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A new species of fox from the *Australopithecus sediba* type locality, Malapa, South Africa

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The 1.977 Ma site of 'Malapa' (Gauteng, South Africa) has yielded important new fossils, including the type specimens of the new hominin species *Australopithecus sediba*. Recently, we reported the first Carnivora specimens to have been recovered from the site. That sample included members of Felidae, Herpestidae and Hyaenidae. That first report also included three associated small canid specimens (an M_2, a rib and a posterior mandibular fragment including the P_4, M_1, coronoid, condylar and angular processes) that we attributed to *Vulpes* cf. *V. chama*. In this paper, we compare these specimens to a broad sample of modern and fossil foxes and conclude that these specimens are distinct enough to be referred to a new species, here described and named *Vulpes skinneri*.

Keywords: **Mammalia, Carnivora, Canidae, *Vulpes*, *Australopithecus sediba*, Pliocene, Pleistocene, South Africa**

INTRODUCTION

The site of Malapa was first discovered in 2008 and reported in 2010 (Berger *et al.*, 2010; Dirks *et al.*, 2010). The locality has since gained recognition as the type site for a new species of hominin, *Australopithecus sediba* (Berger *et al.*, 2010). Subsequently, the completeness of some of the *Au. sediba* specimens and their importance to human evolution have been demonstrated, along with a reconstruction of their possible diet (Carlson *et al.*, 2011; Kibii *et al.*, 2011; Kivell *et al.*, 2011; Zipfel *et al.*, 2011; Berger, 2012; Henry *et al.*, 2012). The accompanying fauna, much of which remains unpublished, is extensive. The Carnivora were recently published (Kuhn *et al.*, 2011), based on 81 identified specimens representing five families and including both extinct species such as the "false" sabertooth cat, *Dinofelis barlowi*, and still extant forms such as the leopard (*Panthera pardus*), black-footed cat (*Felis nigripes*) and brown hyaena (*Parahyaena brunnea*) (Kuhn *et al.*, 2011). Of special note was the referral of three specimens to *Vulpes* cf. *V. chama*, and this component of the fauna forms the subject of this contribution.

The evolutionary history of foxes (Tribe Vulpini) is much less well understood than that of the larger dogs of the *Canis* group. The most extensive studies to date of extant dog species (Zrzavý & Ricánková, 2004; Lindblad-Toh *et al.*, 2005) have found the Vulpini to be paraphyletic, with the grey and island foxes (genus *Urocyon*) as the sister group to all other extant Canidae (Figure 1). The remaining Vulpini (here Vulpini *sensu stricto*) form a monophyletic group that is the sister to the tribe Canini (South American "foxes" + *Canis* group). The Vulpini *sensu stricto* includes the genera *Vulpes* (true foxes, including species that have previously been placed in the genera *Fennecus* and *Alopex*), *Otocyon* (bat-eared fox), and *Nyctereutes* (raccoon dog). The phylogenetic position of the latter has been debated for many years (Tedford *et al.*, 1995, Reynolds, 2012) and most morphological analyses have placed it with the South American canids. However, molecular analyses now place it firmly within the Vulpini.

The fossil record of Vulpini *sensu stricto* is generally poor. The tribe is likely to have originated in North America from *Leptocyon*-like ancestors (Tedford *et al.*, 2009) sometime in the early Late Miocene. The earliest Vulpini known to date is *Metalopex macconnelli* from the Late Clarendonian (*c.* 10.5 Ma) of California (Tedford & Wang, 2008), though this taxon may be more closely related to *Urocyon* than Vulpini (Figure 2). Somewhat younger species with a firmer connection to Vulpini are *Vulpes stenognathus* and *V. kernensis* from the Hemphillian (*c.* 9 Ma) of Oklahoma and California, respectively (Tedford *et al.*, 2009). Vulpini must have left North America no later than about 8 Ma (due to the presence of *Vulpes riffautae* in Africa, see below), but this migration is not documented in the fossil record of Eurasia, where the earliest Vulpini are of early Pliocene age (Qiu and Tedford, 1990). The subsequent fossil record of Vulpini in Eurasia is fragmentary until the Late Pliocene, but includes *V. alopecoides, V. praecorsac, V. beihaiensis* and *V. chikushanensis*, as well as several species of *Nyctereutes* (Tedford and Qiu, 1991).

The oldest fox in Africa is *Vulpes riffautae* from the Late Miocene (*c.* 7 Ma) of Toros-Menalla, Chad (de Bonis *et al.*, 2007). This may, in fact, be the oldest canid found outside North America, rivalled only by "*Canis*" *cipio* from approximately coeval sediments in Spain (Crusafont Pairó, 1950). After this time, the Vulpini of northern, eastern and southern Africa appear to follow separate evolutionary trajectories. *Vulpes riffautae* is clearly distinct from all living foxes, but its phylogenetic relationships within the tribe are not known.

Nyctereutes spp. has been reported from several regions of Africa. In North Africa, *N. abdesalami*, an undoubted *Nyctereutes* close to Eurasian species, has been reported from

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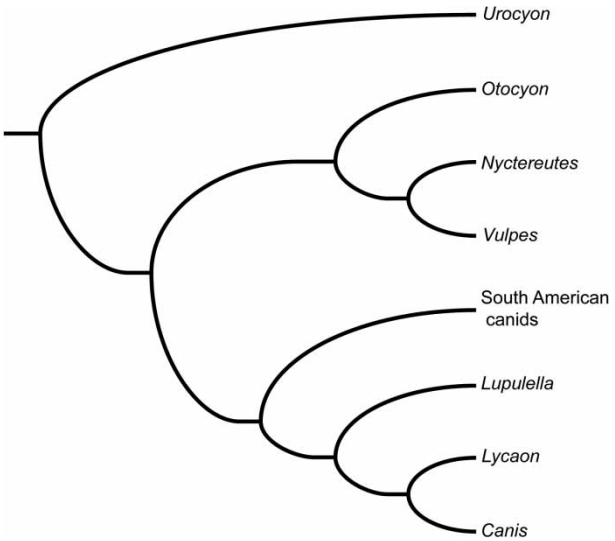

Figure 1. Simplified cladogram of extant Canidae, following Lindblad-Toh *et al.* (2005).

