Eucyon khoikhoi sp. nov. (Carnivora: Canidae) from Langebaanweg 'E' Quarry (early Pliocene, South Africa): the most complete African canini from the Mio-Pliocene

ALBERTO VALENCIANO[1,2,3,*], JORGE MORALES[4] and ROMALA GOVENDER[1,2]

[1]*Research and Exhibitions Department, Iziko Museums of South Africa, Cape Town, South Africa*
[2]*Department of Biological Sciences, University of Cape Town, Palaeobiological Research Group, Cape Town, South Africa*
[3]*Departamento de Ciencias de la Tierra and Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, Zaragoza, Spain*
[4]*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain*

A new medium-sized canid, **Eucyon khoikhoi sp. nov.**, is described from the early Pliocene site of Langebaanweg 'E' Quarry (South Africa). It possesses a robust dentition with large upper- and lower-second molars, an m1 talonid without a transverse cristid between the entoconid and the hypoconid, and a well-developed hypoconulid shelf. Our cladistic analysis of the earliest better-known African canini, places *E. khoikhoi* as the most basal taxon of an African clade composed of *E. wokari*, ?*Nyctereutes barryi*, ?*Schaeffia mohibi* and *Schaeffia adusta* (living side-striped jackal). We suggest an alternative arrangement for the poorly known East African *E. intrepidus* from the Late Miocene and *E. kuta* from the Middle Pliocene. *Eucyon intrepidus* could belong to the same clade as *E. khoikhoi*, unlike *E. kuta*, whose dentition suggests a closer relation with the *Lupulella* group. Thus, these results support the paraphyly of *Eucyon*, demonstrating the need for an in-depth review of the genus. *Eucyon khoikhoi* has a body mass comparable to *E. kuta* and the European *E. debonisi* and *E. monticinensis*. We conclude that *E. khoikhoi* may have had a comparable role in the ecosystem to the extant hypocarnivorous *S. adusta*.

ADDITIONAL KEYWORDS: fossil – jackal – Neogene.

INTRODUCTION

Canids are one of the most diverse and cosmopolitan groups of medium- to large-size carnivorans (Wilson & Mittermeier, 2009). It is composed of at least of 23 genera and 35 species, and occupies all major terrestrial habitats on every continent except Antarctica (Sillero-Zubiri, 2009). All living Canidae belong to the subfamily Caninae Fischer, 1817, and forms a monophyletic group, but canids have two additional extinct North American subfamilies: Hesperocyoninae Martin, 1989 and Borophaginae Simpson, 1945. Caninae has a sister-group relationship with Borophaginae, and both clades link to the more primitive Hesperocyoninae (Tedford *et al.,* 2009). Caninae appear in the fossil record in the Early Oligocene of North America, almost at the same time as Borophaginae (Wang *et al.,* 1999; Tedford *et al.,* 2009), but the subfamily maintains a low diversity until the Late Miocene when the first Vulpini, *Metalopex* Tedford & Wang, 2008 and the first Canini *Eucyon* Tedford & Qiu, 1996 and *Canis* Linnaeus, 1758 are identified in North America. The cladogenesis of Caninae is coincident with its dispersal to Eurasia, which can be dated to at least 7.5 Myr with *Canis cipio* Crusafont, 1950 known from the Spanish localities of Concud and Los Mansuetos (Pons-Moyà & Crusafont, 1978). A second migration in the Old World occurs with *Eucyon* in south-western Europe in Spain (Montoya *et al.*, 2009) and in the three African localities of Kapsomin, Lukeino Fm, Kenya (Morales *et al.*, 2005), Lemudong'o, Kenya (Howell & García, 2007) and Amba East Vertebrate Locality 1, Sagantole

*Corresponding author. E-mail: a.valenciano@unizar.es

Fm, Ethiopia (Haile-Selassie & Howell, 2009). Later, during the Pliocene, the Caninae are widely recorded from both Eurasia and Africa comprising the genera *Eucyon*, *Canis*, *Nyctereutes* Temminck, 1838, *Otocyon* Müller, 1836 and *Vulpes* Frisch, 1775 (e.g. Hendey, 1974; Rook, 1992, 2009; Tedford & Qiu, 1996; Sardella, 2008; Geraads *et al.*, 2010; Sotnikova & Rook, 2010; Werdelin & Peigné, 2010; Dehghani & Werdelin, 2011; Werdelin *et al.*, 2014a, b; Piñero *et al.*, 2017; Bartolini-Lucenti, 2018; Bartolini-Lucenti *et al.*, 2018), and in North and South America, e.g. *Canis* Linnaeus, 1758, *Cerdocyon* Smith, 1839 and *Chrysocyon* Smith, 1839 (Tedford *et al.*, 2009), becoming one of the most common carnivore groups in terrestrial mammalian sites.

Canids from Langebaanweg have not been studied in detail, but Hendey (1974) described some isolated teeth as Canidae *incerta sedis*. Later, he tentatively assigned these samples to two forms, *Vulpes* sp. and aff. '*Canis*' *brevirostris*, noting the difficulty in distinguishing the 'E' Quarry civet and canid specimens (Hendey, 1981a), without specifying the catalogue numbers for each canid. According to specimen labels, and notes found in the original boxes from the 1970s, we can hypothesize that the fox that was mentioned, refers to specimen SAM-PQL-31272, 'Jessie's fox', and the fragmentary specimens SAM-PQL-69621A composed of several fragments (currently SAM-PQL-72219, and 72220), SAM-PQL-50110, 50111 and 50497. The description of these remains to vulpines is comprehensible, because of the fragmented nature of the fossils, damaged dentition does not allow a direct comparison and its gracile appearance is reminiscent of a vulpine. Although the Langebaanweg sample has never been properly described, it is briefly discussed in Rook (1993), Montoya *et al.* (2009) and Werdelin & Peigné (2010). Most of the *Eucyon* fossils came from the Muishond Fontein Pelletal Phosphorite Member (MPPM), with the exception of one fragmented forelimb (SAM-PQL-20424, 233331) that came from Langeberg Quartzose Sand Member (LQSM) (Supporting Information, Table S1). This sample is heterogeneous and varies in size and robustness, which can be explained by sexual dimorphism, like other populations of *Eucyon*, e.g. *Eucyon debonisi* Montoya *et al.*, 2009 from Venta del Moro (Late Miocene, Spain). It also includes the first deciduous dentition for the genus.

The main aim of this work is to describe the unpublished material of Canidae from Langebaanweg, which comprise one skull, several mandibles, dentition and postcranial bones. With more than 50 specimens of at least four individuals, it constitutes the largest sample of *Eucyon* from Africa and is a unique opportunity to expand our knowledge of the occurrence of the genus on the continent, such as its evolutionary relationships and palaeobiogeographical implications for the family Canidae.

THE LANGEBAANWEG FOSSIL SITE

Along the nearly 2000 km of the southern African west coast there are few onshore deposits, but where they do occur, they are rich in palaeontological and archaeological remains (Pether *et al.*, 2000; Roberts, 2006a,b). Langebaanweg (32°57′19.4″S, 18°6′49.9″E) is located on the stable platform on the west coast of South Africa, 13 km inland from the current coastline and less than 2° north of the southern tip of Africa (Hendey, 1981a, b; Roberts *et al.*, 2011). During the Late Miocene–Early Pliocene, Langebaanweg was about 1 km from the river mouth where it debouched into Saldanha Bay (Hendey, 1981b). The Varswater Formation at the 'E' Quarry spans the Middle Miocene (Langhian) to the Early Pliocene (Zanclean; Tankard, 1974; Hendey, 1989; Roberts, 2006a,b; Roberts *et al.*, 2011). The fossil-rich LQSM and MPPM are concentrated within an 'abbreviated' stratigraphic interval of *c.* 26–30 m above sea level (Roberts *et al.*, 2011: 208) and are associated with numerous transgressive–regressive episodes (Tankard, 1974; Hendey, 1989; Roberts, 2006a,b; Roberts *et al.*, 2011). The palaeoenvironmental history of Langebaanweg includes a high-energy shallow marine system during the Late Miocene (Messinian), incorporating sandy and rocky beaches represented by the Konings Vlei Gravel Member, while the earliest Early Pliocene (Zanclean), the Langeberg Quartzose Sand Member, was deposited in a lagoonal or estuarine setting protected from wave action but open to the sea (Kensley, 1972; Kensley, 1977; Roberts *et al.*, 2011). The Muishond Fontein Pelletal Phosphorite Member (MPPM), comprising Beds 3aN and Bed 3aS, accumulated in a shallow embayment sheltered from the open ocean by granitic islands during the Early Pliocene transgression (Smith & Haarhoff, 2006). Recently, a study suggested that there was a watering hole fed by an aquifer that seeped into the bedrock or in a dune depression (Brumfitt *et al.*, 2013). The bone bed accumulated during several drought cycles as animals died in the area due to starvation and were buried by sediment or as a result of downslope exposure in a low-energy environment (Brumfitt *et al.*, 2013).

