Bat-eared fox (Canidae, *Otocyon*) from the Pleistocene of northern Namibia

Martin Pickford[1], Jorge Morales[2], Helke Mocke[3], Dominique Gommery[4] and Brigitte Senut[5]

1. CR2P (MNHN, CNRS, SU), 8, rue Buffon, 75005, Paris, France <martin.pickford@mnhn.fr>
2. Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC - C/José Gutiérrez Abascal 2, 28006, Madrid, Spain <jorge.morales@mncn.csic.es>
3. Geological Survey of Namibia, Aviation Road, Windhoek, Namibia <helke.mocke@mme.gov.na>
4. CR2P (MNHN, CNRS, SU), Campus Pierre et Marie Curie, T.46-56, E.5, 4, Place Jussieu, 75005, Paris, France <dominique.gommery@sorbonne-universite.fr>
5. CR2P (MNHN, CNRS, SU), 8, rue Buffon, 75005, Paris, France <brigitte.senut@mnhn.fr>

Abstract :- Fossils of the bat-eared fox, *Otocyon*, have been found at various localities in Southern and Eastern Africa, often in archaeological contexts. In Namibia the genus has previously only been recorded from four Holocene localities. We herein describe a specimen from Kombat, Otavi Mountains, which is likely to be of Pleistocene age. The origin of the bat-eared fox lineage is still poorly understood. One scenario in the literature, which has been contested, is that it originated in Eurasia (or ultimately North America) and then spread to Africa before going extinct in Eurasia. Our preferred interpretation is that the earliest phases of the evolution of bat-eared foxes as a distinct lineage from other canids occurred in Africa during the Early Pliocene, because, by the mid-Pliocene a species is known from the Upper Laetoli Beds (3.85-3.6 Ma) Tanzania, and an Early Pleistocene species (*Prototocyon recki*) is known from Olduvai Bed I, Tanzania (ca 2.0-1.8 Ma) and the lineage is quite common in southern African Late Pliocene, Pleistocene and Holocene localities.

Introduction

The Namibia Palaeontology Expedition, a collaborative project between the Geological Survey of Namibia, Windhoek, and the Centre de Recherche en Paléontologie, Paris (CR2P), has been carrying out palaeontological research in the country since 1991. Screening of unconsolidated sediments in the 'A' fissure at Kombat E-900 (Fig. 1, 3, 4) has yielded abundant fossils including the first remains of equids and canids recorded from the deposits.

This paper describes and interprets the canid fossil from the site and discusses the origin of the bat-eared foxes. It is hypothesised that they may well have originated in southern Africa during the Early Pliocene, evolving from a species of Canidae that had dispersed to Africa (from North America via Eurasia) in the Latest Miocene or Early Pliocene.

The main evolutionary tendencies of the bat-eared fox group include a slight reduction in body size, the acquisition of accessory molars and the development of an «insectivorous»

morphology of the molar crowns (Kieser, 1995), a thick pelage, and large ears (hence the common name of the species).

Clark (2005) postulated that the large ears of *Otocyon megalotis* might play a role in thermo-regulation, an adaptation to the arid environment it lives in. However, field observations indicate that its large ears are used to locate underground insects, such as harvester termites (*Hodotermes mossambicus*) that comprise one of its main sources of food and other cryptic insects such as beetles (Stuart *et al.*, 2003). In support of the latter idea the authors wrote that "*the distribution of harvester termites .... and bat-eared fox .... in southern Africa, when superimposed on a map, show a 95% overlap.*"

After bat-eared foxes had evolved in southern Africa, it is inferred that they then spread northwards to East Africa during the middle of the Pliocene, but did not disperse as far as the Tropic of Cancer nor to Eurasia.

Previous Work

The fossiliferous fissure fillings at Kombat, Otavi Mountains were first described by Pickford and Senut (2010) who estimated that the deposits in the 'A' fissure at E-900 were Holocene, but, following recent collections from the infillings, it is more likely that they are of Late Pleistocene age. A sedimentary infilling in the nearby 'C' fissure contains similar unconsolidated deposits and a variety of lithic implements and waste flakes of Middle Stone Age aspect.

Fossil remains of bat-eared foxes have been recorded from a number of localities in Southern and Eastern Africa (Avery, 2019; Savage, 1978; Werdelin and Peigné, 2010) (Fig. 1, 2; Table 1). Most of the records (13 from Pleistocene deposits, 10 of Holocene age) are simple mentions in faunal lists. An exception is the genus and species, *Prototocyon recki* Pohle,

1928, from the Early Pleistocene of Tanzania, which is known from cranial elements (Pohle, 1928) and an almost complete mandible (Petter, 1973) (Fig. 7).

Because of the general lack of descriptions and illustrations of the fossils attributed to *Otocyon*, we herein describe and illustrate the specimen from the Kombat 'A' fissure. Even though the representation of bat-eared foxes at the site is currently based on a single fossil, the Kombat specimen prompts enquiries about the origins of the lineage, mainly because the specimen is substantially larger than any of the extant material available for study, and it is slightly larger than the extinct species *Prototocyon recki* (Fig. 8). The possibility thus exists that extant bat-eared foxes are smaller than their Pleistocene and Pliocene ancestors.

Figure 1. Distribution of fossil localities that have yielded remains of *Otocyon* and *Prototocyon*. Pleistocene sites are named; for locations and names of Holocene sites see Fig. 2. The white dotted outlines depict the distribution of extant *Otocyon megalotis*.

Country	Locality	Latitude	Longitude	Pleisto-cene	Holo-cene	References
Kenya	Lainyamok	01°49'S	36°10'E	x	o	Potts and Deino, 1995
Namibia	Kombat E-900 Fissure 'A'	19°42'S	17°44'	x	o	This paper
South Africa	Boegoeberg	28°46'S	16°34'E	x	o	Klein *et al.*, 1999
South Africa	Cave of Hearths	24°10'S	29°11'E	x	o	Savage, 1978
South Africa	Lincoln Cave (Sterkfontein)	26°01'S	27°44'E	x	o	Reynolds *et al.*, 2003, 2007; Wadley, 2015
South Africa	Pinnacle Point	34°11'S	22°05'E	x	o	Armstrong, 2016; Marean *et al.*, 2004; McGrath *et al.*, 2015; Rector and Reed, 2010; Wadley, 2015
South Africa	Plovers Lake	25°59'S	27°47'E	x	o	Brophy *et al.*, 2006, 2014; De Ruiter *et al.*, 2008; McKee *et al.*, 1995; Reynolds, 2010; Thackeray and Watson, 1994; Wadley, 2015
South Africa	Sterkfontein	26°01'S	27°44'E	x	o	Ewer, 1958; McKee *et al.*, 1995; O'Regan, 2007; Reynolds, 2010; Reynolds and Kibii, 2011; Reynolds *et al.*, 2003, 2007; Turner, 1987
South Africa	Swartkrans	26°02'S	27°43'E	x	o	Ewer, 1958; McKee *et al.*, 1995; Reynolds, 2010; Turner, 1993; Watson, 1993
South Africa	Tobias Cave (Taung)	27°37'S	24°37'E	x	o	McKee, 1994
Tanzania	Laetoli	03°13'S	35°11'E	x	o	Dehghani, 2008; Werdelin and Dehghani, 2011
Tanzania	Olduvai Gorge	02°59'S	35°21'E	x	o	Petter, 1973; Pohle, 1928
Botswana	White Paintings Rock Shelter	18°25'S	21°30'E	x	x	Robbins, 1990; Robbins *et al.*, 2000
South Africa	Equus Cave	27°37'S	24°38'E	x	x	Klein *et al.*, 1991; Kuhn *et al.*, 2016; McKee *et al.*, 1995
Botswana	Caecae	19°47'S	21°04'E	o	x	Wilmsen, 1989
Botswana	Divuyu	18°45'S	21°44'E	o	x	Denbow, 2011; Turner, 1987
Botswana	Matlapaneng	19°S	23°E	o	x	Turner, 1987
Botswana	Nqoma	18°45'S	21°45'E	o	x	Turner, 1988
Namibia	Big Elephant Shelter	21°42'S	15°40'E	o	x	Wadley, 1979
Namibia	Bremen	25°S	17°E	o	x	Cruz-Uribe and Klein, 1981–1983
Namibia	Maguans Andalusia	25°S	16°E	o	x	Cruz-Uribe and Klein, 1981–1983
Namibia	Striped Giraffe Shelter	21°48'S	15°42'E	o	x	Plug, 1979
South Africa	Abbot's Cave	31°27'S	24°39'E	o	x	Plug, 1993b, 1993c; Plug and Sampson, 1996
South Africa	Doornfontein	28°12'S	23°02'E	o	x	Beaumont and Boshier, 1974; Klein, 1979; Thackeray *et al.*, 1983
South Africa	KN6-3C	30°13'S	17°14'E	o	x	Dewar, 2007
South Africa	Schroda	22°11'S	29°25'E	o	x	Plug, 2000; Voigt, 1980
South Africa	Spoeg River	30°18'S	17°16'E	o	x	Webley, 2001a, 2001b
Tanzania	67 km W of Itigi and WNW of Kilimatinde	05°41'S	33°53'E	o	x	Reck and Pohle, 1922

Table 1. Localities having yielded fossil remains of *Otocyon* and other bat-eared foxes (x - present; o - no record)