Ahl al Oughlam, Morocco (Geraads, 1997), while in eastern Africa ?*N. barryi* from Laetoli, Tanzania and *N. lockwoodi* from Dikika, Ethiopia have been referred to the genus (Geraads *et al.*, 2010; Werdelin and Dehghani, 2011). All of the above are of Pliocene age – though Ahl al Oughlam may be very slightly younger than the Plio-Pleistocene boundary. In South Africa another species of raccoon dog, *N. terblanchei*, has been described from several clearly Pleistocene sites, including Kromdraai A (type site) and ''Kromdraai-Coopers'' (or ''KA 2''), and Sterkfontein Mb 5. The species was originally described as a species of jackal by Broom (1948) and subsequently transferred to *Nyctereutes* by Ficcarelli *et al.* (1984). A contrary view has, however, recently been expressed by Reynolds (2012), who believes that the material should be referred to a species of jackal or fox (ironically, in the current molecular phylogenetic scheme, *Nyctereutes* is a fox).

The bat-eared fox, *Otocyon,* is poorly represented in the fossil record. It is not known from North Africa and only from a single Pleistocene record in South Africa, at Plovers Lake. In eastern Africa it is known from a single record at Laetoli (Werdelin and Dehghani, 2011) and from more extensive material at Olduvai, Tanzania (Petter, 1973). Both of these records have been referred to the genus *Prototocyon*, which is only doubtfully distinct from *Otocyon*. The extant genus has been reported from the Middle Pleistocene of Lainyamok, Kenya (Potts and Deino, 1995).

The genus *Vulpes*, on the other hand, is poorly known from North and eastern Africa, but relatively frequently reported from South Africa. Apart from Middle and Late Pleistocene records of *V. vulpes*, the genus is only known from a single North African record, a group of specimens from Ahl al Oughlam thought to be close to *V. rueppelli* (Geraads, 1997). The eastern African record is even poorer. It is restricted to an undescribed skull from the Mursi Fm., Ethiopia that may be a Vulpini, and a likewise undescribed *Vulpes* sp. mandible fragment from Koobi Fora, Kenya. In South Africa, by contrast, two extinct species of *Vulpes* have been described, and there are also a number of records of fossil *V. chama*. The extinct species are *V. pattisoni* from Taung (the status of this species is discussed below) and *V. pulcher* from Kromdraai A and Swartkrans (Broom, 1939, Broom, 1948, Ewer, 1956). Finally, *V. chama* has been reported from various times in the Pleistocene: Drimolen, Elands Bay Cave, Elandsfontein Main Site, Makapansgat Mbs 3 and 4, Plovers Lake, Saldanha Sea Harvest, Sterkfontein, Swartklip, and Swartkrans (Werdelin and Peigné, 2010).

MATERIALS AND METHODS:

The specimens we describe herein are the posterior mandibular fragment (Figure 3), an M_2 (Figure 4) and a rib (Figure 5) that were originally referred to *Vulpes* cf. *V. chama* (Kuhn *et al.*, 2010; Kuhn *et al.*, 2011).

Comparative data (Table 1) were obtained from extant specimens housed at the American Museum of Natural History, New York (AMNH), the Palaeosciences Centre at the University of the Witwatersrand, Johannesburg (U.W.), the small mammal collection and zooarchaeology collection at the Ditsong Museum of Natural History, formerly the Transvaal Museum, Pretoria (TM or AZ), and the Swedish Museum of Natural History, Stockholm (SMNH). Data were collected from several species of *Vulpes,* representing the genus' modern body size range (from *V. zerda* to *V. vulpes* – ~ 1 kg and up to 14 kg, respectively; Larivière, 2002, Larivière and Pasitschniak-Arts, 1996), including all specimens of *V.*

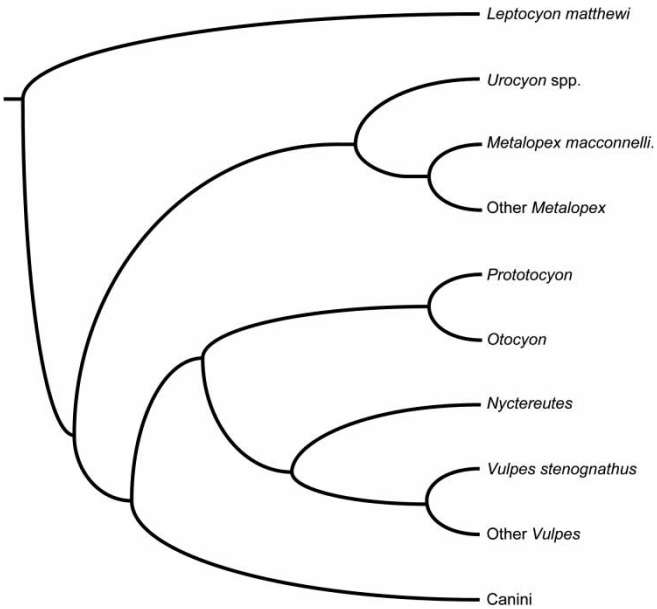

Figure 2. Cladogram of Vulpini, including some fossil taxa mentioned in the text. Modified after Tedford *et al.* (2009).