The 'E' Quarry is a prime locality for palaeoecological studies, because it has yielded a rich Early Pliocene (5.2 Mya) faunal assemblage and palaeopalynological information during a period of change from moderate to cooler climates (Hendey, 1976, 1981a, b; Roberts *et al.*, 2011). Langebaanweg ranks among the richest Neogene fossil vertebrate sites in Africa and in the world (Hendey, 1981a; Werdelin, 2010), comprising

more than 230 taxa of invertebrates and vertebrates (Hendey, 1981a, 1989). Langebaanweg also has an outstanding record of Carnivora (Werdelin, 2006). After Hendey completed the first monographic studies on the mammals of Langebaanweg (Hendey, 1972, 1974, 1976, 1978a, b, c, 1980, 1981a, 1989), this fauna became a reference for Mio-Pliocene studies of carnivorans.

There are at least 19 species of carnivorans in MPPM and LQSM (Werdelin, 2006), comprising mustelids, canids, one hemicyonid/ursid (*Agriotherium* Wagner, 1837), pinnipeds, felids, hyaenids, herpestids and viverrids, with the larger ones better known (Werdelin *et al.*, 1994; Werdelin & Lewis, 2001; Morales *et al.*, 2005; Werdelin, 2006; Werdelin & Sardella, 2007; Stynder, 2009; Govender *et al.*, 2011, 2012; Tseng & Stynder, 2011; Oldfield *et al.*, 2012; Stynder *et al.*, 2012, 2018; Hartstone-Rose & Stynder, 2013; Stynder & Kupczik, 2013; Govender, 2015; Hartstone-Rose *et al.*, 2016; Valenciano & Govender 2020a, b).

ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; ICP, Institut Català de Paleontologia Miquel Crusafont, Barcelona, Spain; IPS, collection from the ICP; F:AM, collection housed in the Frick Collection of the Division of Paleontology, AMNH, New York, USA; ISAM, Iziko South African Museum, Cape Town, South Africa; KNM, Nairobi National Museum, National Museums of Kenya, Nairobi, Kenya; MGUV, Museu de Geologia de la Universitat de València, Burjassot, Spain; MNCN, Museo Nacional de Ciencias Naturales Madrid, Spain; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; SAM-PQL, Quaternary Palaeontology (Langebaanweg), Iziko South African Museum, Cape Town, South Africa; SAM-ZM, Zoology Mammals, Iziko South African Museum, Cape Town, South Africa; VAL, Anatomical Museum of Valladolid University, Valladolid, Spain.

MATERIAL AND METHODS

NOMENCLATURE AND MEASUREMENTS

Dental nomenclature follows Ginsburg (1999), Smith & Dodson (2003) and Tedford *et al.* (2009). Anatomical descriptions are based primarily on Barone (1999, 2000) and Evans & de Lahunta (2010, 2013), and the terminology conforms to the standard of the *Nomina anatomica veterinaria* (NAV; Waibl *et al.*, 2005). Measurements were taken using Mitutoyo Absolute digital callipers to the nearest 0.1 mm (Tables 1–3; Supporting Information, Fig. S1; Table S2).

STUDY MATERIAL

We have re-analysed the material described by Hendey (1974) as Canidae *incertae sedis*, and the new material of this family housed in the Cenozoic collections at the Iziko South African Museum (ISAM). The comparative sample includes original fossils of: *Eucyon debonisi* Montoya *et al.*, 2009 from Venta del Moro (Spain), comprising dentition and fragmentary mandibles housed at MNCN and MGUV (Montoya *et al.* 2009), and the two M1 of *Eucyon intrepidus* Morales *et al.*, 2005 from Lukeino Fm (Kenya) housed at Orrorin Community Organization, Kipsaraman, Baringo County, Kenya; *Canis cipio* Crusafont, 1950 (IPS 1988, maxilla) from the Late Miocene of Concud (Spain) and an isolated m1 (IPS 46489) from Los Mansuetos (Spain), both *c.* 7.1–7.9 Mya housed at ICP (Pons-Moyà & Crusafont, 1978); crania, mandibles and dentition housed at AMNH of *Eucyon davisi* (Merriam, 1911) (F:AM 63007, 63009, 630, 09B, 63038, 63058) from the Late Miocene of North America, *Eucyon davisi* from the Pliocene of China (F:AM 97028, 97027, AMNH 97048, 97057, 97058, 97059, 97061), *Eucyon ferox* (Miller & Carranza-Castañeda, 1998) (F:AM 27388, 63035, 63061, 63062, 49298) from the Pliocene of North America and *Eucyon zhoui* Tedford & Qiu, 1996 (F:AM 97048) from the Pliocene of China. We analysed the casts of the following taxa: *Eucyon monticinensis* (Rook, 1992) (BRS 87/04 mandible, BRS 24/12 M1, BRS 24/9 M1, BRS 27/6 m1, BRS 27/8 right upper canine, BRS 27/14 ulna, BRS 27/15 radio, BRS 27/16 humerus and BRS 27/13 tibia) from Brishiguela (Italy); *E. intrepidus* KNM NK 41284 (M1) and KNM NK 41285 (m1) from Lemudong'o locality 1 (Kenya) (Howell & García 2007) and the m1 AME.1/144 from Amba East Vertebrate Locality 1, Kuseralee Member, Sagantole Fm (Haile-Selassie & Howell, 2009); *Eucyon wokari* García, 2008 ARA 6/21 (fragmented m1 and a complete m2) from Aramis Member, Sagantole Fm, in the Middle Awash Valley, Ethiopia; and *Eucyon davisi* (LOC 69 113/ VCMP 112197 m1-p4; LOC 887/UCMP M1-M2) from Thousand Creek, Oregon, USA. Additionally, *E. davisi* from North America and China, *E. zhoui* from China and *E. ferox* from North America were studied via photographs of the originals and by their original publications; *Eucyon odessanus* (Odintzov, 1967) by pictures of the casts housed at AMNH. *Eucyon kuta* Werdelin *et al.*, 2014b from the Woranso-Mille Area (Ethiopia), 3.82–3.57 Mya, ?*Nyctereutes barryi* Werdelin & Dehghani, 2011 from the Upper Laetoli Bed (Tanzania) 3.7–3.4 Mya (Su & Harrison, 2007) and *Lupulella mohibi* Geraads, 2011, from the site 'Grotte des Rhinocéros' (OH1-GDR) in Oulad Hamida 1 Quarry (Morocco), *c.* 0.5 Mya, and from other sites in the Casablanca area

(Morocco) dated to 0.8–0.4 Mya (Geraads, 2011) by their original publications.

The taxonomic status of the African jackals, traditionally placed in the genus *Canis* has been discussed (e.g. Hilzheimer, 1906; Ewer, 1956; Petter, 1969; Hendey, 1974; Zrzavý & Řičankova, 2004; Prevosti, 2010; vonHoldt *et al.*, 2011; Koepfli *et al.*, 2015; Atickem *et al.*, 2017; Viranta *et al.* 2017; Zrzavý *et al.*, 2018; Perri *et al.*, 2021; Taron *et al.*, 2021). Herein, we follow the hypothesis that resurrects the genus *Lupulella* Hilzheimer, 1906 for *Canis mesomelas* Schreber, 1775 (recently followed for several researchers, e.g.: Geraads, 2011; Atickem *et al.*, 2017; Viranta *et al.* 2017; Zrzavý *et al.*, 2018; Perri *et al.*, 2021), as well as *Schaeffia* Hilzheimer, 1906 for *Canis adustus* Sundevall, 1847. The revalidation of the genus *Lupulella* has been a direct consequence of the accumulation of evidence that has questioned the monophyly of the genus *Canis*, which is only sustainable if all the members of the subtribe Canina *sensu* Tedford *et al.* (2009) are classified within *Canis* (Viranta *et al.* 2017; appendix 1, comments on use of *Lupulella*).The revalidation of *Schaeffia* aligns with this same view, as we demonstrate in our phylogeny, which is in agreement with the proposed one by Zrzavý & Řičankova (2004).