Geological and Palaeontological Contexts

The bedrock in the Kombat E-900 area consists of Proterozoic dolostones and phyllite/shales that were subsequently mineralised with diverse sulphides during the Proterozoic (Deane, 1995; Nghoongoloka *et al*., 2020).
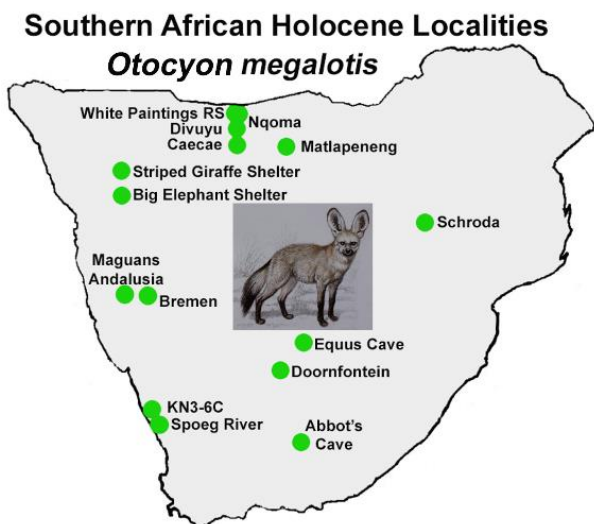

Figure 2. Southern African Holocene localities having yielded remains of *Otocyon megalotis*; image of bat-eared fox from Skinner and Smithers (1990)

During the Cenozoic Era, near-surface fissures and caves developed in the dolostone of the Upper Hüttenberg Formation, and as a result the E-900 zone at Kombat is characterised by narrow fissures and small caves that have acted as receptacles for sediments of diverse kinds (Pickford and Senut, 2010; Fig. 3, 4). The latter authors estimated the age of the fissure fillings as Recent, but subsequent surveys suggest that the 'A' fissure filling, which is unconsolidated, is more likely to be Late Pleistocene in age. The nearby 'C' fissure at E-900 yields lithic implements of Middle Stone Age aspect, and there are older well-indurated fissure fillings near the vehicle adit of the mine. The Asis Ost cave breccia, which is close by, is of Late Pleistocene to Recent age on the basis of the faunal remains that it has yielded.

The sedimentary infilling of the 'A' fissure at E-900 consists of unconsolidated dark brown, sandy to clayey sediment rich in small euhedral quartz crystals and small angular clasts of bedrock (dolostone and phyllite/schist) derived from the subjacent Proterozoic bedrock. Fossils are scattered randomly in the sediment, many of them being broken into fragments. The fossils are generally dark brown to black, but many have turquoise or green colouration due to copper minerals that have impregnated the bone or enamel and dentine of the teeth.

A comprehensive list of localities that have yielded fossil remains of bat-eared foxes is given in Table 1. The fauna currently known from fissure 'A' is listed in Table 2.

Figure 3. Kombat E-900 open pit showing the positions of fissures 'A', 'B' and 'C' in dolostones of the Upper Hüttenberg Formation; fissure 'B' is poorly fossiliferous and the 'C' fissure contains abundant Middle Stone Age lithic implements and waste flakes.
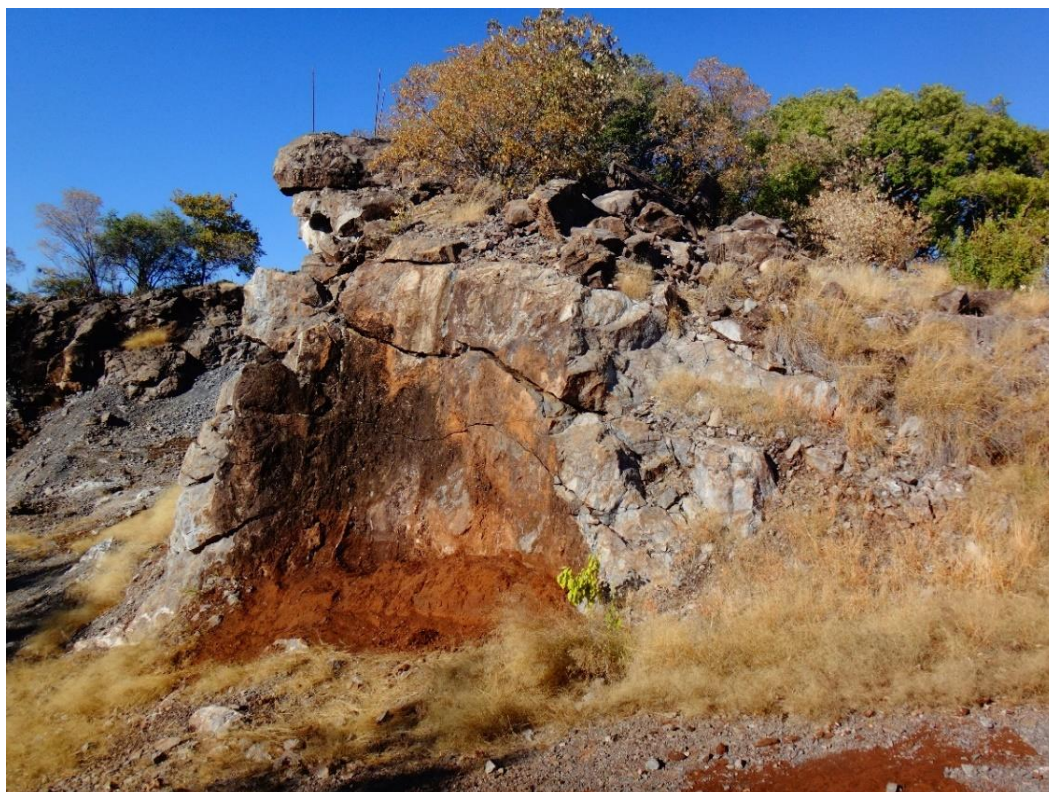
Figure 4. The 'A' fissure at Kombat E-900 with its infilling of fossiliferous dark brown sediment (image taken in May, 2024)

Amphibia
Ophidea
Lacertidae
Aves
Chiroptera
Erinaceidae
Carnivora
     Felidae (Leopard?)
     Canidae
          Otocyon cf *megalotis*
Rodentia
     Otomyinae
     Steatomys
     Aethomys
     Pedetes
     Petromyscus

     Petromus
     Others
Lagomorpha
     Pronolagus sp.
Chrysochloridae
Hyracoidea
     Procavia capensis
Macroscelidea
     ?*Petrodromus*?
Perissodactyla
     Equidae
          Equus sp.
Artiodactyla
     Bovidae
          Antidorcas sp.
          2 other spp.

Table 2. Faunal List - Kombat E-900 'A' fissure

Material and Methods

GSN KOM 80'24 is an isolated lower molar from the 'A' fissure at the Kombat E-900 pit, Otavi Mountainland, northern Namibia (Fig. 5). It is coloured turquoise and black due to impregnation of copper, iron and manganese into the enamel.

The specimen was compared with material of extant *Otocyon megalotis* (Fig. 6) and with a cast of the extinct species *Prototocyon recki* from Olduvai Gorge, Bed I, Tanzania (Fig. 7), housed at the Palaeontology Collection, Muséum National d'Histoire Naturelle, Paris (Petter, 1973). Reference was also made to the literature (Koyasu, 1993; Kieser, 1995), which deals with the dentition of *Otocyon megalotis*.

Measurements of teeth were taken with sliding calipers to the nearest tenth of a millimetre (Table 3). Photographs were captured with a Sony Cybershot digital camera, and treated with Photoshop Elements 15 to increase contrast and to remove unwanted background.

Systematic Palaeontology

Order Carnivora Bowdich, 1821

Family Canidae Fischer von Waldheim, 1817

Genus *Otocyon* Müller, 1836

Species *Otocyon* cf *megalotis* Desmarest, 1822

Material. KOM 80'24, left m/2 (Fig. 5).

Locality and Age. Kombat E-900, 'A' Fissure (19°42'35''S : 17°43'55''E), Late Pleistocene (Fig. 3, 4).

Description

The crown of KOM 80'24 is ovoid in occlusal view, with the anterior part slightly broader than the posterior part. The protoconid and metaconid are well developed both in volume and in height, with the metaconid being the taller of the two cusps. The mesial valley is narrow, bordered buccally by a mesial cristid that extends towards the low, vestigial paraconid positioned in the centreline of the tooth. The basal cingulum on the protoconid is well developed. The talonid is shorter and narrower than the trigonid, and is dominated by a large hypoconid that is almost as tall as the protoconid.

The entoconid is smaller than the hypoconid and is slightly compressed transversely and is positioned obliquely with respect to the transverse axis of the tooth. Between the two cusps of the talonid there is a small, low, cuspid. There is a weak pre-entoconid cristid and distally the hypoconulid closes the talonid valley, which is deep.

The crown is 7.0 mm in mesio-distal diameter, the mesial lophid is 5.0 mm broad, and the distal lophid is 4.5 mm broad.
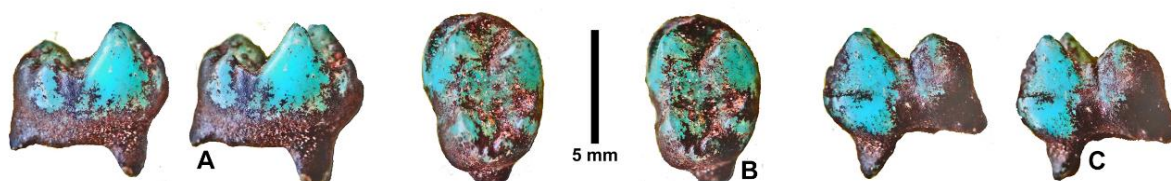

Figure 5. Stereo images of GSN KOM 80'24, left m/2 of *Otocyon* sp. From Kombat E-900 (fissure 'A'), Otavi Mountainland, Namibia. A – lingual view, B – occlusal view, C – buccal view

Discussion

The strong development and height of the trigonid cusps (protoconid-metaconid) and the talonid (hypoconid-entoconid) of the Kombat molar are characters that occur in posterior lower molars of *Otocyon megalotis*, being features that distance it from molars of other extant canids such as *Vulpes*, *Lupulella* and *Nyctereutes* and their fossil species. In addition, the latter forms tend to have relatively elongated, narrower, m/2s with low talonid cusps. On this basis, even though the Kombat fossil seems rather large for *Otocyon megalotis* (ca 20% greater than the mean of m/2 : Table 3; Fig. 8) its morphology agrees closely with the corresponding teeth of this species.