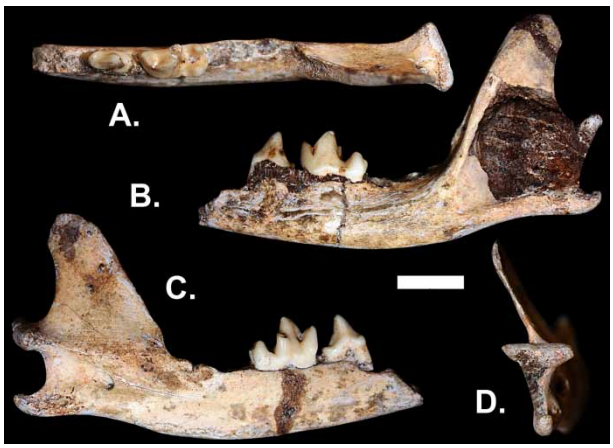

Figure 3. Holotype specimen U.W. 88-812. Views: A, Superior; B, Lateral; C, Medial; D, Posterior. Scale is 10 mm × 2 mm.

Figure 4. Paratype M_2 (U.W. 88-814; right) compared with M_2 of *V. chama* (AMNH 81760; left) in occlusal (top) and lateral (bottom) views. Scale is 5 mm × 1 mm.

chama (the taxon most similar to the Malapa material) from each institution. Data were also collected from several individuals of *Otocyon megalotis* and *Nyctereutes procyonoides* – canids that are roughly similar in body size to the new species – for further out-group comparisons. Jackals (*Canis sensu lato*) and wild dogs (*Lycaon*) are much larger than the Malapa fox specimens, and were therefore excluded from the metric comparisons. Variables were analysed using default settings in JMP 9.0.2 (SAS Institute Inc.). Correlation matrices were used for principal component analysis (PCA).

SYSTEMATIC PALEONTOLOGY

Carnivora Bowdich, 1821
Canidae Fischer von Waldheim, 1817
Caninae Fischer von Waldheim, 1817
Vulpini Hemprich and Ehrenberg, 1828–1834
Genus *Vulpes* Frisch, 1775
Vulpes skinneri nov. sp.

Figure 5. Paratype rib (U.W. 88-183; A, caudal; B, cranial) compared with the third ribs of *V. chama* (C and D; cranial) and *O. megalotis* (E; cranial) from the Ditsong Museum. C = AZ 1192, D = AZ 2329, E = AZ 2084. Scale is 10 mm × 2 mm.

Table 1. Comparative sample size, means and standard deviations. See Figure 6 for description of measurements.

	U.W. 88-812, 814	*V. chama* (*N* = 32)		*V. macrotis* (*N* = 4)		*V. pallida* (*N* = 3)		*V. velox* (*N* = 9)		*V. vulpes* (*N* = 9)		*V. zerda* (*N* = 10)		*N. procyonides* (*N* = 2)		*O. megalotis* (*N* = 10)		*V. pattisoni* (*N* = 1)		*V. pulcher* (*N* = 2)[a]		*V. riffautae* (*N* = 2)[b]	
		μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
p4 L	6.68	6.76	0.59	7.59	0.42	5.62	0.50	7.27	0.64	9.28	0.98	5.11	0.34	6.61	0.26	5.39	0.48			7.90	0.50	6.65	0.05
p4 W	3.12	3.16	0.41	3.17	0.34	2.49	0.23	3.21	0.26	4.04	0.48	2.19	0.30	3.08	0.08	3.16	0.15			3.20	0.00	2.45	0.05
m1 L	10.26	10.70	0.77	10.43	0.81	8.74	0.56	11.49	0.65	14.37	1.50	7.40	0.86	11.35	0.45	6.24	0.51			13.05	0.95	10.30	
m1 Tri L	6.33	7.07	0.66	7.48	0.57	5.45	0.76	8.27	0.27	9.62	1.00	5.01	0.40	7.02	0.23	3.44	0.35					7.00	
m1 W	4.88	4.86	0.51	4.51	0.42	4.00	0.38	4.78	0.35	5.84	0.50	3.47	0.21	4.55	0.10	4.12	0.36			4.80	0.20	4.00	
m2 L	6.47	5.79	0.61	4.54	0.25	4.91	0.26	4.92	0.51	6.34	0.42	4.71	0.99	5.22	0.07	5.13	0.61	6.96		6.55	0.55	5.50	0.00
m2 W	5.22	4.59	0.55	3.74	0.28	3.18	0.41	4.19	0.37	5.00	0.37	3.52	0.27	4.00	0.20	4.48	0.27	5.28		4.70		3.60	
Sub m1 H	14.92	16.40	1.29	13.94	1.82	12.54	1.46	15.93	1.51	20.79	1.53	10.82	0.54	15.88	0.52	14.91	1.13						
Sub m1 W	5.41	5.27	0.48	5.79	1.46	3.73	0.14	5.67	0.50	6.82	0.73	3.65	0.21	6.22	0.81	5.28	0.35						
Cor-Ang	30.50	28.03	1.41	25.66	0.79	22.79	2.70	30.01	2.08	37.89	2.25	20.53	0.94	30.57	0.62	29.98	2.62						
Con-Ang	14.42	12.70	1.07	12.01	0.93	10.57	0.51	14.33	1.51	16.69	1.11	9.47	0.44	22.92	9.99	15.46	1.69						
Con W	10.62	10.20	0.78	10.04	0.43	9.06	1.07	11.40	0.57	14.47	1.20	7.80	0.62	12.56	0.28	12.37	0.64						
Con DV	3.79	3.76	0.45	3.83	0.71	3.39	0.28	4.13	0.63	5.46	0.86	2.89	0.32	5.13	0.52	5.71	0.66						

[a] From Ewer, 1956. Data listed without standard deviations are from one of the two specimens.
[b] From de Bonis *et al.*, 2007. Data listed without standard deviations are from one of the two specimens.