The extant specimens used for comparison are housed in the following collections: *Canis aureus* Linnaeus, 1758 (NRM), *Canis latrans* Say, 1823 (NRM), *Canis lupaster* Hemprich & Ehrenberg, 1832 (VAL), *Canis lupus* Linnaeus, 1758 (MNCN and NRM), *Lupulella mesomelas* (Schreber, 1775) (SAM-ZM and MNCN), *Otocyon megalotis* (Desmarest, 1822) (SAM-ZM), *Schaeffia adusta* Hilzheimer, 1906 (NRM), *Vulpes chama* (Smith, 1833) (SAM-ZM) and *Vulpes vulpes* Linnaeus, 1758 (MNCN).

CLADISTIC ANALYSIS

We performed a cladistics analysis of 12 operational taxonomic units (OTU) and 50 cranial and dental characters based on Tedford *et al.* (1995, 2009), Daguenet & Sen (2019), Ruiz-Ramoni *et al.* (2020) and this work, in order to examine the phylogenetic position of the new species *Eucyon khoikhoi* relative to better-known Late Miocene–Early Pliocene *Eucyon* taxa from the Northern Hemisphere and some extinct Pliocene and Pleistocene African canids with uncertain taxonomical determination from North and East Africa, besides a sample of living canids. We studied *Eucyon davisi* from North America (USA), *Eucyon ferox* from North America (Mexico and USA), *Eucyon debonisi* from Europe (Spain), the enigmatic *Canis cipio* from Europe (Spain) and Plio-Pleistocene

African canids with dubious generic assignations (*Eucyon wokari*, ?*Nyctereutes barryi* and *Lupulella mohibi*), the living African jackals *Lupulella mesomelas* (black-backed jackal), *Schaeffia adusta* (side-striped jackal) and *Canis lupaster* (African golden wolf), as well as the Holarctic *Canis lupus* (grey wolf) and *Vulpes vulpes* (red fox). The extant metric data of the dentition used for the phylogeny are based on Hendey (1974), Tedford *et al.* (2009), Bertè (2017), Viranta *et al.* (2017) and the specimens observed in the collections by us. All characters were equally weighted and unordered. The complete list of taxa, characters and the character–taxon matrix are available in Supporting Information, Data S1; Table S3. We excluded the poorly known East African *Eucyon intrepidus* and *Eucyon kuta*. The selected outgroup was *V. vulpes*. The cladistic analysis was performed using in PAUP*4.0b10 (Swofford, 2002). This analysis yielded three parsimonious trees with 97 steps by the branch-and-bound-search, with a consistency index (CI) of 0.5258, a homoplasy index (HI) of 0.4742 and a retention index (RI) of 0.5929. Clade support was calculated using bootstrap analysis with 1000 replicates and Bremer support values.

SYSTEMATIC PALAEONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

SUBORDER CANIFORMIA KRETZOI, 1943

FAMILY CANIDAE FISCHER, 1817

SUBFAMILY CANINAE FISCHER, 1817

TRIBE CANINI FISCHER, 1817

SUBTRIBE CANINA FISCHER, 1817

GENUS *EUCYON* TEDFORD & QIU, 1996

1993 *Eucyon* nov. gen. (Tedford & Qiu, *in stampa*), Rook: 12.
1996 *Eucyon* nov. gen. Tedford & Qiu: 27.
2009 *Eucyon* Tedford & Qiu, in press, Rook: 726.

Type species: Canis davisi Merriam, 1911.

Diagnosis: In Tedford & Qiu (1996), revised by Tedford *et al.* (2009) and Werdelin *et al.* (2014b).

Remarks: Tedford & Qiu (1996) recognized that with *Eucyon* they were creating a paraphyletic taxon, due to its primitive position at the base of the Tribe Canini. Despite this, the number of

species attributed to the genus has been increasing progressively (Morales *et al.*, 2005; Spassov & Rook, 2006; García, 2008; Montoya *et al.*, 2009; Rook, 2009; Werdelin *et al.*, 2014b; Bartolini Lucenti & Rook, 2020). Recently Zrzavý *et al.* (2018) performed a phylogenetic analysis of living and extinct Caninae using morphological, developmental, ecological, behavioural and molecular characters. Only three *Eucyon* species were included in their analysis: *E. davisi*, type species of the genus, and two Asian species: *E. zhoui* from the Lower Pliocene and *E. marinae* from the Upper Pliocene. *Eucyon davisi* appears as the basal species of the entire Canini clade, while *E. zhoui* and *E. marinae* nest in a paraphyletic basal clade to the subtribe Canina. These same authors point out the paraphyletic character of the genus *Canis*, whose species are grouped into at least two different and distant clades.

EUCYON KHOIKHOI SP. NOV.

(FIGS 1–8)

1974 Canidae *incerta sedis* Hendey: 67.
1981a *gen. and sp. not det*. ? aff. '*Canis*' *brevirostris* Hendey: 50.
1981a *Vulpes* sp. Hendey: 50.
1993?*Eucyon* sp. Rook: 45.
2008 cf. *Eucyon* García: 589.
2009 *Eucyon* sp. Rook: 741.
2009 *Eucyon* sp. Montoya, Morales & Abella: 719.
2010 *Eucyon* sp. Werdelin & Peigné: 609, fig. 33.2A.
2016 *Eucyon* sp. Hartstone-Rose *et al*: 2, fig. 1A.

Zoobank registration: urn:lsid:zoobank.org:act: EFC6184C-759D-4AEC-B0DB-CEA578D79898

Diagnosis: Eucyon of similar size to that of the type species of the genus *E. davisi* of North America. Upper premolars (P2–P3) relatively short and robust, separated by a small diastema. P4 robust, with strong protocone. Robust and large M2, with respect to M1. Short and tall lower premolars. p3 with small distal accessory cuspid. Robust p4 with stronger and more extended distal accessory cuspid, and presence of a second distal accessory cuspid, comprising a small talonid. Robust m1, with high protoconid, talonid without transverse cristid between the entoconid and the hypoconid. m2 relatively long compared with m1, with a complete trigonid and a narrow talonid.

Differential diagnosis: Differs from *E. davisi* from North America (Tedford *et al.*, 2009) in a more robust lower dentition (p4–m1 and m2), with a longer m2 in relation to the m1. In relation to the former character,

the M2 long and more robust. The P4 is also more robust. The m1 has a better developed hypoconulid shelfhypoconulid shelf, comprising a markedly higher m1 protoconid. Most of these differences between *E. khoikhoi* and *E. davisi* are observed in the individuals of *E. davisi* from different localities in China (Tedford & Qiu, 1996). The Chinese sample has more robust premolars, especially P4 and p4, and more robust second molars (M2 and m2) than those of the North America populations. Therefore, they are more like *E. khoikhoi*. The Chinese *E. davisi* maintain small M2 and m2 lengths in relation to the first molars, which clearly distinguish them from *E. khoikhoi*. The difference in the length of the second molars with respect to the length of the m1 also allows the new Langebaanweg species to be distinguish from other *Eucyon* spp., which preserve comparable molar dentition: *Eucyon debonisi*, *E. odessanus*, *E. wokari* García, 2008 and *E. zhoui*. It differs from *E. debonisi* by the greater graciliness of the lower dentition in the Spanish species, particularly in the premolars and the carnassial teeth (P4 and m1). It differs from *E. wokari* in the anomaly of the alveolus in the maxilla for an M3, in the morphology of the m1 talonid, which in the Ethiopian species has transverse cristids that connect the hypoconid to the entoconid (Garcia, 2008). *Eucyon marinae* Spassov & Rook, 2006 differs from *E. khoikhoi* in the advanced morphology of the lower premolars and m1, which, although it lacks the transverse cristid between the hypoconid and the entoconid, the hypoconid is extremely large with respect to the entoconid, a trait that could indicate that this species moved away from the most common morphotypes of the *Eucyon* species. *Eucyon kuta* differs from *E. khoikhoi* in the robustness of the p2–3, unknown in other species of the genus, as the authors of the species point out. *Eucyon monticinensis* (Rook, 1992) possesses, despite the limited sample, a notable intraspecific variability, which, like *E. debonisi*, could be interpreted as sexual dimorphism (Montoya *et al.*, 2009). The M1 are at the maximum of robustness of the group, different from *E. khoikhoi*, and correspond with the size and proportions of the m1 of the type (Rook, 1992). It also differs from *E. khoikhoi* in the greater graciliness and size of the m2, traits that are common in both Italian and Spanish species. It differs from *Eucyon intrepidus* in its larger size and more robust M1 and m1. This species has the smallest M1 recorded in the Upper Miocene of Africa, close to the smallest specimens of *E. debonisi* and *E. khoikhoi*.