Catalogue	Number	Locality	Tooth	Mesio-distal length	Bucco-lingual breadth
MNHN	2007-19	Cap de Bonne Espérance	m/2 lt	5.5	4.4
MNHN	1973-135	Ethiopia	m/2 lt	5.4	4.0
MNHN	1973-136	Ethiopia	m/2 lt	4.9	3.5
MNHN	1972-392	Ethiopia	m/2 lt	6.0	4.2
MNHN	1933-2794	Ethiopia	m/2 lt	5.7	4.2
MNHN	1933-115	Ethiopia	m/2 lt	5.6	3.8
MNHN	1969-481	Ethiopia	m/2 lt	5.6	4.2
MNHN	1977-19	Somalia	m/2 rt	5.3	4.0
MNHN	1965-205	Ménagerie	m/2 rt	5.4	4.4
MNHN	2007-19	Cap de Bonne Espérance	m/3 lt	4.9	4.2
MNHN	1973-135	Ethiopia	m/3 lt	5.0	4.0
MNHN	1973-136	Ethiopia	m/3 lt	4.8	3.9
MNHN	1972-392	Ethiopia	m/3 lt	5.2	4.0
MNHN	1933-2794	Ethiopia	m/3 lt	5.0	4.2
MNHN	1933-115	Ethiopia	m/3 lt	4.7	3.5
MNHN	1969-481	Ethiopia	m/3 lt	5.2	3.9
MNHN	1977-19	Somalia	m/3 rt	5.5	4.0
MNHN	1965-205	Ménagerie	m/3 rt	5.1	4.0

Table 3. Measurements (in mm) of posterior lower molars of *Otocyon megalotis* housed in the Collection of Comparative Anatomy, Muséum National d'Histoire Naturelle (MNHN), Paris (lt – left; rt – right)

In *Otocyon megalotis* the m/2 tends to be somewhat larger than the m/3 but in the bivariate plots there is overlap of the measurements of these teeth (Fig. 8). In addition the talonid of the m/2 is usually only slightly narrower than the trigonid, whereas in the m/3 the talonid is in general noticeably narrower than the trigonid. The molar from Kombat has a relatively narrow talonid which resembles the proportions seen in m/3s of *Otocyon megalotis*, but its overall cuspal morphology indicates that it it more likely to be an m/2.
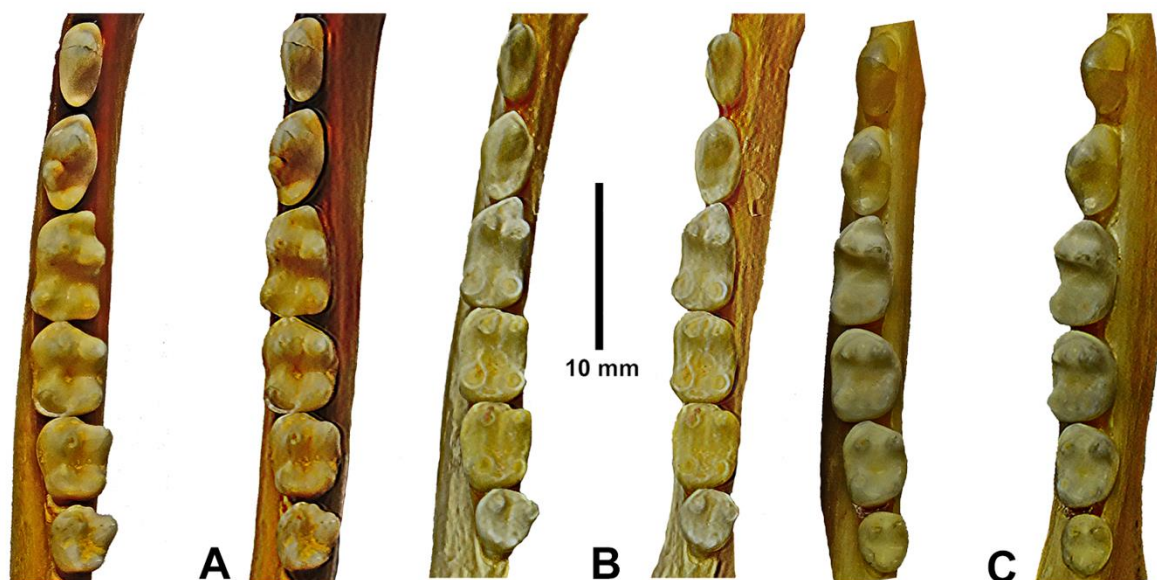

Figure 6. Stereo occlusal views of lower cheek teeth (p/3-m/4) of extant *Otocyon megalotis*. A – MNHN 1965-205 (right teeth reversed), B – MNHN 1973-135 (right teeth reversed), C – MNHN 1969-481 (left teeth).
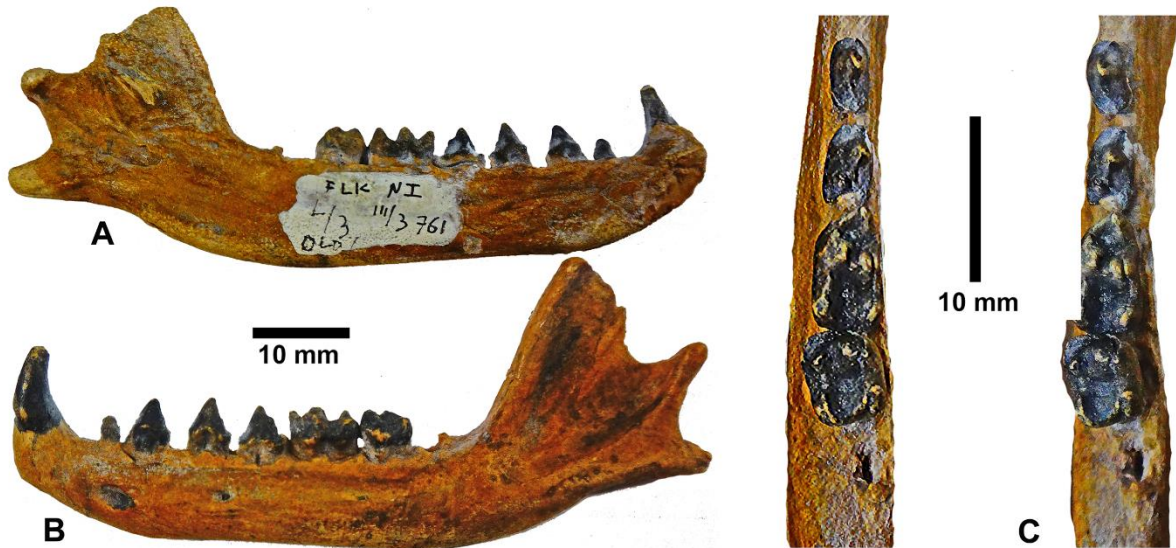
Figure 7. FLK N1 761, left mandible of *Prototocyon recki* from Olduvai Bed I, Tanzania (cast in MNHN, Paris); A – lingual view, B – buccal view, C – stereo occlusal view of p/3-m/2 and alveolus of m/3 (enlarged)
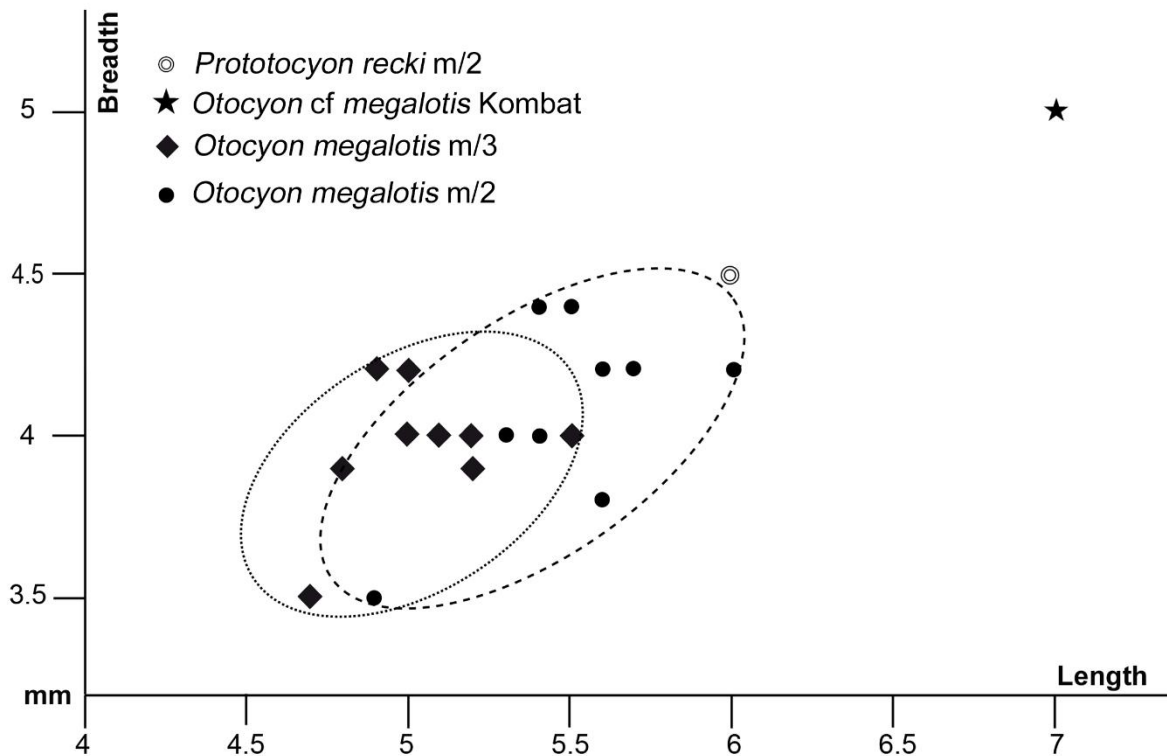

Figure 8. Bivariate (length-breadth) plots of posterior lower molars (m/2 and m/3) of extant *Otocyon megalotis* (MNHN collection) and the Kombat fossil. Measurements of *Prototocyon recki* are from Petter (1964). Our measurements of the m/2 in a cast of *Prototocyon recki* in the MNHN are 5.6 x 5.1 mm.

