *N. procyonoides* Gray, 1834, the raccoon dog, which occurs naturally in eastern Asia.

RIASSUNTO — [Prima segnalazione di una specie di *Nyctereutes* Temminck, 1838, nei depositi Plio-Pleistocenici del Sud Africa] — Fossili da depositi plio-pleistocenici del South Africa, che erano stati riferiti ad una specie di sciacallo, sono nel presente lavoro attribuiti al genere *Nyctereutes*. Questo canide, largamente diffuso nel Rusciniiano e nel Villafranchiano dell'Eurasia, è segnalato per la prima volta in Africa. Oggi *Nyctereutes* è presente in Asia orientale con una sola specie, *N. procyonoides* Gray, 1834.

INTRODUCTION

We report on material of Plio-Pleistocene age from South Africa, previously assigned to the genus *Canis* Linnaeus, which we believe should be reassigned to the genus *Nyctereutes* Temminck, 1838. *Nyctereutes* is represented by a single species, *N. procyonoides* Gray, 1834, the raccoon dog, which occurs naturally in eastern Asia. Various species of *Nyctereutes* are known from Eurasian deposits of Plio-Pleistocene age (Soria and Aguirre, 1976; Kurtén, 1968; Savage and Russell, 1983), but none have previously been recorded from Africa. Most of the material discussed here is held in the Transvaal Museum, Pretoria, South Africa, and is from sites in the Sterkfontein Valley, some 40 km southwest of Pretoria. Sites in this area are best known for their finds of Plio-Pleistocene hominids of the genus *Australopithecus* Dart, 1925. One item, from the southern Cape Province site of Elandsfontein, is held in the South African Museum, Cape Town.

HISTORY OF THE MATERIAL

Table 1 lists the African material discussed here. In 1948 Broom briefly described a crushed, unnum-

bered canid skull with associated mandibles from the portion of the Kromdraai site now known as Kromdraai A. He concluded that the specimen represented a new species of jackal which he named *Thos terblanchei*. In a later and more detailed description of the fossil material in which she itemised the Kromdraai specimen as 1290, Ewer (1956) proposed that both fossil and modern jackals should be placed in the genus *Canis* rather than in *Thos* Oken, 1816. However, she also threw the origin of the specimen into some confusion by claiming that the adhering matrix is considerably lighter in colour than that associated with other Kromdraai A specimens. The question has been discussed by Hendeby (1974) and by Brain (1981), both of whom concluded that the provenance of the type specimen is therefore uncertain. However, further examination of the matrix adhering to specimen 1290 and to specimens from Kromdraai A by one of us (AT) suggests that insufficient allowance has been made for variations in matrix colouration. An old and undated catalogue book of material held in the collections of the Transvaal Museum lists the skull of a « fox » from the site of Kromdraai, item 1290. Against this entry, in what is clearly Broom's handwriting, is added the note « type of *Thos ter-*

blanchei Br Coll R Broom ». There are a number of amended entries in the catalogue book, where provenance details have later been altered, but no such amendment has been made in the case of specimen 1290. We take the view that the provenance of the type specimen is reasonably well supported.

Ewer (1956) also referred two specimens from a nearby site known as Coopers to the same species as Broom's material: K₂ 82, a left mandibular fragment with M₁, M₂, alveolus of M₃ and part of the condyle, and K₂ 83, a right snout region with most of the palate, premaxilla, maxilla, and anterior jugal and the carnassial and both upper molars.

Hendey (1974) suggested that specimen 15605 from Elandsfontein in the southwestern Cape Province might be referred to *C. terblanchei*. He noted that the fragmentary nature of the specimen precluded assessment of most of the characters said to distinguish *C. terblanchei* from *C. adustus* Sundevall, 1846, the side-striped jackal, but argued that the features which are visible in 15605 match most closely with those of Broom's original specimen. Hendey also drew attention to the presence of a subangular lobe on the mandible of the type of *C. terblanchei*, and noted the presence of that feature in a small number of extant canids including *N. procyonoides*, but concluded that *C. terblanchei* might be regarded « simply as a less advanced form of *C. adustus* ».