Etymology: Named after the Khoikhoi (KhoeKhoen) people, formally a nomadic pastoralist indigenous population of southern Africa who thrived for over 1000 years in various regions of South Africa including

the Western Cape, where this species was discovered. We honour Khoi heritage and ancestry.

Holotype: SAM-PQL-31272, comprising the skull, two hemi-mandibles, two fragmentary humerii, two radii, including a right complete and a left fragmentary one, and five cervical vertebrae, including the atlas, axis and cervical 3–5.

Paratype: SAM-PQL-72215, right maxillary including M1–M2.

Referred specimens: SAM-PQL-40041, old and pathological individual comprising the fragmentary left hemi-mandible with p1, broken p4 and m1–3, the fragmentary right hemi-mandible with p1–m2, the right proximal epiphysis of the scapula, the right proximal epiphysis of the humerus, the right proximal epiphysis of the ulna, the left distal epiphysis of the radius, the complete right metacarpals II–V (Mc IV, broken), the left both pyramidal and magnum, the right ectocuneiform, eight sesamoids, four first phalanges, three second phalanges, one ungual phalanx and one caudal vertebra (fourth caudal); SAM-PQL-24976B, right I3; SAM-PQL-24976B, left Cx; SAM-PQL-15526B, left P2; SAM-PQL-15184B, left P4; SAM-PQL-72203, right fragment of P4, including the protocone; SAM-PQL-72204, left fragment of P4, including the protocone; SAM-PQL-72205, left fragment of P4, including the protocone; SAM-PQL-72207, left fragmentary P4; SAM-PQL-72208, right M1; SAM-PQL-69621B, left maxillary, including M1–2; SAM-PQL-15588 B/C, right M1; SAM-PQL-50497, left M1; SAM-PQL-15219B, left M1; SAM-PQL-15705A, left M2; SAM-PQL-72217, right M2; SAM-PQL-72206, left M2; SAM-PQL-72218, indeterminate root; SAM-PQL-40308, fragmentary left hemi-mandible with m1–3 alveoli, two fragmented tibiae and eight fragments of vertebrae; SAM-PQL-72228, right cx; SAM-PQL-50112, left cx; SAM-PQL-72221, fragmentary right cx; SAM-PQL-72222, fragmentary right cx; SAM-PQL-69621d, fragmentary right cx; SAM-PQL-72223, left fragmentary hemi-mandible with m2-3 alveoli; SAM-PQL-50111, right fragmentary hemi-mandible with m2–3 alveoli; SAM-PQL-722219, right fragmentary hemi-mandible with complete p1, p3–4 and a broken p3 at the base crown; SAM-PQL-72220, left fragmentary hemi-mandible with broken p3-p4 and mesial part of m1 at the base of the crown, plus distal root of m1; SAM-PQL-69621A, fragmentary right hemi-mandible with broken p3–m2 at the crown base and with m3 alveolus; SAM-PQL-50110, left fragment of hemi-mandible with c and p1 alveoli and a fragmentary p2; SAM-PQL-50497A, left fragmentary hemi-mandible with both m1 and m3 alveolus and a complete m2; SAM-PQL-15381 A/1, left p2; SAM-PQL-72216, left m1; SAM-PQL-72166,

left fragment of the m1 trigonid; SAM-PQL-50113A, distal fragment of a right m1, including protoconid, metaconid and talonid; SAM-PQL-50113B, right m2; SAM-PQL-72225, right m1 talonid; SAM-PQL-72212, left m2; SAM-PQL-72211, fragmentary left m2; SAM-PQL-16120A, right m3; SAM-PQL-72213, right m3; SAM-PQL-72209, right Dp2; SAM-PQL-72210, left dp4; SAM-PQL-72214, fragmentary talonid of a left dp4; SAM-PQL-72226A, left fragment of dp3; SAM-PQL-72226B, left dp4; SAM-PQL-20424, right fragmentary humerus with most of the shaft and the distal epiphysis; SAM-PQL-23331, right radius; SAM-PQL-15323, atlas; SAM-PQL-15174, axis; SAM-PQL-15160, third cervical vertebra.

Type locality: Langebaanweg 'E' Quarry, Western Cape, South Africa.

Age: Langebaanweg 'E' Quarry spans the Middle Miocene (Langhian, 16–12 Mya) to the Early Pliocene (Zanclean, 5.2 Mya) (Tankard & Rogers, 1978; Hendey, 1989; Roberts, 2006a,b; Roberts *et al.*, 2011). The bone bed occurs at the base of the MPPM within the channel fill of the LQSM (Roberts *et al.*, 2011). The specimens of *Eucyon khoikhoi* are recovered from the MPPM and LQSM which dates to Early Pliocene, 5.2 Mya (see Roberts *et al.*, 2011).

Description

Skull and upper dentition: The type skull SAM-PQL-31272 is well preserved, without deformation (Fig. 1; Tables 1, 2). Portions of the palatine, and both pterygoid and the basisphenoids, are missing. The cranial sutures and the absence of wear of the dentition, suggests it is a young adult. Dorsally, the overall morphology is reminiscent to *C. aureus*. It has long nasal bones, with the muzzle similar to that of *V. chama*, *C. aureus* and *C. latrans* and relatively shorter compared to *L. mesomelas*. A small infraorbital foramen is located above P3. It has a big and round orbital bone. It has a frontal sinus invading the base of the postorbital process, but a minor dorsal depression is present on the process, being less marked to those the one of the African vulpini *V. chama* and *O. megalotis*.

The forehead is not as high as in *C. lupus*, resembling those of the jackals *C. aureus* and *L. mesomelas*, the coyote (*C. latrans*) and vulpini. On the right, the sharper and robust frontal process of zygomatic is preserved in the zygomatic arch.

A thick and broad sagittal crest is present in the parietal area. The occipital protuberance extends beyond the occipital area, and connects with the prominent nuchal crests, which are more laterally expanded than those of living jackals and *V. chama* and *O. megalotis*. The cranium is lateromedially wide

Figure 1. Skull of *Eucyon khoikhoi* from Langebaanweg. Individual SAM-PQL-31272 (holotype). A, left side; B, right side; C, dorsal view; D, ventral view; E, rostral view; F, caudal view. Scale bar equals 5 cm.

at the temporal level. In ventral view, the palatine fissure is large but broken.

The palatine sulcus is not preserved. The major palatine foramen is situated between P4 and M1, as in *C. aureus* and *V. chama*, and in a more caudal position than *L. mesomelas*. Neither the pterygoid bones nor hamulus processes are preserved, but both left oval and caudal foramina are preserved. The bulla is large and swollen. The right one has the ectotympanic bone missing, the petrosal bone and the bullar septum are partially preserved. The rostroventral area of the right one is broken. A large foramen lacerum and a small musculotubal canal are located in the most rostral area of the bulla. It has a round external acoustic meatus and a round and smaller stylomastoid foramen, similar to that of *L. mesomelas* and much smaller than the analysed vulpini. In the distal part of the bulla, the tympano-occipital fissure is large and oval. A small hypoglossal canal is located distally to the fissure. The paroccipital process is ventrally projected. It is well developed and extends over the bulla, displaying a strong bone bar. Both mastoid and paroccipital processes are similar to those of *C. latrans*, *C. aureus*, *L. mesomelas* and unlike *V. chama* and *O. megaloti*. In caudal view, the nuchal area is triangular, comprising a complete occipital condyle.

The incisors are set in a parabolic row. I3 is larger than I2. There is a diastema between the I3–C and between the P1 and P2. The I3 is tall with a single cusp, lingually curved. There is a small distolingual cingulum (Fig. 2A, B). The C is oval, showing a marginal lateromedial compression. Its crown is high and thin. In distal view it is slightly sigmoidal (Fig. 2C). P1 single rooted. P2 and P3 relatively short, without mesial accessory cusps. P2 with residual accessory cusp associated with the distal crista. P3 with well-developed distal accessory cusp (Fig. 2) and P4 has no parastyle. It has a carnassial notch. The protocone is low, conical and located in line with the mesial border of the paracone. The fragmentary specimen SAM-PQL-72205 has the protocone more mesially projected. An inflection is present between the protocone and the mesial border