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Diagnosis

Canidae similar in size to *V. chama.* Lower carnassial trigonid mesiodistally short and tall, hypoconulid small, closely associated with hypoconid and separated from entoconid. Angular process of mandible substantial and low relative to the condyle and coronoid processes. Second lower molar large, especially relative to carnassial trigonid. Lower fourth premolar lacking distal accessory cuspid.

Holotype

U.W. 88-812: posterior left mandibular fragment including P_4 and M_1 housed at the Palaeosciences Centre, University of the Witwatersrand.

Referred specimens

U.W. 88-814: Left M_2 also housed at the Palaeosciences Centre.

U.W. 88-813: Left rib, probably R3 also housed at the Palaeosciences Centre.

Etymology

V. skinneri, honouring the late Professor John Dawson Skinner, long-time director of the University of Pretoria Mammal Research Institute and author of many seminal works on African mammals, including all three editions of *The Mammals of the Southern African Subregion* (Smithers and Skinner, 1983; Skinner and Smithers, 1990; Skinner and Chimimba, 2005).

Occurrence

Early Pleistocene (1.977 Ma), Malapa Cave, Sterkfontein Valley, Gauteng, South Africa.

Description

U.W. 88-812 is a posterior left mandibular fragment including P_4 and M_1, alveoli for M_2 and M_3, and all posterior mandibular morphology including angle, condyle, coronoid process and mandibular foramen. The specimen is broken anterior to P_4 and is missing some of the mesial P_4 alveolus. U.W. 88-814 is a complete left M_2 crown including most of the distal root. U.W. 88-813 is a complete left rib, probably R3. All three specimens were found in the same breccia block, which is devoid of other similarly sized specimens. They are likely to belong to a single individual. Consistent with other fossils from Malapa, the specimens do not exhibit taphonomic degradation (i.e. no insect damage, carnivore chew marks or perimortem abrasion).

The P_4 is fairly tall, though well within the range of other *Vulpes* (Table 1). Like most similarly sized canids, it has no mesial accessory cuspid. Though it has a distinct and sharp postcingulid (common in small canids), its complete lack of a distal accessory cuspid appears to be unique among all small canids.

Though the M_1 is not particularly tall, its short length – particularly that of the trigonid – makes it appear so (Figures 3 and 6). Indeed, it is nearly as tall as it is long (Table 1). Though broken, the base of the metaconid is nearly as long mesiodistally as that of the paraconid, suggesting that these two cusps were of similar height (Figure 6). The hypoconid is slightly taller than the entoconid and there is a very small hypoconulid (Figure 3 – particularly visible in lateral view) that is closely associated with the hypoconid and separated from the entoconid.

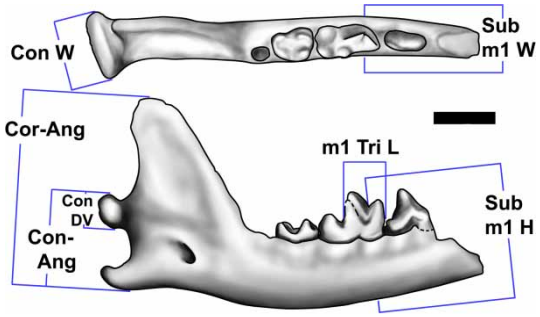

Figure 6. Mandibular measurements in superior and medial view. These measurements were taken in addition to standard L, W, and H (measured from the cementoenamel junction on the buccal side of the tooth to the top of the highest buccal cusp point) on P_4, M_1 and M_2. In this rendered image, the paratype M_2 (U.W. 88-814) has been added to the holotype specimen (U.W. 88-812) and the metaconid and anteromedial P_4 alveolus have been reconstructed (broken line). Con W = maximum width of the condyle, Con-Ang = minimum distance from the top of the condyle to the bottom of the angle, Con DV = maximum dorsoventral height of the condyle, Cor-Ang = minimum distance from the top of the coronoid process to the bottom of the angle, m1 Tri L = length of the carnassial trigonid from the front of the paraconid to the back of the metaconid, Sub m1 H = height of the mandible from the carnassial notch to the bottom of the corpus perpendicular to the corpus (from Hartstone-Rose *et al.*, 2007; Hartstone-Rose, 2008), Sub m1 W = width of corpus at Sub m1 H. Scale is 10 mm × 2 mm.

A complete left M_2 crown with most of the distal root intact (U.W. 88-814 Figure 4) is similar in dimensions to the M_2 alveolus present in the U.W. 88-812 mandible and we believe it is from the same individual. It has four distinct cusps and a strong buccally oriented mesiobuccal cingulum that apparently extends much further distally than in *V. chama*. (With a larger sample size, this might indeed be a good character to distinguish *V. chama* from *V. skinneri.*) Because of this cingulum, the trigonid is wider than the talonid. The protoconid and metaconid are of almost equal height. The entoconid is taller than the hypoconid and connected to it by a distinct postentoconulid. Unlike most *V. chama* and other vulpines, there are no other cuspulids or distinct cingulids. Though the mesiolingual shelf is more substantial than that found in *V. chama*, in all other respects (including its simplicity) it is within the morphological range of *V. chama*.