More recently still, Brain (1981) tentatively suggested that a left maxillary specimen, SE 125 from Member 5 of the Sterkfontein site, might also be referred to *Canis terblanchei*. The specimen has only an *in situ* canine and the alveoli of the other teeth.

In our view, features to be seen in specimen 1290 match most closely with those to be found in *Nyctereutes*. A cast of the right side of the skull and attached right mandible of specimen 1290, together with a complete cast of the now detached left mandible and a cast of specimen K₂ 82, were made in the Transvaal Museum and used by GF and DT for more detailed assessment of the material in direct comparison with modern and fossil specimens of *Nyctereutes* held in European institutions.

DATING OF SPECIMENS

The problems of dating the South African hominid and other mammalian-fossil sites and their contents are well known. The general absence of material suitable for the application of absolute dating techniques is a serious obstacle to interpretation, and has meant that considerable reliance must continue to be placed on relative dating of vertebrate assemblages from the sites in comparison with those from dated deposits in East Africa. Useful summaries of the problems, and of the possible correlations which may be made, are given by Cooke (1983), Partridge (1982) and Vrba (1982).

Specimen 1290 is from the portion of the site known as Kromdraai A (Brain, 1981), while hominid remains have been found only in Kromdraai B. The two deposits occur in parallel, east-west trending solution cavities separated by about 17 metres. It has been customary at times in the past to assume that both deposits formed contemporaneously, but studies of the respective assemblages have thrown doubt on this interpretation (Brain, 1975, 1981; Freedman and Brain, 1972; Hendey, 1973). Following recent excavation in B breccia (Vrba, 1981), it has become apparent that both the Kromdraai A assemblage and that previously recovered from Kromdraai B are from deposits of unknown but considerable formation time. On the basis of the bovid component of the assemblages, Vrba (1982) has tentatively suggested that the A and cemented B deposits at Kromdraai may date to around 1.0-1.5 Myr and around 2.0 Myr respectively, but clearly a more precise figure cannot be assigned to any individual items at present. Material from the Coopers site has no clear date assigned to it since the material is simply too scanty. Member 5 of Sterkfontein has been suggested to date to around 1.5 Myr (Vrba, 1982), and thus we may place such a possible date on the maxillary specimen SE 125. The specimen from Elandsfontein referred to *Canis terblanchei* is undated, but has been argued to be of similar age to the type specimen from Kromdraai on the basis of morphology (Hendey, 1974). These inferred dates are summarised in Table 1.

EXPLANATION OF PLATE 1

Mandibulae of:

Fig. 1a, b - *Nyctereutes terblanchei* (Broom). South Africa, Ka 1290.

Fig. 2 - *N. terblanchei* (Broom). South Africa, K₂ 82.

Fig. 3, 4 - *N. sinensis* (Schlosser). Choukoutien Loc. 1 (Pei, 1934: Fig. 5E, 5B).

