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The carnivore guild circa 1.98 million years: biodiversity and implications for the palaeoenvironment at Malapa, South Africa

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Abstract The Malapa fossil assemblage was likely accumulated as a result of a death trap. Given this, the carnivoran species found there must have lived in proximity, close proximity for the smaller species, to the site, offering the possibility of expanding our interpretation of the habitats available to *Australopithecus sediba* via pinpoint palaeoenvironmental interpretation. To date, the identified carnivorans are the most abundant identified non-hominin taxa at Malapa, and given their territorial behaviour, are important when interpreting the palaeoecology of the site. The extinct false saber-tooth felid (*Dinofelis barlowi*) suggests that the presence of closed environments and the ancestral form of modern water mongoose (*Atilax mesotes*) indicates the presence of water in the vicinity. Canids generally support the presence of open habitats. The first appearance in the fossil record of *Vulpes skinneri* and *Felis nigripes* indicates the presence of drier open grassland/scrub. The Malapa carnivorans support widespread shifts in carnivore turnover circa 2.0 Ma in Africa and suggest, together with other lines of evidence, the occurrence of a regional transitioning environment during the time of *Au. sediba*.

Keywords Paleoecology · Carnivore · Malapa · *Australopithecus sediba*

Introduction

The Malapa fossil locality, north of Sterkfontein and Swartkrans and due east of Gladysvale (Fig. 1), has yielded a rich assemblage of *Australopithecus sediba* and non-hominin vertebrate fauna (Berger et al. 2010; Dirks et al. 2010; Kuhn et al. 2011). The mosaic nature of *Au. sediba* anatomy, deemed a *Homo*-like *australopith*, together with its geological age of ~1.98 Ma, suggests that this taxon is a potential candidate to occupy a key evolutionary place in the *Australopithecus*-*Homo* transition (Kivell et al. 2011; Kibii et al. 2011; Zipfel et al. 2011; Pickering et al. 2011a; Berger 2013; Churchill et al. 2013; Schmid et al. 2013; DeSilva et al. 2013). The associated vertebrate fauna is also remarkable, representing a taxonomically diverse assemblage that includes new species as well as last-and-first appearances of taxa in the Plio-Pleistocene fossil record. To date, the identified Carnivora dominate the Malapa assemblage. The identified bovids, equids, and non-hominin primates are less abundant and hence the ecological interpretations of Malapa benefit from assessments of the adaptations and habitats associated with the carnivoran clade. Here, we review the ecology at Malapa using the carnivorans as an environmental proxy and further describe the surrounding palaeoenvironments using data derived from isotopic analysis and identification of fossilized plant remains in support of the carnivoran assemblage.

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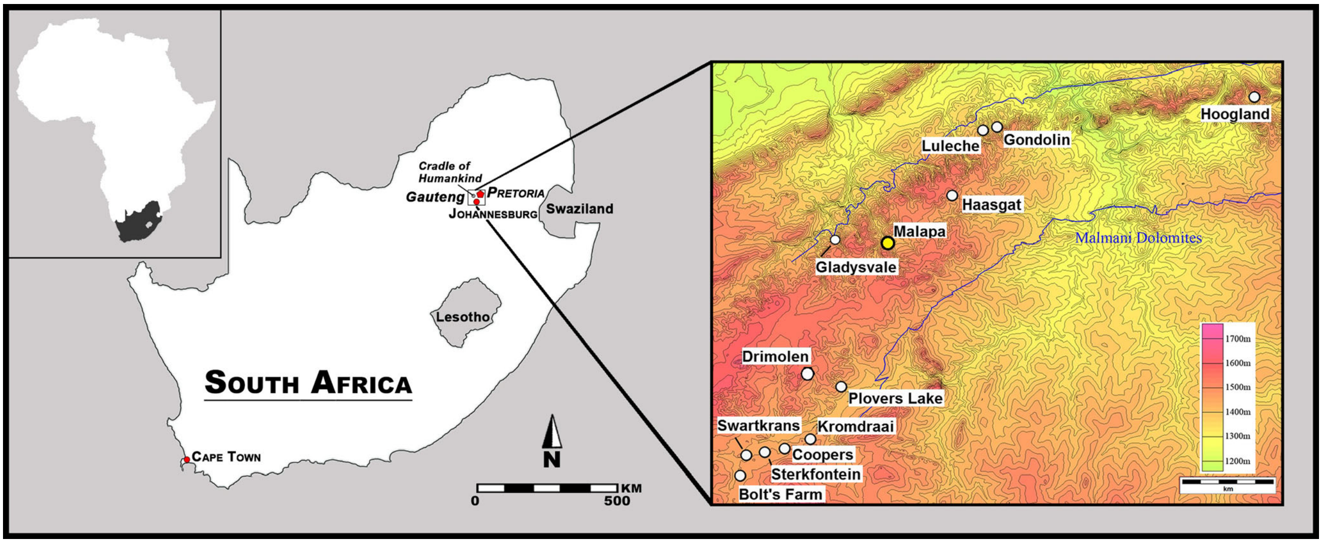