The simple oval M_3 alveolus present on U.W. 88-812 measures 3.0 mm mesiodistally and 2.1 mm buccolingually. As in most canids, the coronoid process rises from the corpus at roughly 45°. It is narrower at its coronal point than in some *V. chama* (compare Figure 7 A and B) but within the range of this highly variable morphology. Likewise, the posterior margin of the coronoid process is more concave than in many vulpines, but again within the morphological range of many specimens. It is not hook-shaped as in *O. megalotis* (cf. Figure 7 E.). The condyle is nearly identical to that of *V. chama*, though the angle is slightly more substantial than in most cape foxes. The mandibular angle is also lower in the Malapa specimen (see next section). The mandibular foramen is unremarkable as is the corporal cross section.

U.W. 88-813 is a left rib – probably the 3rd. It possesses a complete head that has two facets, separated by a crest, for articulation with the corresponding as well as preceding vertebral body costal facets. The neck appears cranio-caudally flattened, with two margins (internal/ventral and external/dorsal) and two surfaces (cranial and caudal). Both the dorsal and the ventral margins are concave ventrally. The neck is

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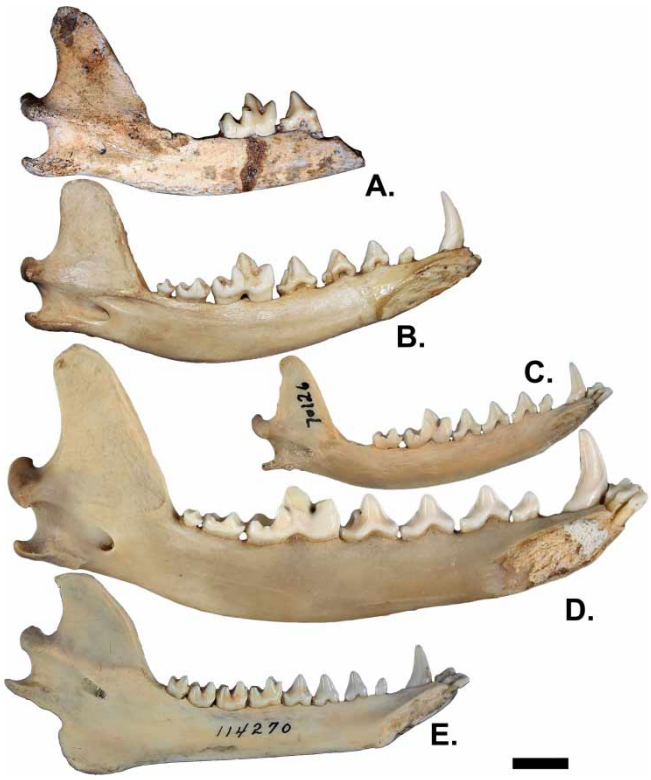

Figure 7. Medial view of fox mandibles. A, U.W. 88-812; B, *V. chama* (BPI/C 621 – Bernard Price Institute, University of the Witwatersrand); C, *V. zerda* (AMNH 70126); D, *V. vulpes* (AMNH 18245); E, *O. megalotis* (AMNH 114270). Note: although the P_4 distal accessory cuspid is not readily visible on some of these specimens (particularly the smaller specimens), it is present on all these individuals – and all comparative specimens studied for this manuscript – when viewed in occlusal or lateral views. This medial view was selected for this comparison as it better shows the M_1 morphology (particularly the base of the metaconid) and the posterior mandibular morphology – which is partially obscured by breccia in lateral view (Figure 1). Scale is 10 mm × 2 mm.

narrow proximally and widens distally at the tubercle. The tubercle is well developed and protrudes from the dorsal margin. There is a well-developed articulating facet on the tubercle for articulation with the transverse process of the corresponding vertebra. The tubercle position corresponds with the dorsal angle of the rib. The shaft is flattened and has two margins (internal/medial and external/lateral) and two surfaces (cranial and caudal). There is a slight torsion resulting in an obliqueness of the shaft. The transverse axis of the shaft lies closer to the cranio-caudal plane. This orientation of the axis causes the cranial surface to face externally/laterally and the caudal surface to face slightly internally/medially. The shaft is narrow proximally, widens distally and appears more flattened as the costal pit (for the costal cartilage) is approached. A shallow costal groove is visible on the caudal surface of the proximal half of the shaft. The cranial surface is roughened compared to the smoother caudal surface. Two breaks are visible, one immediately distal to the tubercle and the second proximal to the mid-shaft region. These breaks occurred during preparation of the specimen and do not affect the measurements of the parts of the rib.

The differences between the features of the ribs of *V. chama* and *O. megalotis* are subtle (Figure 5). However, based on the observed non-metric features, there is a closer affinity of U.W. 88-813 with *V. chama* than with *O. megalotis*. The main metric variable (from our admittedly small sample of two *O. megalotis* and four *V. chama*) that supports this affinity is neck shape (neck ventro-dorsal/cranio-caudal). By this ratio, *O. megalotis* exhibits a rounder cross-section ratio of $\mu = 1.25$ ($\sigma = 0.002$) than either U.W. 88-813 (1.52) or *V. chama* ($\mu = 1.52$, $\sigma = 0.18$). This qualitative and quantitative affinity extends to other morphologies and measures but the intraspecific variability exhibited by the ribs of modern foxes does not allow this element to be very diagnostically useful. Based on its taphonomic association with U.W. 88-812 and 814 (these three specimens come from the same breccia block and are the only carnivoran material from Malapa of this size range), and the fact that this rib falls within the morphospace of vulpines of this size, we believe that it is parsimonious to include it in *V. skinneri*.