General Discussion

The presence of accessory molars in the small African canid, *Otocyon megalotis*, has intrigued zoologists for well over a century (Huxley, 1880; Lydekker, 1884; Winge, 1895; Carlsson, 1905; Matthew, 1924; Pilgrim, 1932; Petter, 1964, 1973; Ewer, 1965; Clutton-Brock *et al*., 1976; Koyasu, 1993; Kieser, 1995; Nel and Maas, 2004).

Whilst it has been almost universal for zoologists to classify the genus *Otocyon* in the

family Canidae, there has been little consensus regarding the question of its relationships to other genera of canids (Tedford *et al.*, 1995). Is it a member of a separate subfamily - Otocyoninae - distinct from other dogs - Caninae (Clutton-Brock *et al.*, 1976) - or is it a form derived from a *Vulpes*-like ancestor, and thus a Caninae? (Carlsson, 1905). Both views are available in the literature.

Much of the debate revolves around the presence of accessory molars in *Otocyon* (Lydekker, 1884; Koyasu, 1993) and the observation that the molars show morphology derived towards an insectivorous diet (Petter, 1964, 1973; Kieser, 1995). These factors have been interpreted in contrasting ways, the accessory molars and molar morphology being cited either as primitive retentions (plesiomorphies; Huxley, 1880) or as derived characters (apomorphies) (Winge, 1895; Carlsson, 1905). Skinner and Smithers (1990) summarised the situation succinctly when they commented that « *The ancestors of the wild dog and the bat-eared fox are unknown and there are no clues to the links between Miocene and Pleistocene canids* ».

Although not explicitly stated in the literature, there seems to have been an underlying assumption on the part of most authors who have written about the origin of bat-eared foxes, that the canid lineage from which they descended was already of small dimensions. However, the fossils from the Pleistocene of Tanzania (Petter, 1973) and now from Kombat, suggest that the ancestral lineage may have been somewhat larger (10-20% greater) than the extant *Otocyon megalotis*, a possibility that opens up new avenues of interpretation of hitherto doubtfully identified fossil post-cranial bones, for example, some of the specimens from Swartkrans, South Africa, identified as Canidae indet. by Watson (1993).

When commenting on the small Pleistocene canid described by Bose (1880) from the Pinjor-Markanda area, Siwalik Hills, India, Lydekker (1884) wrote « *The most probable interpretation of the genetic affinity of* Canis curvipalatus *is that it is a form derived from the primitive ancestral stock of* Otocyon … ». The supposedly primitive nature of *Otocyon* inferred by Lydekker (1884) was based on the presence of additional molars when compared to other canids. In his logic, Lydekker (1884) was adhering to Huxley's (1880) view that *Otocyon* is a

primitive form, the presence of M4/ being interpreted by him as a survival of the dentition of ancestors of the Canidae and carnivorous marsupials (see Pilgrim, 1932). This interpretation was vigorously challenged by Winge (1895) and, even though Carlsson (1905) supported the systematic viewpoint of Lydekker (1884) she considered that the presence of extra molars in *Otocyon* was a derived condition, and not the retention of a primitive feature.

In tune with Lydekker's (1884) view, Pohle (1928) wrote that the small canid from the Pleistocene of Pinjor, India, could represent the base of the *Otocyon* lineage. He proposed that it was most probably a descendant of *Nothocyon curvipalatus* (Bose) via *Prototocyon recki* Pohle to *Otocyon megalotis* (Desmarest). Under this interpretation, the base of the *Otocyon* lineage would be a genus that originated in North America (*Nothocyon* Wortman and Matthew, 1899). However, Wang and Tedford (1992) transferred this genus to the Arctoidea and some of the species included in it were transferred to *Leptocyon* (a primitive canid) (Tedford *et al.*, 2009).

Pilgrim (1932) discussed the issue of *Canis curvipalatus* in detail, and even though he wrote that « *Pohle's (1928) view that the three species form a genetic group seems to be justified* » *...* he concluded that « *it appears better that the Indian fossil species should be distinguished by a generic name of its own, and for this I propose that of* Sivacyon ». By doing so, Pilgrim (1932) effectively excluded the possibility that the *Otocyon* lineage descended directly from a North American genus. Geraads *et al.* (2015) in contrast, considered that *Sivacyon* was closely related to *Vulpes* (*sensu stricto*) and concluded that there was « *no reason to connect it to* Otocyon *as has sometimes been done* ».

Of historical interest is the phylogeny of Thenius and Hofer (1960) that positioned *Otocyon* close to *Nyctereutes*, *Speothos*, *Dusicyon* and *Chrysocyon*, but with a question mark at the base of its lineage. In their phylogeny, the ultimate ancestral canid from which *Otocyon* was thought to derive was *Cynodesmus*, a North American Miocene genus according to the authors. The *Vulpes* and *Fennecus* group was positioned further off from *Otocyon* than the *Nyctereutes-Dusicyon* group (Fig. 9).
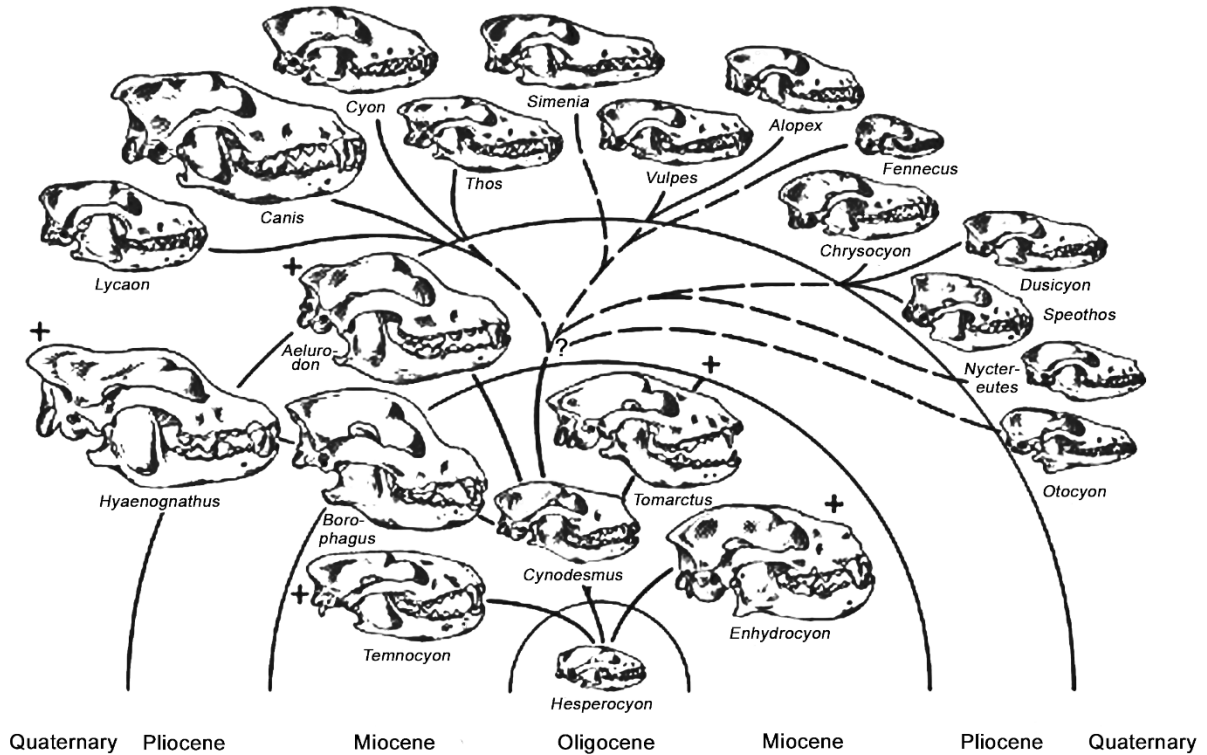
Figure 9. Phylogeny of the Canidae based on Thenius and Hofer (1960). Note the question mark at the base of the *Otocyon* lineage. « + » signifies the extinction of a lineage.

On the basis of observations on fossils from Olduvai Gorge, Tanzania, discovered after the work of Pohle (1928), Petter (1964) discussed the origin of the bat-eared fox lineage. She concluded that Pohle's genus and species *Prototocyon recki* was indeed distinct from *Otocyon*.

Unlike Pohle (1928) and Petter (1964) however, Ewer (1965) considered that the Olduvai bat-eared fox belonged to the same genus as the extant *Otocyon megalotis*, as the combination *Otocyon recki*. In her interpretation, the differences in cranial and dental features between the fossils and extant specimens represented interspecific variations rather than higher level distinctions. In response, Petter (1973) who had examined additional fossils from Olduvai Gorge, including a mandible, considered that *Prototocyon recki* was indeed distinct at the genus level from *Otocyon*. Its dentition is somewhat more primitive than that of *Otocyon megalotis* as noted by Pohle (1928), but overall, she concluded that the species *P. recki* was a typical bat-eared fox, but with one molar fewer in the upper and lower jaws than *Otocyon megalotis*, among other features such as differences in the length of the symphysis and the relative development of the subangular process.

Citing the publications of Wayne *et al*. (1987) and Wayne and O'Brien (1987), Tedford *et al*. (1995) pointed out that in the Canidae, different data sources led to different phylogenies. As concerns the bat-eared fox, they wrote « *Problem taxa include the foxes* Urocyon *and* Otocyon*, considered sister taxa and members of the Vulpini clade osteologically, but either as members of the Canini clade (with* Fennecus*) on chromosome morphology or in a basal unresolved multichotomy with other canines on allozyme evidence* ».