Fig. 1 Map showing location of Malapa in relation to other fossil sites located within the Cradle of Humankind (modified from Adams et al. 2010)

Sedimentological and geochronological data support the hypothesis that Malapa should not be considered a widely spread, time-averaged deposit (Dirks et al. 2010). These data provide strong support for the view that Malapa was a likely death trap with rapid deposition and cementation of the skeletal material deposited on the cave floor (Dirks et al. 2010). The same authors have hypothesised that the cave system had vertical openings with no other egress, thus the scenario of animals falling in and expiring either on impact or over a short period of time. The vertebrate assemblage is characterised by fairly complete pieces, often including articulated post-cranial remains consistent with limited transport of the vertebrate remains before deposition (Berger et al. 2010; Dirks et al. 2010; Kuhn et al. 2011). Thus, it is reasonable to suggest that the carnivoran taxa lived in relatively close proximity to the cave. The tight temporal window represented by this assemblage enables us to assess the range of habitats likely available to *Au. sediba*. The carnivoran sample recovered from Malapa to date contains eleven taxa, six of which are identified to species, three to genus, and two only to family (Table 1). Of note are the last recorded appearance of *Dinofelis barlowi* and the first recorded appearance of the black-footed cat (*Felis nigripes*) and the new fox species, *Vulpes skinneri* (Hartstone-Rose et al. 2013; Kuhn et al. 2011). These data on the last and first appearances at Malapa support widespread turnover in the African carnivore guild close to 2.0 Ma in Africa (Lewis and Werdelin 2010).

The Malapa carnivores and their environments

Habitat-generalist (eurytopic) taxa found at Malapa include the brown hyaena, *Parahyaena brunnea* (Kuhn et al. 2011). Brown hyaenas today are found from the arid beaches of Namibia (Wiesel 2006; Kuhn et al. 2008), to the Kalahari Desert (Owens and Owens 1978; Mills and Mills 1978), to the environments on the outskirts of Johannesburg and Pretoria, South Africa (Kuhn 2014). Considering the adaptability of the brown hyaena today, its presence is of limited use in establishing the habitat surrounding Malapa.

Members of the family Felidae identified at Malapa provide two distinct interpretations of the nearby habitats. Eurytopic large felids identified at Malapa are the leopard (*Panthera pardus*) and a specimen identified simply as a large felid (Kuhn et al. 2011). Leopards are a highly adaptable species, occupying environments as diverse as arid deserts to rainforests (Skinner and Chimimba 2005; Hunter and Barrett 2011). Therefore, the presence of *P. pardus* at Malapa is consistent with the presence of either open or closed habitats or both and is of little use in interpreting the habitat surrounding Malapa. The presence of *Dinofelis barlowi*, a taxon characterised by short distal limb elements, which suggests a grappling, ambush hunter, and is suggestive of closed environments (Lewis 1995, 1997; Marean and Ehrhardt 1995; Turner and Antón 1997; Werdelin and Lewis 2001; Berger and Lacruz 2003; Lacruz et al. 2006) within its home range. The brachial index of the known *Dinofelis* skeletons portrays an animal with relatively short, robust forelimbs capable of greater force than those of extant leopards, suggesting a forelimb-driven hunting strategy similar to that of other machairodont felids, such as *Megantereon* and *Smilodon* (Marean and Ehrhardt 1995; Lewis 1997; Turner and Antón 1997; Werdelin and Lewis 2001). The lack of cursorial specialisations, combined with powerful forelimbs, further suggests adaptations to relatively closed habitats, where *Dinofelis* could be a more effective ambush predator (Marean and Ehrhardt 1995; Lewis 1997; Turner and Antón 1997; Werdelin and Lewis 2001).