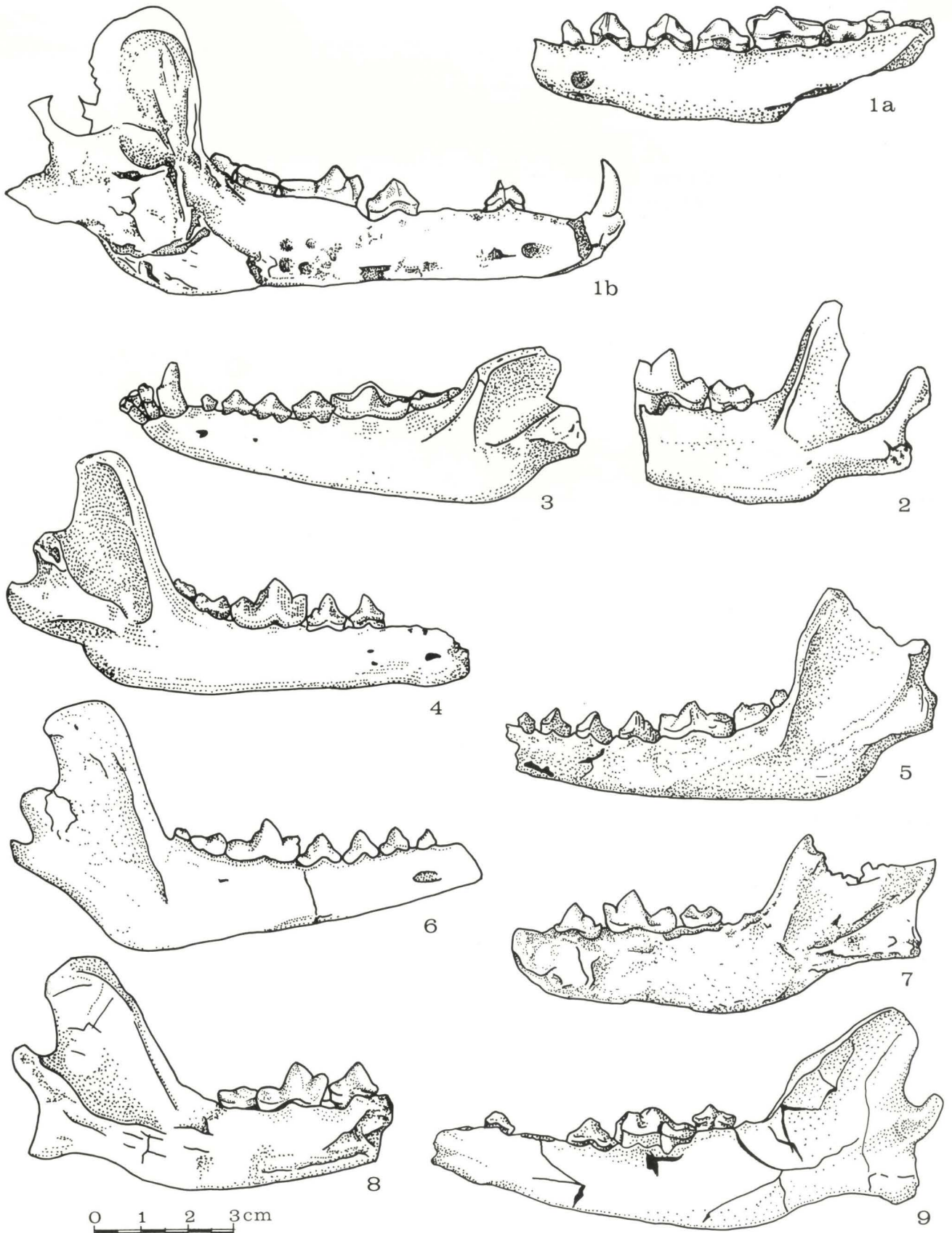
Fig. 5 - *N. sinensis* (Schlosser). Nihowan (Teilhard de Chardin & Piveteau, 1930: pl. 18, Fig. 3).

Fig. 6 - *N. megamastoides* (Pomel). Saint-Vallier (Viret, 1954: pl. 1, Fig. 2a).

Fig. 7 - *N. aff. donnezani* (Deperet). Weze (Czyzewska, 1969: pl. 28, Fig. 3).

Fig. 8 - *N. donnezani* (Deperet). Layna (Soria & Aguirre, 1976: pl. 2, Fig. 1b).

Fig. 9 - *N. donnezani* (Deperet). Perpignan (Deperet, 1890: pl. 3, Fig. 5).



Specimen	Description	Site	Age (Myr)
Ka 1290	Skull and mandibles	Kromdraai A	1.0-1.5
K ₂ 82	left mandible	Coopers	?
K ₂ 83	right snout	Coopers	?
15605	left and right maxillae	Elandsfontein	?
SE 125	left maxilla	Sterkfontein 5	c.1.5

Table 1 - African fossil canids previously described as *Canis terblanchei*. Dates after Vrba (1982).