Werdelin and Peigné (2010) wrote that « *The Canidae are exclusive to North America until the late Miocene, after which* Eucyon- *and* Vulpes-*like taxa appear in Western Europe, Asia, and Africa ….. Recently, Morales* et al. *(2005) described from Lukeino (ca. 6 Ma) what was then the oldest canid of Africa,* Eucyon intrepidus. *Even more recently, however, a foxlike canid has been discovered from older sediments in Chad (Toros-Menalla, ca. 7 Ma;* Bonis *et al., 2007). The family reaches southern Africa in the early Pliocene and northwestern Africa in the mid-Pliocene. The final radiation of the Canidae (Caninae) in the Pleistocene is seen mainly in eastern Africa, but also in South Africa and*

Algeria ». However, the dating of the Chad material is not secure, the assemblage of fossils from Toros Menalla consisting of surface finds ranging in age from 10 Ma to 4 Ma (Pickford, 2008a). It is thus insecure to consider that *Vulpes*-like canids existed in Africa during the Late Miocene, even though other canids (*Eucyon*) are well represented in the continent, in Kenya at Lukeino (Morales *et al*., 2005) and Lemudong'o (Howell *et al*., 2007).

The earliest plausibly well-dated occurrences of *Vulpes* in Africa are from the Pliocene of the Mursi Formation, Ethiopia (ca 4 Ma, Geraads *et al*., 2015), Makapansgat (Ewer, 1957) and Matjihabeng (De Ruiter *et al*., 2010) South Africa, and possibly Ahl Al Oughlam, Morocco (Geraads, 1997, 2008) with younger material known from various sites in northern, eastern and southern Africa (Avery, 2019; Werdelin and Peigné, 2010).

Several recently published phylogenetic scenarios, including some based on molecular biology, appear to place *Otocyon* as the most primitive member of the family in its own clade (Clutton-Brock *et al*., 1976) but others (Zrzavý and Řičánková 2004) classify it close to *Vulpes*, *Nurocyon* and *Nyctereutes*, but in varying positions depending upon the data analysed.

On the basis of cranial and dental characters, and using numerical analysis, Clutton-Brock *et al*. (1976) generated a centroid linkage dendrogram (Fig. 10) in which *Otocyon* was positioned at the base of the canid radiation, far removed from *Vulpes*, *Urocyon* and *Nyctereutes*, but closer to *Cuon*, *Speothos*, *Lycaon*, *Dusicyon* and *Canis*.

On the basis of chromosomal data Wayne *et al*. (1987) positioned *Otocyon* close to *Urocyon* and *Fennecus*, but far from *Nyctereutes* and *Vulpes*, whereas Wayne and O'Brien (1987) on the basis of allozyme data positioned *Otocyon* close to *Urocyon* and *Nyctereutes*, far from *Vulpes* and *Fennecus*, and well removed from *Speothos* and *Lycaon*.

In contrast, basing their cladogram on morphological data, Tedford *et al*. (1995, figs 8 and 9) positioned *Otocyon* and *Urocyon* close together, with *Nyctereutes* close to *Speothos*, but far from *Fennecus* and *Vulpes*. In their figure 2, however, Tedford *et al*. (1995) positioned *Otocyon* close to *Urocyon* and *Vulpes*, but distanced it from *Nyctereutes* and *Speothos*, with *Cuon* and *Lycaon* even further removed from it (Fig. 10).

Tedford *et al*. (2009) positioned *Otocyon* and *Prototocyon* far from Canini, but closer to *Urocyon* and slightly further from *Vulpes*.

Westbury (2018) placed *Otocyon* close to *Nyctereutes* and *Vulpes*, with *Urocyon* further off, and with *Cuon*, *Speothos*, *Lycaon* and *Canis* even further off (Fig. 10).

On the basis of all unweighted characters analysed, Zrzavý *et al*. (2018) positioned *Otocyon* close to *Nyctereutes* and *Nurocyon* and to some, but not all, species of *Vulpes*, with *Cuon*, *Canis* and *Speothos* far removed from it. Using nHC and molecular characters (Fig. 10), the same authors proposed that *Otocyon* was close to *Nurocyon*, *Nyctereutes* and *Vulpes*, with *Urocyon* some way off, followed by *Canis*, *Cuon*, *Lycaon* and *Speothos*, along with a diversity of other canid taxa.

On the basis of mitochondrial DNA analyses, Geffen *et al*. (1992) wrote that « *The grey fox,* Urocyon cinereoargenteus*, and the bat-eared fox,* Otocyon megalotis*, are not closely related to each other or to any of the sampled fox taxa* » (*Fennecus*, *Vulpes*). Thus, in their view, *Otocyon* is an outlier in canid phylogeny, not closely related to other fox-like taxa.

In contrast, Bardeleben *et al*. (2005) hypothesised that *Otocyon* was close to *Nyctereutes*. They wrote « *Differences between trees derived from the nuclear data and those from the mitochondrial data include the grouping of the bush dog and maned wolf into a clade with the South American foxes, the grouping of the side-striped jackal* (Canis adustus) *and black-backed jackal* (Canis mesomelas) *and the grouping of the bat-eared fox* (Otocyon megalotis) *with the raccoon dog* (Nyctereutes procyonoides) ».

After analysing morphological and molecular datasets, Zrzavý and Řičánková (2004) wrote that « Otocyon *and* Nyctereutes *are the most problematic canid genera, causing an unresolved branching pattern of* Otocyon*,* Vulpes*,* Nyctereutes *and DC (dog-like canid) clades* » whereas, on the combined basis of morphology, behaviour, genes and fossils, Zrzavý *et al*. (2018) concluded that « Otocyon*,* Nyctereutes *and* Nurocyon *form a clade* ». This proposal is interesting because *Nurocyon* Sotnikova, 2006, is a large canid first described from Chono-Kariakh in Transbaikalia, Mongolia (Pliocene, MN 14) (Rook, 2009).
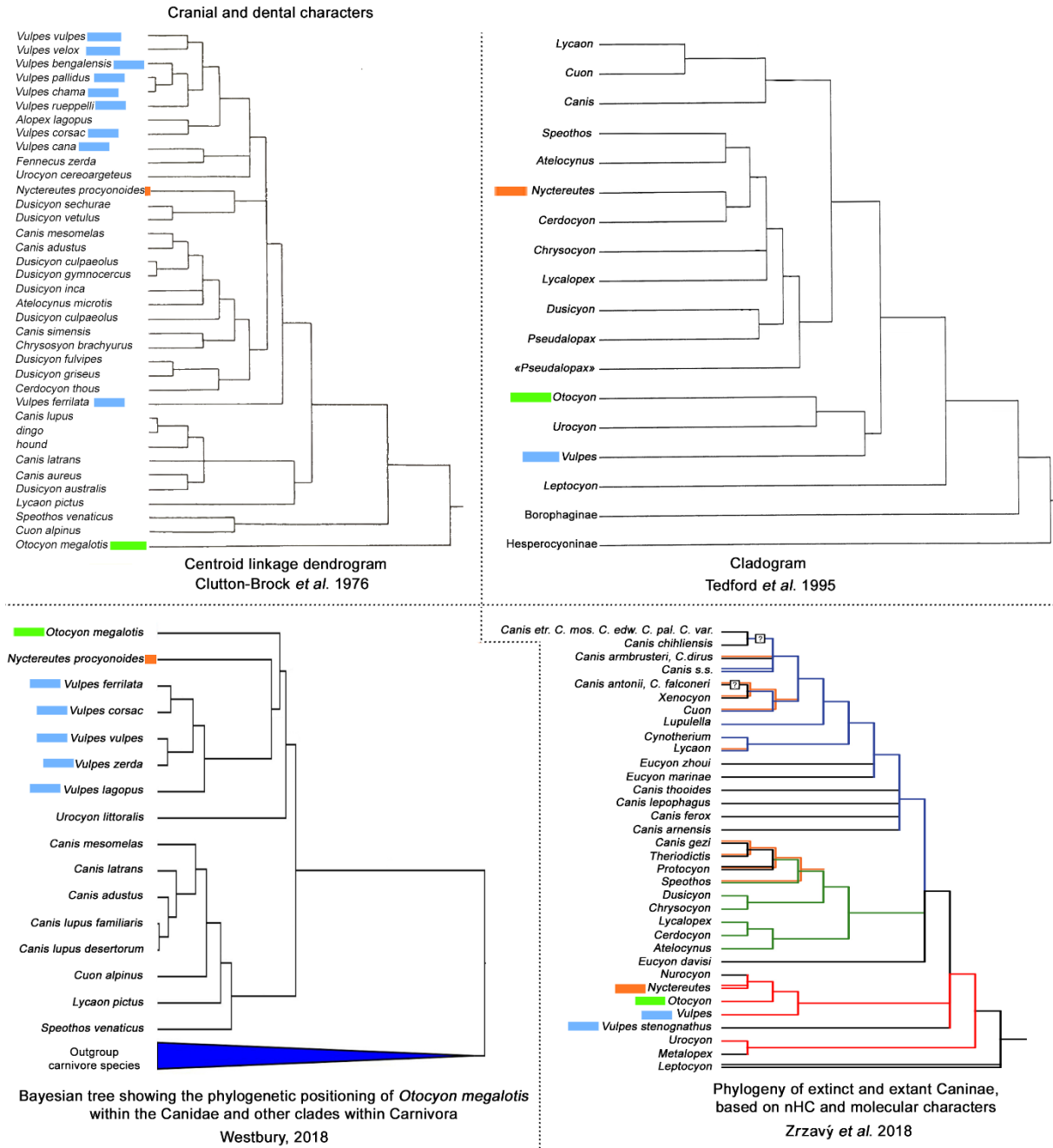
Figure 10. Four 'phylogenies' of Canidae containing *Otocyon*. For ease of reading, *Otocyon*, *Vulpes* and *Nyctereutes* have been highlighted in green, blue and brown respectively.