The Malapa fox can be qualitatively distinguished from the larger African canids (genera *Canis sensu lato* and *Lycaon*) by its smaller size. Likewise, it is larger than the North African fennec fox (*V. zerda*). It can be distinguished from the genera *Otocyon* and *Nyctereutes*, both of which were potentially present in southern Africa around 2 Ma (though the raccoon dog is disputed; Reynolds, 2012), by its lack of a subangular lobe. It is also dentally distinct from both taxa, especially *Otocyon* which has a supernumerary molar and hypocarnivorous teeth with tall, piercing cusps (Figure 7). It is morphologically similar to *V. chama*, though it differs in some metric comparisons. Importantly, it differs from all these taxa (and perhaps all modern canids) in its complete lack of a distal accessory cuspid on the fourth lower premolar, a feature not found in any canid we have studied, nor by others in large samples of *V. vulpes* (Szuma, 2002; Nentvichova and Andera, 2008). It also differs from all modern *Vulpes* in the height of the M_1 metaconid; though broken, it was clearly more than half the height of the protoconid.

Metric comparisons

Quantitatively, the Malapa fox falls within the size range of *V. chama* for all linear metrics and is metrically more similar in size to *V. chama* than it is to other members of the genus (Figure 8). However, it is distinguishable from *V. chama* by several ratios (and is more similar in relative proportions to *V. zerda*, though considerably larger; Figure 8). The most substantial quantitative difference between the Malapa fox and *V. chama* is the relationship between the size of the M_2 (a geometric mean of M_2 L and W) and the length of the M_1 (particularly its trigonid). This ratio emerges as an important factor in a PCA, including all of the specimens in the sample and all dental lengths and widths (Figure 9 and Table 2). In the bivariate plot of PC 1 (accounting for 68.8% of the variation and driven entirely by size – though influenced more by the P_4 and M_1 than the M_2) and PC 2 (accounting for 13.7% of the variation and predominantly driven by an inverse relationship between M_2 measurements and M_1 lengths – L and Trigonid L), *V. skinneri* is outside of the range of *V. chama*. Thus, based on a global analysis of all specimens and all dental lengths and widths, the Malapa fox is beyond the periphery of the range of what may be its modern descendent. (PC 3, driven by an inverse relationship between P_4 measurements and M_2 L, does not sort any of the species into logical patterns and is therefore not shown.)

When the driving factors of PC 2 (M_1 trigonid length inversely related to M_2 area) are examined separately, this positioning of the Malapa fox in the periphery of the range of *V. chama* is confirmed (Figure 10). The fact that the

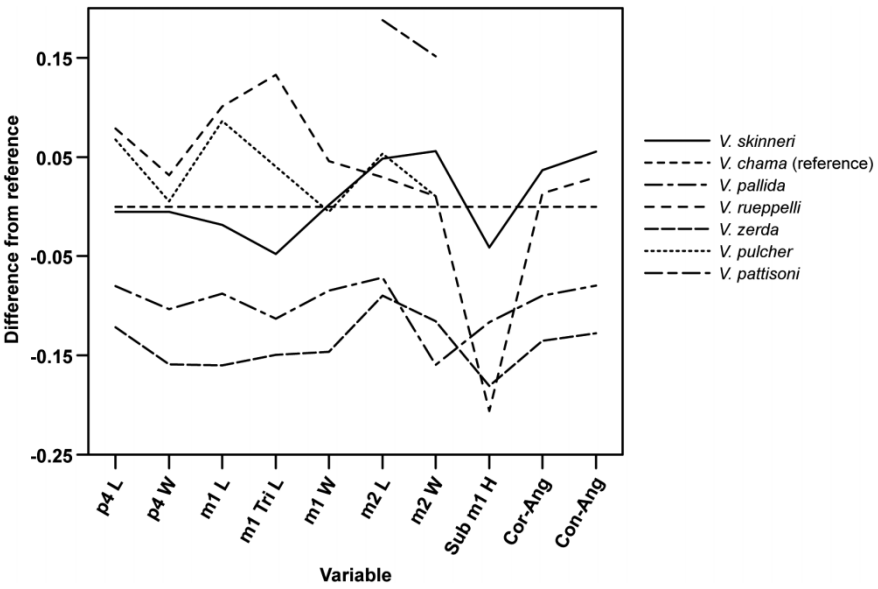

Figure 8. Ratio diagram of select metrics. Note that *V. skinneri* is generally most similar in size to *V. chama;* however ignoring size, it is most similar in shape to *V. zerda*. Importantly, *V. skinneri* and *V. chama* are no more similar than other species in the data set that are generally agreed to be distinct species.

relationship between the M_1 trigonid length and the M_2 occlusal area is driving this variation – particularly that it separates *V. skinneri* from *V. chama* – is important. Though it may seem inappropriate to compare a length and an area in this manner simply to illustrate an emergent statistical finding, these variables are functionally significant, in that the M_1 trigonid is the functional region that relates most specifically to the consumption of flesh (Van Valkenburgh, 1989, 1996; Hartstone-Rose, 2008), while the molar grinding surfaces (M_1 talonid, M_2 and M_3 areas) are the regions that correspond most directly to omnivory in carnivorans (Hartstone-Rose, 2008). By this measure, *V. skinneri*, with its large M_2 area relative to its M_1 trigonid length, may have been more omnivorous than the slightly more hypercarnivorous *V. chama*.