The presence of black-footed cat, *Felis nigripes*, represents its first and only appearance in the fossil record to date. *F. nigripes* is a South African endemic species with highly constrained home ranges (males ~20 km^2, females ~10 km^2)

Table 1 Carnivora species identified at Malapa and their associated environmental niche

Family	Taxon	Environment
Hyaenidae	*Parahyaena brunnea*	Eurytopic but includes grasslands/savannah and semi-arid environments
Felidae	*Dinofelis barlowi* Extinct	Heavy tree cover
	Panthera pardus	Eurytopic but includes grasslands/savannah and semi-arid environments
	Felis nigripes	Grasslands/savannah, scrub, arid and semi-arid environments
	Large Felidae indet.	Unknown
Viverridae	cf. *Genetta* sp.	Eurytopic but includes grasslands/savannah and semi-arid environments
Herpestidae	*Atilax* cf. *mesotes* Extinct	Modern congener prefers a wet environment
	cf. *Cynictis*	Semi arid to arid grasslands, fynbos heath and open bushland
	cf. *Rhynchogale*	Open savannah, open woodland, and open bushland
Canidae	*Vulpes skinneri* Extinct	Grasslands/savannah, scrubland, fynbos—arid and semi-arid environments
	Larger Canidae indet.	In Africa tending toward grassland/savannah open woodland and other arid and semi-arid environments

See text for discussion of environmental assessments and references used to create them

(Macdonald et al. 2010). Their habitat is restricted to semi-desert, Karoo scrub, dry savannah, and open short-grass habitats, and the animal seeks vegetation cover during the day (Skinner and Chimimba 2005; Macdonald et al. 2010). Black-footed cats are highly susceptible to habitat loss (Silwa et al. 2010) and so are key habitat indicators. Thus, assuming their behaviour has not radically changed, their presence at Malapa indicates that the cave itself was located in close proximity to an arid to semi-arid grassland/scrub at the time of deposition.

A species referable to *Genetta* is present at Malapa. *Genetta* is a widespread genus, with species inhabiting a variety of environments (Lariviére and Calzada 2001; Skinner and Chimimba 2005). Both *G. genetta* and *G. tigrina* currently occur in the region surrounding Malapa (Skinner and Chimimba 2005; Kuhn 2014) and inhabit all of the likely biomes surrounding Malapa during the time of deposition (Lariviére and Calzada 2001). Thus, the presence of *Genetta* sp. at Malapa cannot be used to refine environmental characteristics associated with the assemblage but may suggest that the habitats surrounding Malapa have changed little over time, which being grasslands in close association with thick woodlands supported by spring-fed water sources.

Three genera of mongoose (Herpestidae) have been found at Malapa. Two of these may represent species of *Cynictis* and *Rhynchogale* although the available material is insufficient to ascertain species attribution, while the extinct, *Atilax* cf. *mesotes*, is represented by more diagnostic material (Kuhn et al. 2011). The extant *Cynictis penicillata* inhabits semi-arid to arid grasslands, fynbos heath and open bushland, and maintains home ranges of 0.1–1.02 km^2 (Skinner and Chimimba 2005; Hunter and Barrett 2011). The extant *Rhynchogale melleri* is known from open savannah, open woodland, and open bushland, but more recent evidence suggests that it may have a broader tolerance of habitats, including open grassland (Skinner and Chimimba 2005; Hunter and Barrett 2011). The presence of termitaria of the genera *Macrotermes* and *Hodotermes* is important to the distribution of *R. melleri* (Skinner and Chimimba 2005; Hunter and Barrett 2011) as these insect genera are generally found in open woodland and grassland. The third Malapa herpestid, *Atilax* cf. *mesotes*, is an extinct species whose only modern congener is *A. paludinosus*, the marsh mongoose. As the common name suggests, *A. paludinosus* is usually found along rivers, streams, marshes, swamps, and tidal estuaries, but specimens have been found up to half a kilometre from water sources (Skinner and Chimimba 2005).