Thus the debate about the affinities of *Otocyon* within the Canidae remains unresolved, even though diverse approaches to phylogeny reconstruction have been attempted including classic comparative anatomy (Huxley, 1880; Thenius and Hofer, 1960; Tedford *et al*., 1995), numerical methods (Clutton-Brock *et al*., 1976), and molecular biology (Bardeleben *et al*., 2005; Westbury, 2018; Zrzavý *et al.,* 2018).

The uncertainty about the phylogenetic position of *Otocyon* reflects that concerning the uncertainty of the position of jackals in general, and, above all, that of the hunting dog, *Lycaon*.

In our opinion, *Otocyon* is most likely to be a Vulpini. But we note that *Fennecus zerda* presents certain similarities to *Otocyon megalotis* (and to *Prototocyon recki*) in the morphology of the m/1 and m/2 (large broad talonid in the m/1; m/2 with the metaconid hypertrophied). However, the similarities between the

upper dentition of *Otocyon* and *Fennecus* are weaker.

The role of biogeography in the origin of *Otocyon* has been less frequently evoked in the literature, but historically early scenarios tended to look towards Asia (Lydekker, 1884) or Asia and North America (Pohle, 1928) as the region where the lineage originated. It is widely accepted that the Family Canidae (including Canini and Vulpini) is of North American origin (Tedford *et al*., 1995; Werdelin and Peigné, 2010) and that it dispersed to Eurasia and eventually to Africa during the latter part of the Miocene, reaching Kenya by ca 6 Ma (*Eucyon intrepidus*, described by Morales *et al*., 2005 and Rook, 2009). In this sense, the ancestors of *Otocyon* were ultimately of North American origin, but when the peculiarities of the dentition and mandible, along with the enlarged ears, dense furry pelage and relatively small body dimensions are taken into account, the most likely region in which the genus became distinct from other lineages of canids, was in Sub-Saharan Africa, in particular Southern Africa. Such a possibility has not previously been clearly articulated.

In support of a southern origin of the bat-eared fox lineage is the observation that *Otocyon* moults its fur on an annual basis. Such an adaptation is common in taxa that survive in higher latitudes where seasonal climatic changes are dominated by a winter/summer cycle, but is less common in tropically adapted species in which the alternations are more of a wet season/dry season nature. The bat-eared fox grows thick fur during the cooler months of the southern winter and moults it at the onset of the warmer months (Skinner and Smithers, 1990).

If the above biogeographic and developmental scenarios are valid, then *Otocyon* would be an exclusively African lineage and has remained so ever since its origin. It possibly descended from a form such as *Eucyon* Tedford and Qiu (1996) which was one of the earliest members of the family Canidae to disperse to the African continent, the oldest securely dated specimen being aged ca 6 Ma (*Eucyon intrepidus*, Lukeino Formation, Kenya; Morales *et al*., 2005). This scenario would imply a moderate reduction in body dimensions, modifications of dental morphology and the acquisition of extra molars and other featuressuch as the length of the mandibular symphysis (Petter, 1973).

Alternatively, the possibility exists that a currently unknown *Vulpes*-like form may have dispersed from North America to Africa via Eurasia during the Early Pliocene. The earliest *Vulpes*-like canids in North America date from ca 7 Ma, and genera such as *Metalopex* and *Urocyon* are known in that continent from the Latest Miocene and Pliocene respectively (Tedford *et al*., 2009). In Africa (discounting the Chad fossil, the age of which is poorly constrained), Vulpini are known from the mid-Pliocene of Mursi, Ethiopia (Geraads *et al*., 2015), and Makapansgat, South Africa (Ewer, 1957), and younger sites (Avery, 2019).

The supposed Late Miocene dating of the Toros-Menalla (Chad) specimens (Bonis *et al*., 2007) is doubtful. If correct, however, then it would imply an exceptionally rapid dispersal of *Vulpes* to Africa after the origin of the lineage in North America.

Whatever the case, the evolution of *Prototocyon* and *Otocyon* implies the development of additional molars, the modification of molar cuspal morphology and the proportions of the posterior teeth towards a more insectivorous diet, modification of the subangular process of the mandible where the digastric muscle inserts (Tedford *et al*., 1995; Skinner and Smithers, 1990; Clark, 2005), elongation of the mandibular symphysis (Petter, 1973), and very probably the enlargement of the ears, as well as the evolution of a more dense pelage and bushier tail. Because bat-eared foxes live and breed in underground dens their limbs are relatively short when compared with those of other foxes and jackals, but the metatarsals are long (personal observations) suggesting that the ancestor probably had longer femur and tibia than the extant form.

If the Pliocene and Pleistocene bat-eared foxes were somewhat larger (10-20%) than the extant forms, as indicated by the Olduvai and Kombat specimens, then some of the canid post-cranial fossils previously excluded from the group, because they were larger than those of *Otocyon megalotis*, could belong to it. Among the many fossils from the South African cave sites such as Swartkrans, that have been listed as « canid indet. » (Watson, 1993) because they were slightly too big to match their counterparts in *Otocyon megalotis*, there could be some that represent ancient bat-eared foxes.

At present, *Otocyon* occurs in two disjunct regions of Sub-Saharan Africa (Fig. 1) separated by more than 1000 km (Skinner and Smithers, 1990). The greatest area of distribution is Southern Africa, but the species is also widespread in the drier parts of Eastern Africa.

All fossils attributed to *Otocyon* and *Prototocyon* have been found within the same zones as the living species. The currently available fossil record, when combined with the apparent absence of fossils of bat-eared foxes from Northern Africa, the Middle East and Eurasia, suggests that the lineage evolved in Southern Africa, and then, like several other mammals (Pickford, 2008b) spread northwards to the more arid parts of East Africa, but did not disperse any further. This scenario accords with other biogeographic evidence which suggests that Southern Africa was an important centre of evolution (Pickford, 2004, 2008b) and not an evolutionary cul-de-sac as some people have thought.

From a palaeoenvironmental perspective the presence of *Otocyon* at Kombat E-900 accords with the other faunal elements (Table 2) suggesting that the climate and vegetation was comparable to what it is today - semi-arid woodland-savannah with summer rainfall.

Conclusions

The sedimentary infilling of the 'A' fissure at Kombat E-900, Otavi Mountainland, Namibia, has yielded a rich and diverse assemblage of fossil vertebrates which, taken together, indicate a Late Pleistocene age. The nearby 'C' fissure with a similar sedimentary infilling contains lithic implements and waste flakes that suggest a broad correlation to the Middle Stone Age. The 'B' filling is poorly fossiliferous, but the few specimens that it has yielded are similar to material in the 'A' fissure.

Among the fossils from the 'A' fissure, there is a lower molar attributed to a bat-eared fox on the basis of the close morphological similarities that it shares with posterior lower molars of the extant species *Otocyon megalotis*. However, the Kombat tooth is appreciably larger (ca 20%) than the mean of the corresponding element in the extant species. Given the restricted nature of the sample, however, we refrain from naming a new species, and attribute the specimen to *Otocyon* cf *megalotis*.

The observation that some fossils of Pleistocene bat-eared foxes (*Prototocyon recki* and the Kombat fossil) are somewhat larger than the corresponding parts of the extant species suggests that there has probably been a reduction in body size in this lineage through geological time.

Finally, following the dispersal of the family Canidae from North America to Africa (via Asia) at the end of the Miocene (with forms such as *Eucyon* and of vulpines during the Pliocene), it is plausible that *Otocyon* evolved exclusively within Africa (more likely Southern Africa than East Africa) and did not subsequently disperse to other continents, nor even to parts of Africa north of the Tropic of Cancer.

A holistic approach to the origin of the bat-eared fox lineage, taking into account its skeletal and dental morphology, molecular biology, behaviour, body dimensions, physiology (including seasonal adaptations such as moulting), as well as its admittedly relatively sparce fossil record, indicates that it most probably evolved in Southern Africa from a lineage of canids that dispersed to Africa during the latest Miocene, probably ultimately from North America via Eurasia.

For a period of over two centuries, scenarios based on only one or two of the data sources have failed to resolve the issues concerning canid phylogenetics and systematics.

References

Armstrong, A. 2016. Small mammal utilization by Middle Stone Age humans at Die Kelders Cave 1 and Pinnacle Point Site 5-6, Western Cape Province, South Africa. *Journal of Human Evolution*, **101**, 17-44.

Avery, D. M. 2019. *A Fossil History of Southern African Land Mammals*. Cambridge University Press, 315 pp.

Bardeleben, C., Moore, R. L. and Wayne, R. K. 2005. A molecular phylogeny of the Canidae based on six nuclear loci. *Molecular Phylogenetics and Evolution*, **37**(**3**), 815-831.

Beaumont, P. B. and Boshier, A. K. 1974. Report on test excavations in a prehistoric pigment mine near Postmasburg, northern Cape. *South African Archaeological Bulle*tin, **29**, 41-59.

Bonis, L. de, Peigné, S., Likius, A., Mackaye, H. T., Vignaud, P. and Brunet. M. 2007. The oldest African fox (*Vulpes riffautae* n. sp., Canidae, Carnivora) recovered in late Miocene deposits of the Djurab desert, Chad. *Naturwissenschaften*, **94**, 575-580.

Bose, P. N. 1880. On undescribed fossil Carnivora from the Sivalik Hills. *Quarterly Journal of the Geological Society, London*, **36**, 119-136.

Bowdich, T. E. 1821. *An Analysis of the Natural Classifications of the Mammalia, for the Use of Students and Travellers*. Paris, J. Smith, 180 pp.

Brophy, J. K., De Ruiter, D. J., Athreya, S. and De Witt, T.J. 2014. Quantitative morphological analysis of bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng Province, South Africa. *Journal of Archaeological Science*, **41**, 376-388.