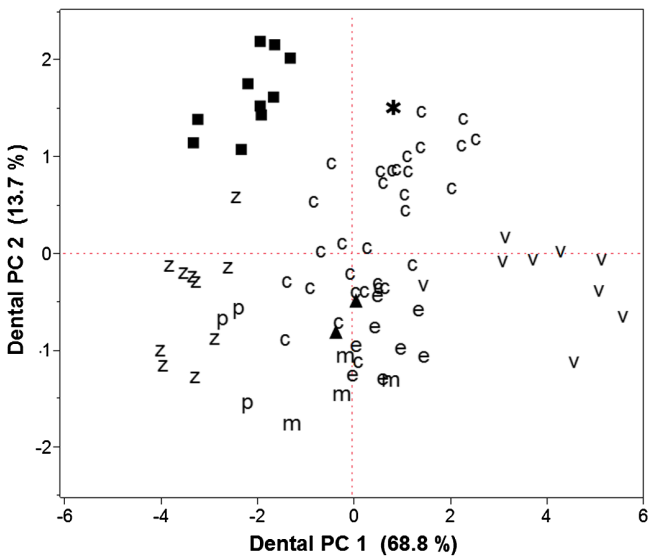

Figure 9. Bivariate plot of first two dental principal components. All specimens were equally weighted and P_4, M_1 and M_2 length, width, and M_1 trigonid length were included. Eigenvectors in Table 2. Asterisk = U.W. 88-812/814, c = *V. chama*, p = *V. pallida*, z = *V. zerda*, m = *V. macrotis*, e = *V. velox*, v = *V. vulpes*, squares = *O. megalotis*, triangles = *N. procyonoides*. None of the other fossil specimens were complete enough to include in the principal components analyses.

Simple comparisons also bear this out. For instance, *V. skinneri* is the only species of *Vulpes* to have an M_2 that is much longer than the M_1 trigonid. Furthermore, the length of the M_1 talonid, combined with the length of the M_2 (i.e. the crushing regions that are preserved in these specimens), is more than 1.6 times the length of the M_1 trigonid, while this ratio is 'only' 1.3 in *V. chama*.

Though not driving forces in the variation (i.e. they do not emerge as major factors in any principal components), the heights of the condyle and coronoid processes also clearly separate the Malapa fox from *V. chama* when plotted against another size variable – especially the small M_1 lengths (Figure 11). Given that both condyle and coronoid heights are measured from the inferior margin of the mandibular angle (Figure 6), the similarity of the segregation of the Malapa fox from the *V. chama* sample by both these variables is less attributable to the height of the condyle and coronoid than it is to the size and ventral projection of the angle. In other words, these metrics (as seen in Figure 11 and the similar Con-Ang graph, not shown) quantify the size of the apparently more substantial mandibular angle present in the U.W. 88-812 specimen (compare Figure 7 A and B).

Table 2. Dental principal component eigenvectors.

Variable	PC 1	PC 2	PC 3
p4 L	0.41966	−0.24174	−0.02692
p4 W	0.36830	0.18810	**−0.50819**
m1 L	0.41133	**−0.36775**	0.14859
m1 Tri L	0.39046	**−0.46149**	0.09213
m1 W	0.41813	0.10915	−0.19600
m2 L	0.29665	**0.39136**	**0.80206**
m2 W	0.32211	**0.62681**	−0.16951

*Boldface numbers indicate the most significant variables determining the structure of PC2 and PC3.

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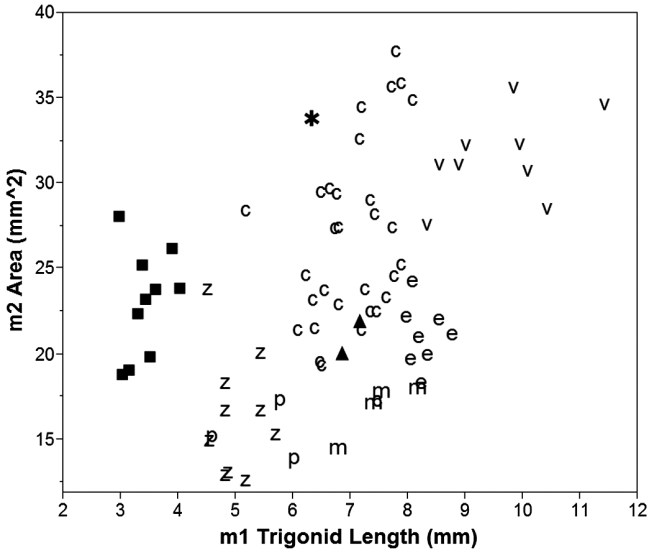

Figure 10. Bivariate plot of M_1 Trigonid L against M_2 L × W. See Figure 7 for key.

DISCUSSION

Two extinct species of fox have been described from the South African Early Pleistocene cave sites, both of them by Broom (1939, 1948). One, *Vulpes pulcher* from Kromdraai A and possibly Swartkrans), is noted by both Broom (1939) and Ewer (1956) to be significantly larger than extant *V. chama*. Even though Figure 8 shows this to be true only of certain variables, dentally the Malapa specimen is closer in size to the extant species. This size difference, as well as the differences in dental proportions, makes it unlikely that the Malapa fox is conspecific with *V. pulcher*. Additionally, the P_4's of both specimens of *V. pulcher* (KA 1289 and SK 236, both in the Ditsong Museum collection) have the distal accessory cusp, which is noticeably absent from the Malapa specimen.

The second species is *V. pattisoni*, described by Broom (1948) on the basis of a lower jaw fragment with an M_2 and alveoli for C_1-M_1 (Broom, 1948, Figure 15 A, B; here reproduced as part of Figure 12). Broom's (1948) description of the specimen is as follows (in its entirety):

> This little fox is almost exactly the same size as the living *Vulpes chama*, but the teeth as judged by the sockets differ appreciably. The canine in the fossil form is distinctly larger than in the living *V. chama*, and the first premolar is much nearer to the canine. As will be seen by the drawings given the fossil form differs considerably from that in *V. chama* in the arrangement of the teeth. From the front of the first premolar socket to the back of the 2nd molar the measurement is 41.5 mm (pp. 22–23).