Two canids are known from Malapa. They include a large-sized form represented by a femoral fragment and the smaller *Vulpes skinneri*. The extant African fauna includes two species of canid of a comparable size to the Malapa femur, *Lycaon pictus and Canis simensis*. Fossils of the *Lycaon* genus have been previously reported in the Cradle of Humankind (Broom 1948; Hartstone-Rose et al. 2010; Werdelin and Peigné 2010), but the Malapa fragment is not adequate for diagnosis below the family level. While the Malapa specimen can only be identified as canid, in Africa, large canids are generally indicative of grassland/savannah or open woodland environments. The genus *Vulpes* includes a number of species that show clear preference for open habitats and semi-arid to arid conditions and commonly occupy small home ranges. The lone exception to this is *V. vulpes*, which has proven to be an extremely adaptable species (Hunter and Barrett 2011). The most important feature that sets *V. skinneri* apart from all other members of the genus *Vulpes* (both extant and extinct) is the lack of the distal accessory cusp on the P_4 (Hartstone-Rose et al. 2013).

Considering that this feature is present in all other *Vulpes*, including the oldest African species *V. riffautae* (de Bonis et al. 2007), it must be considered a derived feature of *V. skinneri* that disqualifies it from the direct ancestry of extant cape fox, *V. chama*. However, since *V. skinneri* shares many traits with *V. chama*, we hypothesise that they shared a recent common ancestor and likely inhabited similar environments characterised by semi-arid to arid habitats (Hunter and Barrett 2011), with relatively small territory sizes up to 32.1 km^2 (Skinner and Chimimba 2005).

Carnivoran guild level assessment of Malapa

The carnivoran guild of Malapa is taxonomically diverse, including members of all the extant terrestrial families of African carnivores except Mustelidae (Kuhn et al. 2011)—a rare group in the Cradle of Humankind fossil record (Brain 1981) aside from Bolt's Farm and Plovers Lake (Werdelin and Peigné 2010). It is also diverse in feeding ecology and body size range, including large carnivores previously found in the region (e.g. *D. barlowi* at Sterkfontein, Mb 4), and a diverse assemblage of small species, including small herpestids, viverrids, and two taxa hitherto unknown in the fossil record, *F. nigripes* and *V. skinneri*.

The environmental signature of the Malapa carnivore guild is mixed featuring grassland, woodland, and water in close proximity to the cave, following previous suggestions based upon non-carnivore fauna (Reynolds and Kibii 2011). Although a direct comparison to other environmental reconstructions such as Sterkfontein, based upon migratory bovids and pollen from time averaged deposits, would be remiss as Malapa is a snapshot of that particular environment at a specific time. Some species, such as *V. skinneri*, *F. nigripes*, and the tentatively identified *Cynictis*, indicate the presence of semi-arid grasslands and scrub lands in direct association with the cave. An open habitat may also be inferred from the presence of the larger canid at the site. On the other hand, the identification of *Atilax* suggests standing water within about half a kilometre of the cave, and the existence of *Dinofelis barlowi* infers the occurrence of relatively closed or wooded areas in the vicinity of the cave. The remaining Malapa carnivores are highly eurytopic and so less relevant as habitat descriptors. What the specific carnivores can tell us is that Malapa, at 1.98 Ma, sits in a space where both riverine wooded areas and the beginnings of more arid scrublands/grasslands met.

The larger carnivore species represented at Malapa are similar to those of the older Sterkfontein Mb. 4 assemblage circa 2.6–2.0 Ma (Herries et al. 2010), which includes *D. barlowi*, *P. pardus*, and *P. brunnea*. The younger assemblages of Swartkrans Mb. 1 at 1.9–1.8 Ma (Pickering et al. 2011b) and Kromdraai A at 2.0–1.5 Ma (Vrba 1982; McKee et al. 1995) have also recorded *P. pardus* and *P. brunnea*, but *D. barlowi* is there replaced by *D. piveteaui*. However, ecomorphological data does not indicate any substantial differences in habitat adaptations between these *Dinofelis* species (Werdelin and Lewis 2001). Among the smaller carnivores, *Vulpes* and Felidae are represented at Sterkfontein by *V. chama* at Jacovec Cave; <2.4 Ma (Herries et al. 2013) and *Caracal caracal* at Mb. 2; 2.6–2.2 Ma (Herries et al. 2013). In addition, *Genetta genetta* has been identified from Jacovec Cave, Sterkfontein. On the other hand, *Atilax mesotes* is not known from sites older than 2 Ma but is known from Kromdraai A (<2 Ma), which is the type-site for the species. A broader analysis (Lewis and Werdelin 2010) has suggested that there is increased turnover among South African carnivores at about 2 Ma, and the Malapa assemblage may lie just at the cusp of this event as we see the last *D. barlowi* and the first appearance of *F. nigripes*.