Brophy, J. K., De Ruiter, D. J., Lewis, P. J., Churchill, S. E. and Berger, L. R. 2006. Preliminary investigation of the new Middle Stone Age site of Plovers Lake, South Africa. *Current Research in the Pleistocene*, **23**, 41-43.

Carlsson, A. 1905. Ist *Otocyon caffer* die Ausgangsform des Hundegeschlechts oder nicht? *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere.* **XXII**, 717-754.

Clark, H. O. 2005. *Otocyon megalotis. Mammalian Species*, *American Society of Mammalogists*, **766**, 1-5.

Clutton-Brock, J., Corbet, G. B. and Hills, M. 1976. A Review of the Family Canidae, with a Classification by Numerical Methods. *Bulletin of the British Museum (Natural History) Zoology*, **29**(**3**), 117-119.

Cruz-Uribe, K. 1991. Distinguishing hyena from hominid bone accumulations. *Journal of Field Archaeology*, **18**, 467-486.

Cruz-Uribe, K. and Klein, R. G. 1981–1983. Faunal remains from some Middle and Later Stone Age sites in South West Africa. *Journal of the South West Africa Scientific Society*, **36-37**, 91-114.

De Ruiter, D. J., Brophy, J. K., Lewis, P. J., Churchill, S. E. and Berger, L. R. 2008. Faunal assemblage composition and paleo-environment of Plovers Lake, a Middle Stone Age locality in Gauteng Province, South Africa. *Journal of Human Evolution*, **55**, 1102-1117.

De Ruiter, D. J., Brophy, J. K., Lewis, P. J., Kennedy, A. M., Stidham, T. A., Carlson, K. B. and Hancox, P. J. 2010. Preliminary investigation of Matjhabeng, a Pliocene fossil locality in the Free State of South Africa. *Palaeontologia Africana*, **45**, 11-22.

Deane, J. G. 1995. The structural evolution of the Kombat deposits, Otavi Mountainland, Namibia. *Communications of the Geological Survey of Namibia*, **10**, 99-107.

Dehghani, R. 2008. *Aspects of Carnivoran Evolution in Africa*. PhD Thesis Summary, University of Stockholm, Sweden, 31 pp.

Desmarest, A. G. 1822. Mammalogie ou description des espèces de mammifères. Seconde partie, contenant les ordres de Rongeurs des Edentes, des Pachydermes, des ruminans et des Cetacés, **7**, 277-555. *In*: *Encyclopédie méthodique*, 196 vols, Veuve Agasse, Paris, France.

Denbow, J. 2011. Excavations at Divuyu, Tsodilo Hills. *Botswana Notes and Records*, **43**, 76-94.

Dewar, G. I. 2007. *The Archaeology of the Coastal Desert of Namaqualand, South Africa: a Regional Synthesis*. Unpublished PhD Thesis, University of Cape Town, 320 pp.

Ewer, R. F. 1957. Some fossil carnivores from the Makapansgat Valley. *Palaeontologia Africana*, **4**, 57-67.

Ewer, R. F. 1958. Appendix A: faunal lists for the sites of Sterkfontein, Swartkrans, Kromdraai A and Makapansgat Limeworks. *In*: Brain, C. K. (Ed.) The Transvaal Ape-man Bearing Cave Deposits. *Transvaal Museum Memoir*, **11**, 128-130.

Ewer, R. F. 1965. Large Carnivora. *In*: Leakey, L. S. B. *Olduvai Gorge, 1951*, Cambridge University Press, Vol. 1, 19-22.

Fischer von Waldheim, G. 1817. Adversaria zoologica. *Mémoires de la Société impériale des naturalistes de Moscou*, **5**, 357-472.

Geffen, E., Mercure, A., Girman, D. J., Macdonald, D. W. and Wayne, R. K. 1992. Phylogenetic relationships of the fox-like canids : mitochondrial DNA restriction fragment, site and cytochrome *b* sequence analysis. *Journal of Zoology*. https://doi.org/10.1111/j.1469-7998.1992.tb 04430.x

Geraads, D. 1997. Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Géobios*, **30**, 127-164.

Geraads, D. 2008. Plio-Pleistocene Carnivora of northwestern Africa: a short review. *Comptes Rendus Palévol*, **7**, 591-599.

Geraads, D., Drapeau, M. S. M., Bobe, R. and Fleagle, J. G. 2015. *Vulpes mathisoni*, sp. nov., a new fox from the Pliocene Mursi Formation of Southern Ethiopia and its Contribution to the Origin of African Foxes *Journal of Vertebrate Paleontology*, **35**(**4**) e943765 (7 pages).

Howell, F. C. and García, N. 2007. Carnivora (Mammalia) from Lemudong'o (Late Miocene, Narok District, Kenya). *Kirtlandia*, **56**, 121-139.

Huxley T. H. 1880. On the cranial and dental characters of the Canidae. *Proceedings of the Zoological Society of London*, 238-288, 16 text figs.

Kieser, J. A. 1995. Gnathomandibular morphology and character displacement in the bat-eared Fox. *Journal of Mammalogy*, **76**(**2**), 542-550.

Klein, R. G. 1979. Palaeoenvironmental and cultural implications of late Holocene archaeological faunas from the Orange Free State and north-central Cape Province, South Africa. *South African Archaeological Bulletin*, **34**, 34-49.

Klein, R. G., Cruz-Uribe, K. and Beaumont, P. B. 1991. Environmental, ecological and paleo-anthropological implications of the Late Pleistocene mammalian fauna from Equus Cave, northern Cape Province, South Africa. *Quaternary Research*, **36**, 94-119.

Klein, R. G., Cruz-Uribe, K., Halkett, D., Hart, T. and Parkington, J. E. 1999. Paleoenvironmental and human behavioral implications of the Boegoeberg 1 Late Pleistocene hyena den, Northern Cape Province, South Africa. *Quaternary Research*, **52**, 393-403.

Koyasu, K., 1993. Variability of dentition in the bat-eared fox, *Otocyon megalotis*. *Aichi Gakuin Journal of Dental Science*, **31**(**1**), 63-104.

Kuhn, B. F., Herries, A. I. R., Price, G. J., Baker, S. E., Hopley, P., Menter, C. and Caruana, M. V. 2016. Renewed investigations at Taung: 90 years after the discovery of *Australopithecus africanus*. *Palaeontologia Africana*, **51**, 10-26.

Lydekker, R. 1884. Indian Tertiary and Post-Tertiary Vertebrata. *Palaeontologica Indica*, (**10**) **II**, i-xv + 1-363, 45 plates.

Marean, C. W., Nilssen, P. J., Brown, K. S., Jerardino, A. and Stynder, D. D. 2004. Palaeo-anthropological investigations of Middle Stone Age sites at Pinnacle Point, Mossel Bay, South Africa: archaeology and hominid remains from the 2000 field season. *Paleoanthropology*, **1**, 14-83.

Matthew, W. D. 1924. Third contribution to the Snake Creek Fauna. *Bulletin of the American Museum of Natural History*, **50**, 59-210, 63 text figs.

McGrath, J. R., Cleghorn, N., Gennari, B., Henderson, S., Kyriacou, K., Nelson-Viljoen, C., Nilssen, P., Richardson, L., Shelton, C., Wilkins, J. and Marean, C. 2015. The Pinnacle Point shell midden complex: a Mid- to Late Holocene record of Later Stone Age coastal foraging along the southern Cape coast of South Africa. *South African Archae-ological Bulletin*, **70**, 209-219.

McKee, J. K. 1994. Catalogue of fossil sites at the Buxton Limeworks, Taung. *Palaeontologia Africana*, **31**, 73-81.

McKee, J. K., Thackeray, J. F. and Berger, L. R. 1995. Faunal assemblage seriation of southern African Pliocene and Pleistocene fossil deposits. *American Journal of Physical Anthropology*, **96**, 235-250.

Morales, J., Pickford, M. and Soria, D. 2005. Carnivores from the Late Miocene and basal Pliocene of the Tugen Hills, Kenya. *Revista de la Sociedad Geológica de España*, **18**, 39-61.

Müller, S. 1836. Jahresbericht über die Fortschritte der anatomisch-physiologischen Wissenschaften im Jahre 1834. *Archiv für Anatomie und Physiologie*, **1835**, 1-151, 225-243.

Nghoongoloka, A., Bowell, R., Kamona, F. and Mocke, H. 2020. Re-evaluation of Kombat-style mineralization and implications for exploration in the Otavi Mountainland, Namibia. *Open Journal of Geology*, **10**, 1119-1152.

O'Regan, H. J. 2007. A revision of the Carnivora from Member 5, Sterkfontein, South Africa, based on a reassessment of published material and site stratigraphy. *Annals of the Transvaal Museum*, **44**, 209-214.

Nel, J. A. J. and Maas, B. 2004. Bat-eared Fox *Otocyon megalotis* (Desmarest, 1822) *In*: Sillero-Zubiri, C, Hoffmann, M. and Macdonald, D. W. (Eds) *Canids : Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, 183-189. IUCN, Gland.

Petter, G. 1964. Origine du genre *Otocyon* (Canidae africain de la sous-famille des Otocyoninae). *Mammalia*, **28**(**2**), 529-538.

Petter, G. 1973. Carnivores pléistocènes du ravin d'Olduvai Tanzanie. *In*: Leakey, L. S. B., Savage, R. J. G. and Coryndon, S. C. (Eds) *Fossil Vertebrates of Africa*, Vol. **3**, 43-100. Academic Press, London.

Pickford, M. 2004. Southern Africa: a cradle of evolution. *South African Journal of Sci*ence, **100**, 205-214.

Pickford, M. 2008a. *Libycosaurus petrocchii* Bonarelli, 1947, and *Libycosaurus anisae* (Black, 1972) (Anthracotheriidae, Mammalia): nomenclatural and geochronological implications. *Annales de Paléontologie,* **94**, 39-55.