SYSTEMATIC DISCUSSION

Family Canidae Gray, 1821

Genus NYCTEREUTES Temminck, 1838

NYCTEREUTES TERBLANCHEI (Broom), 1948

In view of the fragmentary nature of much of the material, and of the difficulties which attend comparisons in such circumstances, we have elected to restrict discussion to the original type specimen of *Canis terblanchei* and to the left mandible from the Coopers site, K₂ 82. In both specimens, the characteristic subangular lobe of the mandible may be seen (Pl. 1). For the rest of the material, we suggest that similarity to the two specimens which we will consider has already been adequately discussed, and that affinities, or otherwise, will continue to stand whether of not specimens 1290 and K₂ 82 are referred to another genus.

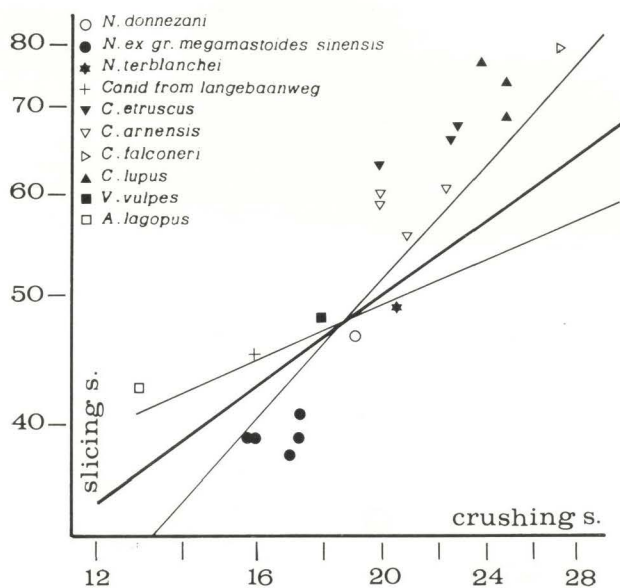
During the Villafranchian, two species, *N. megamastoides* Pomel, 1854 from Europe and *N. sinensis* Schlosser, 1903 from China, are known (Kurtén, 1968; Soria and Aquirre, 1976). Because of the similarities between these two forms we shall refer to them as the *megamastoides-sinensis* group. A pre-Villafranchian form is the species *N. donnezani* Crusafont, 1950.

The skull of the Kromdraai specimen 1290 is very damaged and thus inadequate for diagnosis. But the two mandibles of the specimen show features typical of the genus *Nyctereutes*, particularly in the strongly developed subangular lobe of the right mandible and in the forward rotation of the ascending rami. As a result of that rotation the condyle and the angular process are raised, and the anterior edge of the ascending ramus forms a virtual right angle to the tooth row. These features may also be seen in specimen K₂ 82 from Coopers (Pl. 1). The base of the ascending ramus in 1290 is very massive, while the horizontal portion of the mandible displays a straight lower edge and a progressive disto-medial taper. Such apomorphic features are found to a similar extent in specimens which fall within the *megamastoides-sinensis* group, and also in

the present-day *N. procyonoides*. The development of the lower second and third molars and of the talonid of M₁ in both fossil specimens, together with that of the upper molars in 1290, suggests a higher crushing specialization than that seen in either *Canis* or *Vulpes* Bowditch, 1821. This specialization offers further support for assignment of the specimens to *Nyctereutes* (Martin, 1971).

Although both African specimens approach the Villafranchian *megamastoides-sinensis* group in these dental and gnathic features, the more complete Kromdraai fossil is distinguishable from that group by the ratio of premolar (including M₁ trigonid) length versus molar (including M₁ talonid) length (Text-fig. 1). This feature is developed to an even greater extent in *Canis* and *Vulpes*, and may thus be considered a plesiomorphic character. Interpretation of the character as primitive is supported by the condition seen in the pre-Villafranchian specimens of *N. donnezani* from the Layna (Soria and Aquirre, 1976), Perpignan (Deperet, 1980) and Venta del Moro (Morales and Aquirre, 1976) sites, the latter dated to the Mio-Pliocene boundary, where a ratio similar to that of the Kromdraai specimen may be seen (Text-fig. 1). However, the *N. donnezani* specimens exhibit a greater overall degree of primitiveness in the lesser development of the subangular lobe and in a horizontal ramus morphology more similar to that seen in *Canis* and *Vulpes* (Text-fig. 1 and Pl. 1).