Table 1. Cranial and mandible measurements of the holotype of *Eucyon khoikhoi* SAM-PQL-31272 from Langebaanweg. Skull measurements based on Tedford *et al.* (2009). Mandibles measurements based on our measurements. Abbreviations: BW, braincase width. Maximum breadth of the braincase across the level of parietal-squamosal suture; FSW, frontal shield width. Maximum breadth across the postorbital processes of the frontals; GSL, greatest skull length. Length from anterior tip of premaxillae to the posterior point of the inion; H ascent, hight ascent ramus; H ar-an, hight between articular and angular processes; Hb m1, height of the mandibular ramus below m1; Hb p1, height of the mandibular ramus below p1; JD, jugal depth. Minimum depth of the jugal cranial to the postorbital process, at a right angle to its craniocaudal axis; LB, bulla length. Length from the median lacerate foramen to the suture of the bulla with the paroccipital process; LCM, distance from the distal border of the canine alveolus to the foramen magnum notch; Ld, length diastema between c-p1; Lms, length from m1–3; LPM, maxillary toothrow length. Distance from the mesial edge of the alveolus of P1 to the distal edge of the alveolus of M2; Lps, length from p1 to p4; Lp1–ms, length from p1-m3; MOH, height, maxillary toothrow to orbit. Minimum distance from the outer alveolar margin of M1 to the most ventral point of orbit; M2B, length, M2 to bulla. Minimum distance from the distal edge of the alveolus of M2 to depression in front of the bulla; PCW, postorbital constriction width. Least width across the frontals at the constriction behind the postorbital processes; PWP1, palatal width at P1. Minimum width between the inner margins of the alveoli of the first upper premolars; PWP4, palatal width at P4. Minimum width between the inner margins of the alveoli of the first upper premolars; TL, total length; W cor, maximum craniocaudal width of the coronoid process; ZW, zygomatic width. Greatest distance across the zygoma. Parenthesis means approximated measurements

Skull

LCM	GSL	ZW	BW	LPM	PWP4	PWP1	FSW	PCW	M2B	MOH	JD	LB
121.1	152.2	(80.2)	51.2	(57.2)	24.3	(17.1)	40.7	(29.2)	33.3	(19.0)	8.9	25.8

Mandible

	TL	H ascent	H ar-an	W cor	L d	Lps	Lms	L p1-ms	Hb p1	Hb m1
	110.3	42.4	20.0	21.2	4.4	35.5	26.4	61.2	13.9	14.2

of the paracone in all the P4s (Fig. 2E–H). There is a weak lingual and mesial cingulum (Fig. 2E). There is a wide variability in the measures and morphology in the recovered sample of the first upper molar (Fig. 2). Most of the M1s are worn or broken, except SAM-PQL-31272 and SAM-PQL-50497 (Fig. 2A, M). It is subquadrangular in occlusal view, with a rectilinear mesial wall and the distal one with an inflexion below the metacone. It has a strong parastyle with a well-developed buccal cingulum. Paracone and metacone are subequal in height. The paraconule is small, but well preserved in the specimen SAM-PQL-50497 (Fig. 2M). The protocone is tall and mesially located. It has a large metaconule which connects to the metastyle and the buccal cingula by a tall crista. It has a deep trigone valley. There is a well-developed mesial cingulum, connecting the parastyle with the lingual wall of the protocone. It possesses a tall and bevelled hypocone.

The M2s show a wide intraspecific variability with some specimens having broader talons (Fig. 2J, K) and others reduced ones (Fig. 2P, Q). SAM-PQL-72206, has the biggest M2 of *E. khoikhoi* recovered, with a slightly different morphology and no worn cusps. The M2s have a kidney-shaped occlusal, with a highly developed paracone compared to the metacone, a protocone located in a more central position to those of the M1 and with a strong labial cingulum (Fig. 2M).
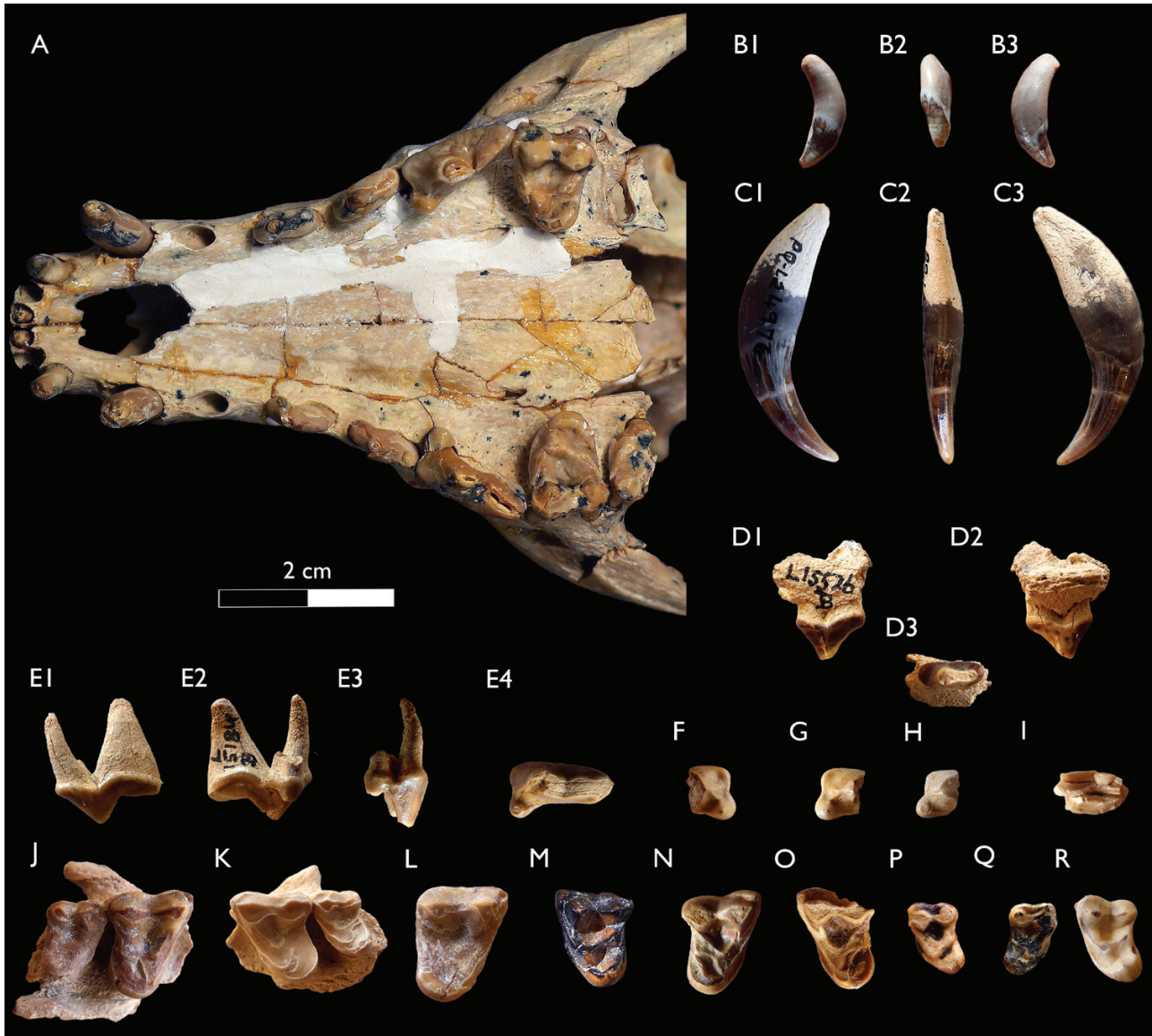
Mandible and lower dentition: The overall morphology of the mandibles of *E. khoikhoi* (Fig. 3; Tables 1, 3) are similar to those of the living jackals of the genera *Canis* and *Lupulella*, being easily distinguish from the African vulpini. SAM-PQL-40041 shows a worn dentition and several dental and bone pathologies. The most complete mandible belongs to the type SAM-PQL-31272. It has a relatively tall coronoid process and a deep masseteric fossa. The articular process is in line with the tooth row and the angular is well developed similar to the canini. The mandibular corpus is low. There are two main foramina on the mandibular corpus, below p1 and p3. There are diastemata between c and p1, and p1–p4. The c is short and robust at the base of the crown. It is distally curved and possesses a lingual keel. Premolars are without mesial accessory cuspid, relatively short and with high main cuspid. There are small diastemata between c–p1, p2–p3, and longer between p2–p1. The p1 is uniradiculate and unicuspidated. The p2 is longer than the p1, double rooted and has no accessory cuspids. The distal area has a small keel. The p3 has a small distal accessory cuspid and a high distal cingulum.