Pickford, M. 2008b. Southern Africa: a cradle of evolution. *Memoir of the Geological Survey of Namibia*, **20**, 539-554.

Pickford, M. and Senut, B. 2010. Karst Geology and Palaeobiology of Northern Namibia. *Memoir of the Geological Survey of Namibia,* **21**, 1-74.

Pilgrim, G. E. 1932. The fossil Carnivora of India. *Palaeontologica Indica, New Series*, **18**, 1-232, 10 plates.

Plug, I. 1993a. KwaThwaleyakhe Shelter: the faunal remains from a Holocene site in the Thukela Basin, Natal. *Natal Journal of Humanities*, **5**, 37-45.

Plug, I. 1993b. The faunal remains from Nanda, an Early Iron Age site in Natal. *Natal Journal of Humanities*, **5**, 99-107.

Plug, I. 1979. Appendix: Striped Giraffe Shelter faunal report. *In*: Wadley L. (Ed.) Big Elephant Shelter and its role in the prehistory of central South West Africa. *Cimbebasia* Series B, **3**, 71-72.

Plug, I. 2000. Overview of Iron Age fauna from the Limpopo Valley. *South African Archaeological Society Goodwin Series*, **8**, 117-126.

Plug, I. and Sampson, C. G. 1996. European and Bushman impacts on Karoo fauna in the nineteenth century: an archaeological perspective. *South African Archaeological Bulletin*, **51**, 26-31.

Pohle, H. 1928. Die Raubtiere von Oldoway. *Wissenschaftliche Ergebnisse der Oldoway-Expedition. 1913*, Neue Folge, **3**, 45-54.

Potts, R. and Deino, A. 1995. Mid-Pleistocene change in large mammal faunas of eastern Africa. *Quaternary Research*, **43**, 106-113.

Reck, H. and Pohle, H. 1922. Über einen vermutlich diluvialen Säugetierrest von der Mittellandbahn in Deutsch-Ostafrika. *Centralblatt für Mineralogie, Geologie und Paläontologie*, Stuttgart, **1922**, 546-557.

Rector, A. L. and Reed, K. E. 2010. Middle and Late Pleistocene faunas of Pinnacle Point and their paleoecological implications. *Journal of Human Evolution*, **59**, 340-357.

Reynolds, S. C. 2010. Where the wild things were: spatial and temporal distribution of carnivores in the Cradle of Humankind Gauteng, South Africa, in relation to the accumulation of mammalian and hominin assemblages. *Journal of Taphonomy*, **8**, 233-257.

Reynolds, S. C. and Kibii, J. M. 2011. Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein Gauteng Province, South Africa. *Palaeontologia Africana*, **46**, 59-88.

Reynolds, S. C., Clarke, R. J. and Kuman, K. 2007. The view from the Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa. *Journal of Human Evolution*, **53**, 160-271.

Reynolds, S. C., Vogel, J. C., Clarke, R. J. and Kuman, K. 2003. Preliminary results of excavations at Lincoln Cave, Sterkfontein, South Africa. *South African Journal of Science*, **99**, 286-288.

Robbins, L. H. 1990. Excavation at the White Paintings Rock-Shelter Tsodilo Hills. *Nyame Akuma*, **34**, 2-4.

Robbins, L. H., Murphy, M. L., Brook, G. A., Ivester, G. H., Campbell, A. C., Klein, R. G., Milo, R. G., Stewart, K. M., Downey, W. S. and Stevens, N. J. 2000. Archaeology, palaeo-environment and chronology of the Tsodilo Hills White Paintings Rock Shelter, northwest Kalahari Desert, Botswana. *Journal of Archaeological Science*, **27**, 1085-1113.

Rook, L. 2009. The wide ranging genus *Eucyon* Tedford and Qiu, 1996 (Mammalia, Carnivora, Canidae, Canini) in the Mio-Pliocene of the Old World. *Geodiversitas*, **31(4)**, 723-741.

Savage, R. J. G. 1978. Carnivora. *In*: Maglio, V. J. and Cooke, H. B. S. (Eds) *Evolution of African Mammals*. Harvard University Press, Cambridge, Massachusetts, 249-267.

Skinner, J. D. and Smithers, R. H. N. 1990. *The Mammals of the Southern African Subregion*. University of Pretoria, South Africa, 771 pp.

Sotnikova, M. V. 2006. A new canid *Nurocyon chonokhariensis* gen. et sp. nov. (Canini, Canidae, Mammalia) from the Pliocene of Mongolia. *Courier Forschungsinstitut Senckenberg*, **256**, 11-21.

Stuart, C. T., Stuart, T. and Pereboom, V. 2003. Diet of the bat-eared fox (*Otocyon megalotis*), based on scat analysis, on the Western Escarpment, South Africa. *Canid News*, **6(2)**, 1-5.

Tedford, R. H. and Qiu, Z. 1996. A new canid genus from the Pliocene of Yushe, Shanxi Province. *Vertebrata PalAsiatica*, **34**, 27-40.

Tedford, R. H., Taylor, B. E. and Wang, X.-M. 1995. Phylogeny of the Caninae (Carnivora: Canidae) the Living Taxa. *American Museum Novitates*, **3146**, 1-37.

Tedford, R. H., Wang, X.-M. and Taylor, B. E. 2009. Phylogenetic Systematics of the North American Fossil Canidae (Carnivora : Canidae). *Bulletin of the American Museum of Natural History*, **325**, 1-218.

Thackeray, A. I., Thackeray, J. F. and Beaumont, P. B. 1983. Excavations at the Blinkklipkop specularite mine near Postmasburg, northern Cape. *South African Archaeological Bulletin*, **38**, 17-25.

Thackeray, J. F. and Watson, V. 1994. A preliminary account of faunal remains from Plovers Lake. *South African Journal of Science*, **90**, 231-233.

Thenius, E. and Hofer, H. 1960. *Stammesgeschichte der Säugetiere*. Springer Verlag, Berlin, Göttingen, Heidelberg, 312 pp.

Turner, A. 1987. New fossil carnivore remains from the Sterkfontein hominid site Mammalia: Carnivora. *Annals of the Transvaal Museum*, **34**, 319-347.

Turner, A. 1993. New fossil carnivore remains from Swartkrans. *In*: Brain, C. K. (Ed.) Swartkrans: A Cave's Chronicle of Early Man. *Transvaal Museum Monograph*, **8**, 151-165.

Turner, G. 1987a. Early Iron Age herders in northwestern Botswana: the faunal evidence. *Botswana Notes and Records*, **19**, 7-23.

Turner, G. 1987b. Hunters and herders of the Okavango Delta, Botswana. *Botswana Notes and Records,* **19**, 25-40.

Voigt, E. A. 1980. Appendix. The faunal sample from Msuluzi Confluence. *In*: Maggs, T., Msuluzi Confluence: a seventh century Early Iron Age site on the Tugela River. *Annals of the Natal Museum*, **24**, 140-145.

Wadley, L. 1979. Big Elephant Shelter and its role in the Holocene prehistory of central South West Africa. *Cimbebasia* B, **3**, 1-76.

Wadley, L. 2015. Those marvellous millennia: the Middle Stone Age of Southern Africa. *Azania*, **50**, 155-226.

Wang, X.-M. and Tedford, R. H. 1992. The status of genus *Nothocyon* Matthew, 1899, (Carnivora): an arctoid not a canid. *Journal of Vertebrate Paleontology*, **12**, 223-229.

Watson, V. 1993. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. *In*: Brain, C. K. (Ed.) Swartkrans: A Cave's Chronicle of Early Man. *Transvaal Museum Monograph*, **8**, 35-73.

Wayne, R. K. and O'Brien, S. J. 1987. Allozyme divergence within the Canidae. *Systematic Zoology*, **36**, 339-355.

Wayne, R. K., Nash, W. G. and O'Brien, S. J. 1987. Chromosomal evolution of the Canidae, II. Divergence from the primitive carnivore karyotype. *Cytogenetics and Cell Genetics,* **44**, 134-141.

Webley, L. 2001a. Excavations at /hei-/khomas Vaalhoek in the Richtersveld, Northern Cape. *Southern African Field Archaeology*, **10**, 46-74.

Webley, L. 2001b. The re-excavation of Spoegrivier Cave on the West Coast of South Africa. *Annals of the Eastern Cape Museums*, **2**, 19-49.

Werdelin, L. and Dehghani. R. 2011. Carnivora. *In*: Harrison, T. (Ed.) *Paleontology and Geology of Laetoli, Tanzania: Human Evolution in Context*. Vertebrate Paleobiology and Paleoanthropology Series. Springer, New York, 189-232.

Werdelin, L. and Peigné, S. 2010. Carnivora. *In*: Werdelin, L. and Sanders, W. (Eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, Los Angeles, Chapter **32**, 603-657.

Westbury, M. V. 2018. *Unraveling Evolution through Next Generation Sequencing*. PhD Thesis, University of Potsdam, Germay, 129 pp.

Wilmsen, E. N. 1989. The antecedents of contemporary pastoralism in western Ngamiland. *Botswana Notes and Records*, **20**, 29-39.

Winge, H. 1895. Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa Minas Geraes, Brasilien. *Museo Lundii Afhandlinger, Copenhagen*, **II**(**4**) 3-104, pls i-viii.

Wortmann, J. L. and Matthew, W. D. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. *Bulletin of the American Museum of Natural History*, **XII**, 109-138, PIs vi, 10 text figs.

Zrzavý, J. and Řičánková, V. P. 2004. Phylogeny of Recent Canidae (Mammalia, Carnivora) ; relative reliability and utility of morphol-ogical and molecular datasets. *Zoologica Scripta*, **33**(**4**), 311-333.

Zrzavý, J., Duda, P., Robovský, J., Okřinová, I., and Řičánková, V. P. 2018. Phylogeny of the Caninae (Carnivora): Combining morphology, behaviour, genes and fossils. *Zoologica Scripta*, https://doi.org/10.1111/zsc.12293