If the relatively greater length of the slicing versus the crushing series is indeed a plesiomorphic character, then it might be logical to conclude that the African form stemmed independently from the lineage that led to the *megamastoides-sinensis* group. In that case, *N. donnezani* might be considered a plausible common stock, and the similarities between jaw morphologies in the African and *megamastoides-sinensis* forms seen as evidence of later parallelism. Alternatively, one might argue that the jaw morphology shows the African specimens to be more closely related to the *megamastoides-sinensis* group, with the higher ratio of the slicing versus the crushing dentition then seen as a



Text-fig. 1 - Scatter diagram of slicing and crushing dental series lengths in various canid species. The thin intersecting lines limit the area which probably separates the *Canis* and *Nyctereutes* fields. The bisector is shown as a heavy line. All measurements in millimetres.

N. donnezani from Ruscinian of Perpignan (France) (Deperet, 1890); *N. ex gr. megamastoides-sinensis* from Villafranchian of Kwabebi (U.S.S.R.) (Vekua, 1972), Saint-Vallier (France) (Viret, 1954), Choukoutien (Pei, 1934) and Nihowan (Teilhard de Chardin & Piveteau, 1930) (China); *N. terblanchei* from Kromdraai (South Africa) (Hendey, 1974); *C. etruscus*, *C. arnensis* and *C. falconeri* from Late Villafranchian of the Upper Valdarno (Italy); *C. lupus* from Late Pleistocene of Equi Cave (Italy); *V. vulpes* and *A. lagopus*, recent. Unreferenced items, source authors.

reversion to the more primitive condition. At present, we prefer the first interpretation, largely on the grounds of parsimony.

TIMING OF DISPERSAL INTO AFRICA

The timing of *Nyctereutes* dispersal into Africa is unclear. The overall canid fossil record in the continent is sparse and renders detailed biogeographic reconstruction very difficult for most if not all species. Some modern canids are known, in very small numbers, from Langebaanweg at about 5.0 Myr (Hendey, 1974), but one can also argue for a significant increase in numbers after about 2.5 Myr (Turner, in press) perhaps marking a dispersal correlated with rather more open conditions. None of the African

specimens discussed here can be dated precisely, as pointed out above, but there is no compelling argument for an age prior to 1.5-2.0 Myr. If we are correct in our separation of the Kromdraai material from the more advanced European *megamastoides-sinensis* group, then one could argue for a pre-Villafranchian date for initial dispersal into Africa. The paucity of the record for *Nyctereutes* between that hypothetical event and the likely earliest date of the African material could then be explained as part of the general phenomenon of fossil canid scarcity, although it is possible that an examination of East African fossil canids in the light of our findings might produce further specimens. Whether one could then push the possible date of dispersal back as far as the Mio-Pliocene boundary and the appearance of modern canids at Langebaanweg is, however, a more difficult question to answer.

CONCLUSIONS

For the moment, we consider that only specimens 1290, from Kromdraai, and K₂ 82, from the Coopers site, can be assigned to *Nyctereutes* with confidence. However, even two such specimens carry clear implications for a significant African presence. The overall paucity of the canid record in the continent shows that the rarity of *Nyctereutes* is not unique. There is therefore every reason to expect that further finds will come to light, and we suggest that close attention should be paid to future canid fossil discoveries and perhaps a fresh appraisal made of unidentified specimens in existing collections. The recognition of a carnivore species new to Africa promises fresh insights into the patterns of mammalian dispersal once the time of first arrival can be established.

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