The p4 is robust, comprising stronger and more extended distal accessory cuspid. There is a second accessory cuspid behind the previous one, which is double in the left hemi-mandible of the specimen

Table 2. Upper-teeth measurements (in mm) of *Eucyon khoikhoi* from Langebaanweg. Parenthesis means measurements on alveoli or at the base of the broken crown

Specimens	I3		C		P1		P2		P3		P4		M1		M2		DP2	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
SAM-PQL 15184B											13.8	7.2						
SAM-PQL 72217													9.9	13.1	6.3	9.4		
SAM-PQL 15588B/C																		
SAM-PQL 15526B							7.8	3.3										
SAM-PQL 31272 left	4.3	3.7	6.8	4.8	(4.8)	(3.3)	8.0	3.3	9.0	4.0	14.2	7.0	10.2	12.3	(7.4)	(9.4)		
SAM-PQL 31272 right	4.3	3.7	6.9	5.2	(4.8)	(3.2)	7.6	3.3	(8.9)	(3.6)	13.7	7.1	9.3	12.4	(6.2)	8.3		
SAM-PQL 24976a	4.4	3.5	7.7	5.4														
SAM-PQL 24976b																		
SAM-PQL 72203												6.7						
SAM-PQL 72204												7.0						
SAM-PQL 72205												(6.1)						
SAM-PQL 72208													10.6	13.5	7.9	10.3		
SAM-PQL 72206													9.9	12.1				
SAM-PQL 50497													(9.8)	12.7				
SAM-PQL 15219B													9.5	11.3	6.5	8.4		
SAM-PQL 69621B													10.1	12.3	6.7	8.6		
SAM-PQL 72215															6.6	9.0		
SAM-PQL 15705A																		
SAM-PQL 72209																	9.1	3.5

Figure 2. Upper dentition of *Eucyon khoikhoi* from Langebaanweg. A, SAM-PQL-31272, holotype, details of the dentition, occlusal view. B, SAM-PQL-24976B, right I3: B1, buccal; B2, distal; B3. lingual views. C, SAM-PQL-24976A, left C: C1, buccal; C2, distal; C3, lingual views, D. SAM-PQL-15526B, left P2: D1, buccal; D2, lingual; D3, occlusal views. E, SAM-PQL-15184B, left P4: E1, buccal; E2, lingual; E3, mesial; E4, occlusal views. F, SAM-PQL-72203, fragmentary right P4: occlusal view. G, SAM-PQL-72204, fragmentary left P4, occlusal view. H, SAM-PQL-72205, fragmentary right P4, occlusal view. I, SAM-PQL-72207, left fragmentary right P4, occlusal view. J, SAM-PQL-72215 (paratype), right maxillary with M1–2, occlusal view. K, SAM-PQL-L69621B, left maxillary with M1–2, occlusal view. L, SAM-PQL-72208, right M1, occlusal view. M, SAM-PQL-50497, left M1, occlusal view. N, SAM-PQL-15588B/C, right M1, occlusal view. O, SAM-PQL-15219 B, left M1, occlusal view. P, SAM-PQL- 15705A, left M2, occlusal view. Q, SAM-PQL- 72217, right M2, occlusal view. R, SAM-PQL-72206, left M2, occlusal view. Scale bar 2 cm.

SAM-PQL-31272, but single in SAM-PQL-72220 (Figs 3, 4D). There is a high distal cingulum. The m1 is robust with a low paraconid compared to the protoconid, which is relatively high in relation to the length of the molar. There is a strong metaconid extending slightly beyond the distal wall of the protoconid. Its talonid has a strong hypoconid with the highly developed mesial cristid. The entoconid, although smaller in size than the hypoconid, is strong and extends mesially with a small pre-entoconid, and internally develops a small cristid (Figs 3, 4). However, both hypoconid and entoconid are well separated. The

Figure 3. Mandibles of *Eucyon khoikhoi* from Langebaanweg. A, B, SAM-PQL-31272 (holotype), right hemi-mandible (A), left one (B). A1, B1, buccal; A2, B2, lingual; A3, B3, occlusal views. C, D, SAM-PQL-40041, right hemi-mandible (C), left one (D). C1, D1, buccal; C2, D2, lingual; C3, D3, occlusal views. E, SAM-PQL-40308, left hemi-mandible: E1, buccal; E2, occlusal view.

talonid valley is divided into two parts, the mesial one is deep and the distal one is shorter, which is closed by a bifurcated hypoconulid in a distocentral position (Figs 3, 4). The m2 is also robust. It is oval, with a complete trigonid and a highly developed buccal cingulum (Figs 3, 4H–J).

The paraconid is small and is attached to the protoconid and continues in a high mesial cingulum that

Table 3. Lower-teeth measurements (in mm) of *Eucyon khoikhoi* from Langebaanweg. Parenthesis means measurements on alveoli or at the base of the broken crown

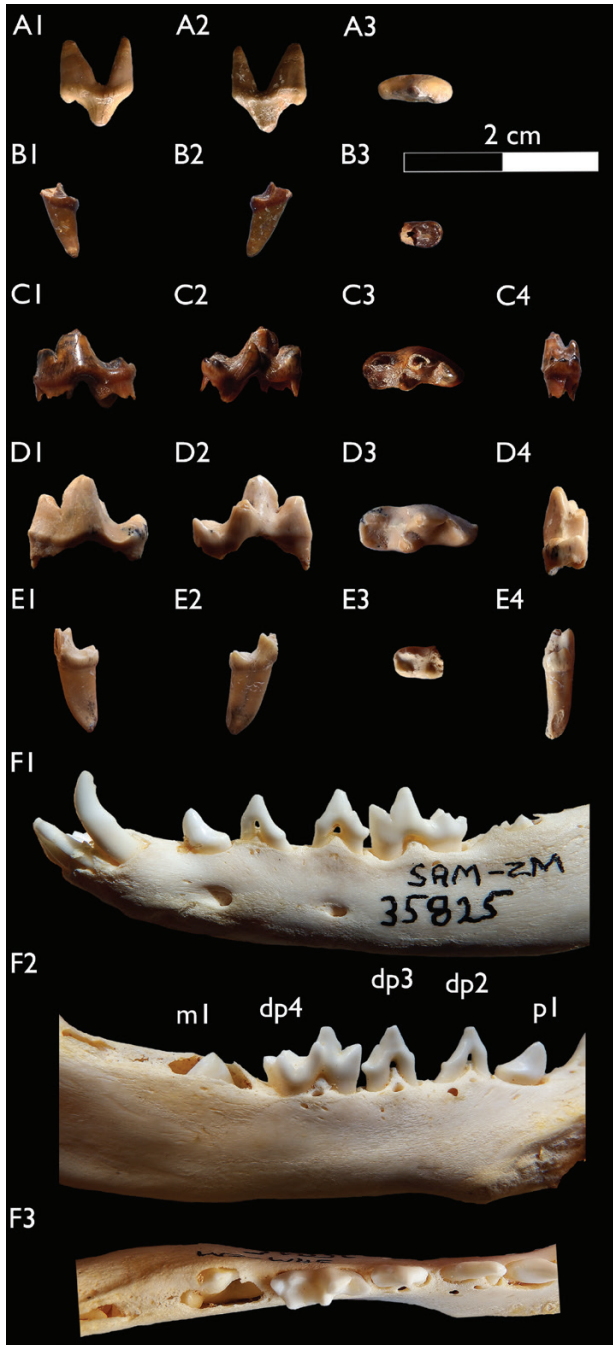| Specimens	c L	c W	p1 L	p1 W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W	m1 L	m1 W	m2 L	m2 W	m3 L	m3 W	dp3 W	dp4 L	dp4 W
SAM-PQL 72216											15.1	6.1							
SAM-PQL 31272 left	6.7	4.7	(4.1)	(2.9)	8.2	3.6	8.7	3.9	10.2	4.9	14.6	6.5	8.1	6.5	(3.4)	(2.8)			
SAM-PQL 31272 right	7.2	4.7	4.0	2.7	8.0	3.5	8.7	3.8	10.2	4.8	14.4	6.8	7.6	6.7	4.3	3.7			
SAM-PQL 72210																		14.2	5.7
SAM-PQL 72211														(5.7)					
SAM-PQL 72212													8.4	6.6					
SAM-PQL 72213															(4.1)	4.3			
SAM-PQL 72214												4.4							
SAM-PQL 72226																	3.7	12.3	5.1
SAM-PQL 72225												6.1							
SAM-PQL 40041 left			4.3	2.9	(6.4)	(2.8)	(7.2)	(3.1)	(8.7)	3.9	14.9	6.6	8.4	7.0	4.5	4.2			
SAM-PQL 40041 right			3.4	2.5	7.1	3.3	7.6	3.2	9.0	3.9	14.5	7.2	9.1	6.6					
SAM-PQL 50112	5.8	4.2																	
SAM-PQL 72221	6.4	4.5																	
SAM-PQL 72228	7.2	5.1																	
SAM-PQL 50110					7.2	3.2													
SAM-PQL 15381 A/1					7.0	2.9													
SAM-PQL 72219			3.7	2.4	(7.2)	(3.0)	7.3	2.9	8.4	3.6									
SAM-PQL 72220							9.3	3.5	10.5	4.3		6.6							
SAM-PQL 72166 right									(10.5)	(3.9)	(16.2)	(5.7)							
SAM-PQL 69621A							9.4	3.5				6.1	(8.7)		4.0	2.8			
SAM-PQL 50113a																			
SAM-PQL 50113b													7.8	5.8					
SAM-PQL 50497A													8.0	6.3					
SAM-PQL 16120A															4.4	4.0			
SAM-PQL 50111													(7.8)		(3.6)	(2.3)			
SAM-PQL 40308													(8.1)		(3.4)	(2.7)			
SAM-PQL 72223													(7.1)	4.6	(3.2)	(2.8)			
SAM-PQL 72166														6.5					