The *Au. sediba* environment

An analysis of a coprolite (likely from a carnivore) recovered from the site identified the presence of fossilized woody remains of *Podocarpus*/*Afrocarpus* spp. among other plant material (Bamford et al. 2010). *Podocarpus*/*Afrocarpus* are conifer genera associated with moist forested areas of abundant rainfall (Bamford et al. 2010). Sediment samples from the hominin layers indicate C_4 grasses of the type found in summer rainfall areas, while the analysis of enamel samples from Malapa Hominin 1 and Malapa Hominin 2 indicate a purely C_3 diet which includes sedge phytoliths (Henry et al. 2012). Of the plants represented here, those with edible rhizomes are mostly perennial and inhabit permanent or seasonal wetlands, whereas sedges from sites with impeded drainage tend to be annual and have small roots or rhizomes. One palm phytolith from the family Arecaceae was also recovered, and these trees require high water tables. Carbon isotope analyses of both bovid and rodent remains also indicate C_4-based diets (Henry et al. 2012). These data support the presence of nearby woodland and grassland in the vicinity of Malapa but also likely suggest mildly cooler temperatures than at present. Lower temperatures and perhaps a degree of relative aridification of Southern Africa were also reported based on the analysis of pollen in deep-sea cores off the Namibian coast between 2.2 and 2.0 Ma (Dupont et al. 2005; Dupont 2006). Other sources identified an early Pleistocene climate cooling with development of a stronger atmospheric circulation circa 2.2–2.0 Ma (Etourneau et al. 2010), whereas aridification related to the intensification of the Walker Circulation (east-west atmospheric circulation along the equatorial belt) was detected at 1.8–1.7 Ma (Hopley et al. 2007). These drier/cooler conditions identified during the deposition of Malapa are similar to those described for the broadly contemporaneous Sterkfontein M5 deposit but not with the older Sterkfontein M4 (Herries et al. 2010; Herries and Shaw 2011). However, both

Sterkfontein M4 and Malapa have recorded the presence of fossilized wood remains (Bamford 1999; Bamford et al. 2010). Clearly climatic conditions around the deposition of Malapa were indicative of a cooling trend. Such drier conditions are consistent with the appearance at Malapa of *V. skinneri* and *F. nigripes*. The occurrence of obligate grazers such as *Equus* and the large alcelaphine *Megalotragus* (Dirks et al. 2010) confirms the presence of open grasslands in the greater region.

Conclusion

The Malapa palaeoenvironment has been previously described as likely including areas of abundant grass and woody vegetation (Henry et al. 2012). The carnivore assemblage thus provides additional evidence for open semi-arid to arid grasslands in direct association with the cave given the small home ranges of *F. nigripes* and *Cynictis* as well as the presence of *V. skinneri*. The presence of *A. mesotes* also suggests that within a short distance, there was a source of water. Thus, the Malapa cave was likely situated either in open habitat or the transitioning ecozone between the open grasslands and the more wooded environments along the edge of the valley previously described by Dirks et al. (2010), with pools of standing water or marsh (quite possibly spring-fed systems) in close proximity. Although the presence of *D. barlowi* likely indicates closed environments, the putative large home ranges for this large body-sized carnivore (Werdelin and Lewis 2001) make a determination of the proximity of this habitat to the cave unclear. *Podocarpus*/*Afrocarpus* provides strong evidence for wooded or forested habitats within the range of *D. barlowi* and *Au. sediba*, confirming another biome in the region. The functional upper limb and thoracic anatomy of *Au. sediba* is indicative of adaptations to tree climbing associated with closed environment (Churchill et al. 2013; Schmid et al. 2013). These data suggest that the full range of palaeoenvironmental conditions available to *Au. sediba* were characterised by wooded areas rich in C_3 grasses and sedges as well as open grasslands and standing water nearby. It may thus be important to consider that the continuous aridification of Southern Africa possibly post ca. 1.9 Ma was a key evolutionary constraint in the putative transition from *Australopithecus* to *Homo* and may also be indicative of changes in the carnivore guild at that time.

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Compliance with ethical standards

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