We are not entirely sure what Broom (1948) meant in saying that the arrangement of the teeth in *V. pattisoni* differs considerably from that in *V. chama*. However, we believe that his comment boils down to a statement that the diastemata between the cheek teeth are smaller in the fossil than in the extant species. This is confirmed by first-hand study of the specimen, housed in the Ditsong Museum of Natural History, Pretoria (Figure 12 C).

Thus, Broom (1948) provides two characters on which to diagnose *V. pattisoni*: a larger lower canine than in *V. chama* and cheek teeth more crowded together. Neither of these characters can be considered particularly significant or diagnostic, not only with regard to comparisons between *V. pattisoni* and *V. chama*, but between the former and any small species of Vulpini. Our inspection of the holotype of *V. pattisoni* confirms that Broom's figure is fairly accurate regarding the M_2 morphology (compare the drawings with the photograph in Figure 12). However, the M_2 of *V. pattisoni* is much larger than any of the species in our comparative sample (Figure 8). Its proportions are also different from the M_2 of *V. skinneri* in that it is relatively more slender than the M_2 of *V. chama* (the standard in Figure 8), while the M_2 of *V. skinneri* is broader. Though M_2 is highly variable in some vulpines (e.g. *V. vulpes*; Szuma, 2002), we believe that its size and proportions in the *V. pattisoni* holotype, and the size and crowding of the alveoli of its other teeth, suggest two things: first, that the Malapa fox is not conspecific with *V. pattisoni*, and second, that the *V. pattisoni* holotype is likely a juvenile, which would explain the relatively crowded cheek teeth. In summary, the Malapa fox material does not match any of the named fossil Vulpini from South African sites.

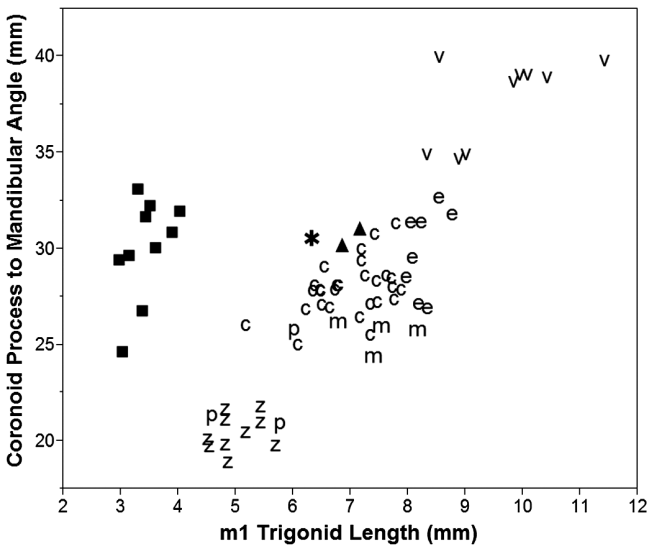

Figure 11. Bivariate plot of M_1 Trigonid L against the Height of the Coronoid Process. The plot of M_1 Trigonid L against the Height of the Mandibular Condyle looks very similar. See Figure 7 for key.

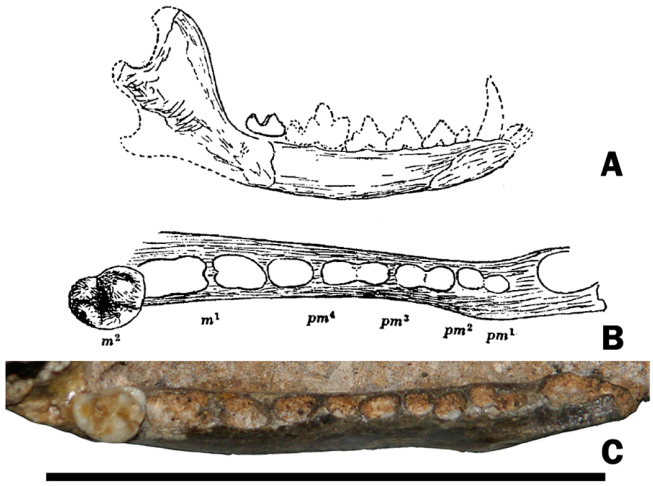

Figure 12. Illustrations that accompanied Broom's (1948) description of *V. pattisoni* (A and B; Figure 15 in Broom, 1948) and photograph of type specimen (C). The scale bar (10 cm) corresponds to the photograph.

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Malapa has yielded some of the most important fossils to be found in South Africa in recent years. The *Au. sediba* specimens continue to reveal significant information about hominin evolution. The taphonomic preservation at the site – substantially better than material from any other site in the Cradle of Humankind World Heritage site – has resulted in an accumulation of specimens that are remarkably complete (several mammalian families are represented by collections of multiple skeletal elements from single individuals) and exquisitely detailed (including microscopic structures not often preserved). The carnivore sample (Kuhn *et al.*, 2011) exemplifies both of these phenomena, preserving associated elements of a felid, a hyaenid and now a canid, as well as preserving small detail including the first recorded fossil specimen of the diminutive *Felis nigripes* and now this delicate fox. Though only these three elements (mandibular fragment, M_2 and rib) have been recovered thus far, these specimens show clear evidence of a new species: *V. skinneri,* which is similar in size to the modern *V. chama*, but has a large M_2 relative to the M_1 trigonid, and a more substantial mandibular angle. Most distinctively, *V. skinneri* completely lacks a distal accessory cuspid in its P_4 – a morphological condition apparently unique among all canids. Thus, *V. skinneri* is the second new species (after *Au. sediba*) to be described from this site.

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