Figure 4. Lower dentition of *Eucyon khoikhoi* from Langebaanweg. A, SAM-PQL-72228, right cx: A1, buccal; A2, lingual; A3, occlusal views. B, SAM-PQL-50112, left cx: B1, buccal; B2, lingual views. C, SAM-PQL-15381 A/1, left p2: C1, buccal; C2, lingual; C3, occlusal views.D, SAM-PQL-72220, right fragmentary hemi-mandible including p1, p3–4: D1, buccal; D2, lingual; D3, occlusal views. E, SAM-PQL-72216 left m1: E1, buccal; E2, lingual; E3 occlusal views. F, SAM-PQL-72166, left m1 trigonid: F1, buccal; F2, lingual; F3, occlusal views. G, SAM-PQL-50113A, right fragmented m1: G1, buccal; G2, lingual; G3, occlusal; G4, distal views. H, SAM-PQL-50497A, left fragmentary hemi-mandible with m2: H1, buccal; H2, lingual; H3, occlusal views. I, SAM-PQL-50113B, left m2: I1, buccal; I2, lingual; I3, occlusal; I4, distal views. J, SAM-PQL-72212, left m2: J1, lingual; J2, occlusal; J3, distal views. K, SAM-PQL-16120A, right m3: K1, buccal; K2, lingual; K3, occlusal views. L, SAM-PQL-72213, right m3: L1, buccal; L2. occlusal views. Abbreviations: h, hypoconid; m, metaconid; par, paraconid; and pr, protoconid. Scale bar 2 cm.

connects with the base of the metaconid, which has an additional cuspid in mesial position, enclosing a small trigonid valley. The metaconid is taller and larger than the protoconid. Buccally, the base of the protoconid is clearly expanded. The talonid is narrower than the trigonid. The hypoconid is the most developed cuspid and is mesially continued by the oblique cristid. The entoconid is bifurcated. The m3 is reduced and has one root. It is round with low cuspids. The largest cuspids are the protoconid and metaconid (Figs 3A1–3, 4K, L).

Deciduous dentition: The deciduous dentition of this new taxon represents the first non-definitive

teeth of *Eucyon* recovered. It is similar to that of the living *L. mesomelas*, although several differences distinguish both canids (Fig. 5). It shows a wide range of variability in terms of size and shape, especially in the lower deciduous carnassial (dp4). The DP2 (SAM-PQL-72209, Fig. 5A) is a slender and long simple tooth, without accessory cusps. Distally a high cingulum is present.

The dp3 recovered is a fragmentary distal portion of the tooth, comprising a noticeable distal cingulum (Fig. 5B). There is a great variability in size in the dp4s founds (Fig. 5C–E). Among them SAM-PQL-72214 is much smaller and narrower to that of SAM-PQL-72210

and SAM-PQL-72226B. The dp4 has a well-developed metaconid, with a more distal position than in the m1. The talonid is wide and simple. It comprises a developed hypoconid and smaller entoconid. An additional hypoconulid is located between both cuspids in the most distal part of the tooth in the specimens SAM-PQL-72226B and SAM-PQL-72214 (Fig. 5C, E).

Postcranial remains: The cervical vertebrae (C1–C5) belong to two individuals (Fig. 6; Supporting Information, Table S2). Morphologically it is similar to *Lupulella*. The transverse foramen of the atlas is smaller to that of the jackal. The caudal articular process of the axis is robust. Although there is no noticeable evidence for the presence or absence of a nuchal ligament *sensu* Wang *et al.* (2008), the morphology of the back of the axis, where the ligament would attach, is similar to that of living canids with this ligament (e.g. extant jackals *Lupulella mesomelas*). The axis SAM-PQL-15174 has several parallel bite marks over the spinous process, which, based on their morphology, can be interpreted as shark bites (Fig. 6G1, G2). Neither the transverse process nor spinous processes are preserved in the C3–C5 (Fig. 6C–E, H). A proximal fragment of a fourth caudal vertebra is present (Fig. 6I1, I2).

The general morphology of the humerii and radii (Fig. 7; Supporting Information, Table S2) are similar to *L. mesomelas* than to those of African vulpini. The type SAM-PQL-31272 has bite marks of a terrestrial carnivoran on both epiphyses of these long bones. SAM-PQL-20424 is more robust and with an elongated humerus. The proximal epiphysis is known from SAM-PQL-40041 (Fig. 8) and the humeral head is round. The humeral diaphysis is straight, with the proximal part curved caudally and laterally compressed. It is rounded to triangular in cross-section distally. The deltoid crest is well developed (Fig. 7A1, A2, D1) and the distal epiphysis is subrectangular in distal view (Fig. 7A5, B). There are two uniform facets on the lateral epicondyle: one proximally for the origin of the extensors of the carpus and digits and one distal to the origin of the m. supinator (Munthe, 1989). There is a distinctive lateral epicondylar crest, where m. extensor carpi radialis originates (Munthe, 1989).

The supratrochear foramen is also well developed. As in living canids, the medial epicondyle is small, where the m. pronator teres originates. The entepicondylar foramen is absent. The radii (Fig. 7C, E; Supporting

Figure 5. Deciduous dentition of *Eucyon khoikhoi* from Langebaanweg compared with the one of the living jackal *Lupulella mesomelas*. A, SAM-PQL-72209, right DP2: A1, buccal; A2, lingual; A3, occlusal views. B, SAM-PQL-72226A, left fragmentary dp3: B1, buccal; B2, lingual; B3, occlusal views. C, SAM-PQL-72226B, left dp4: C1, buccal; C2, lingual; C3, occlusal; C4, distal views. D, SAM-PQL-72210, left dp4: D1, buccal; D2, lingual; D3, occlusal; D4. distal views. E, SAM-PQL-72214, fragmentary left dp4: E1, buccal; E2, lingual; E3, occlusal; E4, distal views. F, SAM-ZM-35825, right hemi-mandible of a juvenile individual of *L. mesomelas*: F1, buccal; F2, lingual; F3, occlusal views. Scale bar 2 cm. Abbreviations: p1, definitive first lower premolar; dp2, decidual p2; dp3, decidual p3; dp4, decidual carnassial; m1, definitive carnassial.
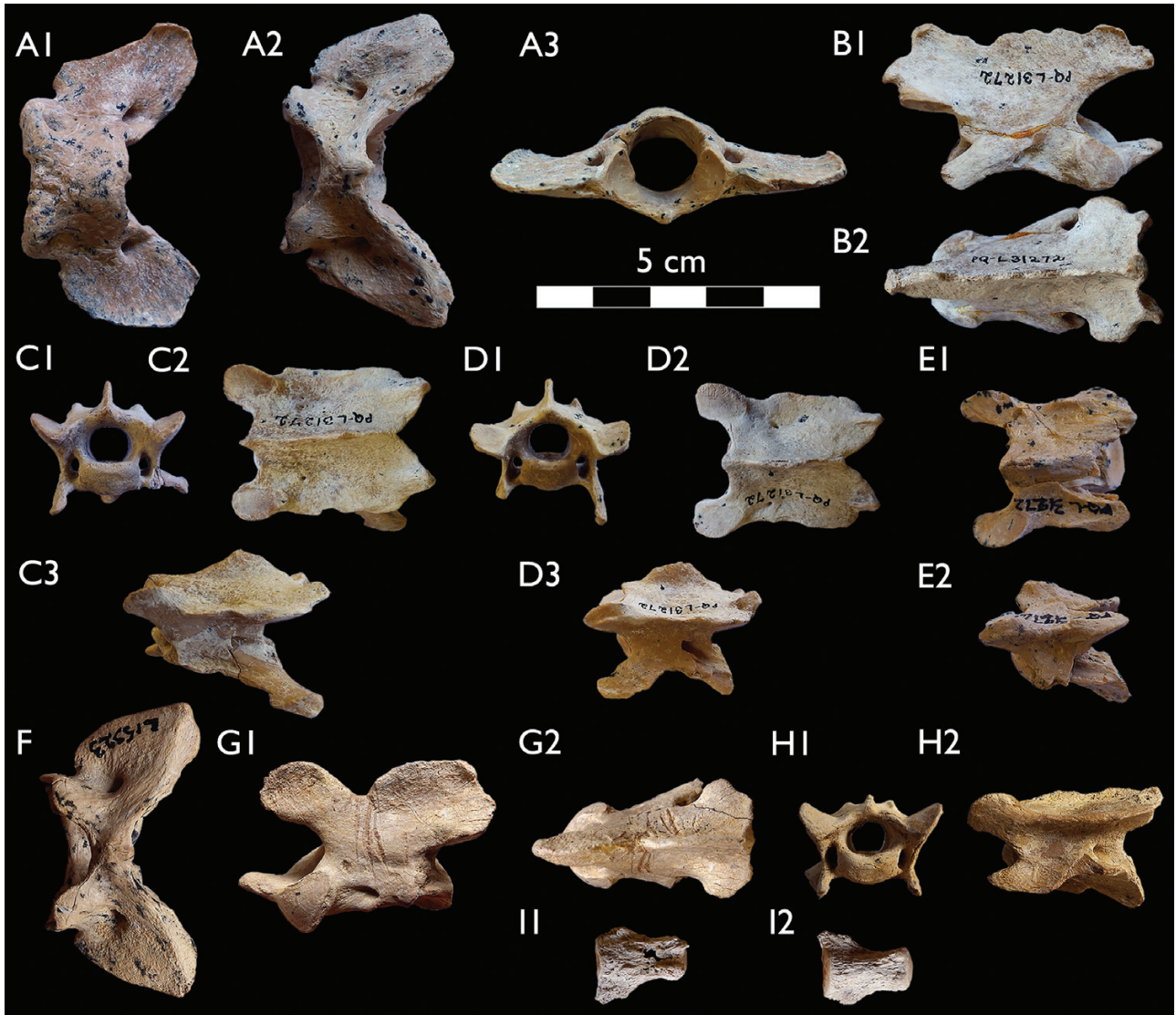
Figure 6. Cervical and caudal vertebrae of *Eucyon khoikhoi* from Langebaanweg. A–E, SAM-PQL-31272. A1–3, atlas: A1, dorsal; A2, ventral; A3, distal views. B1, B2, atlas: B1, lateral; B2, dorsal views. C1–3, third cervical vertebra: C1, cranial; C2, dorsal; C3, lateral views. D1–3, fourth cervical vertebra: D1, cranial; D2, dorsal; D3, lateral views. E1, E2, fifth cervical vertebra: E1, dorsal; E2, lateral views. F, SAM-PQL-15323, atlas, ventral view. G, SAM-PQL-15174, axis: G1, lateral; G2, dorsal views. H, SAM-PQL-15160, third cervical vertebra: H1, rostral; H2, lateral views. I, SAM-PQL-40041, fourth caudal vertebra: I1, dorsal; I2, ventral views. Scale Bar equals 5 cm.

Information, Table S2) are elongated and slightly curved caudally. The *fovea capitis* is oval, deep and has a cranial notch.

A small, radial tuberosity is situated on the lateral edge, where m. biceps brachii and m. brachialis attach. The shaft is craniocaudally compressed. On the first third of the laterocaudal border, the interosseous border is located. The distal epiphysis is mediolaterally large. The ulnar notch is round and small. Medially, there is a small, sharp, knob-shaped styloid process, where the m. brachioradialis inserts. In cranial view,

and following the description of Munthe (1989) for borophagines canids, there are three grooves (Fig. 7E2, E3): a medial deep one for the tendon of the m. adductor pollicis longus, a wider lateral one for the tendon of the m. extensor digitorum communis and between them a wide and shallow groove for the tendon of m. extensor carpi radialis.

The associated postcranial skeleton of the old and pathological individual SAM-PQL-40041 (Fig. 3C; Supporting Information, Table S2), consists of numerous fragmentary remains of the forelimb,

Figure 7. Humeri and radii of *Eucyon khoikhoi* from Langebaanweg. A–C, SAM-PQL-31272. A–B, left fragmentary humerus, A1–5 (left) and B (right). A1, cranial; A2, lateral; A3, caudal; A4, medial; and A5, distal views; B, distal view; C, right radius; C1, proximal; C2, distal; C3, cranial; C4, caudal views. D, SAM-PQL-20424, right fragmentary humerus: D1, cranial; D2, lateral; D3, caudal views. E, SAM-PQL-23331, right radius: E1, proximal; E2, distal; E3, cranial; E4, lateral; E5, caudal; E6, medial views. Scale bar equals 5 cm.

Figure 8. Postcranial remains of *Eucyon khoikhoi* SAM-PQL-40041 from Langebaanweg. A, right distal fragment of the scapula: A1, lateral; A2, medial; A3, ventral views. B, right fragmentary humeral head: B1, caudal; B2. proximal views. C, left fragmentary radius, cranial view. D, right fragmentary ulna: D1, cranial; D2, medial; D3, caudal; D4, proximal views. E1, mounted hand comprising metacarpal II–V, and first, second and ungueal phalanges from the hand or foot, dorsal view; E2, metacarpal II–V, proximal view. F, left magnum: F1, medial; F2, dorsal; F3, lateral views. G, left pyramidal: G1, lateral; G2, medial views. H, right ectocuneiform: H1, lateral; H2, medial; H3, proximal views. I, first phalange: I1, dorsal; I2, lateral; I3, palmar/plantar; I4. proximal views. J, second phalange: J1, dorsal; J2, lateral; J3, palmar/plantar; J4. proximal views. K, ungueal phalange: K1, lateral; K2, dorsal; K3, proximal views. Scale bar equals 5 cm (A1–E1), and 2 cm (E2–K3).

hindlimb and axial skeleton (Fig. 8). Several pathologies are observed, these include, notably, overgrowths of bone on the periosteal surfaces of the long bones, metacarpals, phalanges and caudal vertebrae, as well as endosteal bony growths on the IV metacarpal and radius (Fig. 8). These bones show bite marks, e.g. on the fragmentary scapula (Fig. 8A). Its glenoid cavity is rounded and lateromedially wide, as in *L. mesomelas*, and unlike *V. chama* and *O. megalotis*.

The overall morphology of the ulna is similar to *L. mesomelas*, apart from the lateral and medial tubercles of the tuber olecrani. The ulna of *Eucyon khoikhoi* has similar morphology to *V. chama*, with the medial tubercle prominently larger and projected proximally, beyond the level of the lateral one. In *L. mesomelas*, both tubercles are similar in height. The first metacarpal is unknown. The metacarpals (II–V), carpals (magnum and pyramidal) and tarsals (ectocuneiform) are more robust compared to African vulpini, and similar to *L. mesomelas* and other African jackals. However, some minor traits distinguishes *E. khoikhoi* from *L. mesomelas* and other African jackals, such as the slenderer pyramidal and the wider dorsodistal part of the ectocuneiform. The phalanges (Fig. 8E1, I–K) belong to different digits, but it is difficult to determine whether they belong to the pes or manus. The size difference suggest that they belong to both. The first phalanges have a similar length to *L. mesomelas* and shorter to the African vulpini. They are robust, slightly straight but with ventral curvature. We cannot infer any muscular attachment because of the bone grown on the periosteal surfaces. Two of the three second phalanges are much shorter to the other, which could suggest that they are from the feet. The ungual phalanx is also relatively robust and longer, resembling to those of the living canini. The tibia (SAM-PQL-40308) only preserves a long, slender and sigmoid shaft.

DISCUSSION

Eucyon khoikhoi from Langebaanweg contributes substantially to the knowledge of the initial Canidae radiation in Africa (Fig. 9; Supporting Information, Table S4), because of the quality of the sample, which includes a nearly complete skull, mandibles, dentition and postcranial bones, and for being a site close to the Mio-Pliocene boundary. This age is close to the first records of this family on the continent, known at the moment from three sites at the end of the Miocene (Fig. 10): *Eucyon intrepidus* from Lukeino, Kenya (Morales *et al.*, 2005); *Eucyon* aff. *intrepidus* from Lemudong'o (Howell & García, 2007); and *Eucyon* sp. Amba East Vertebrate Locality 1, Ethiopia (Haile-Selassie & Howell, 2009; Werdelin & Peigné, 2010; Werdelin
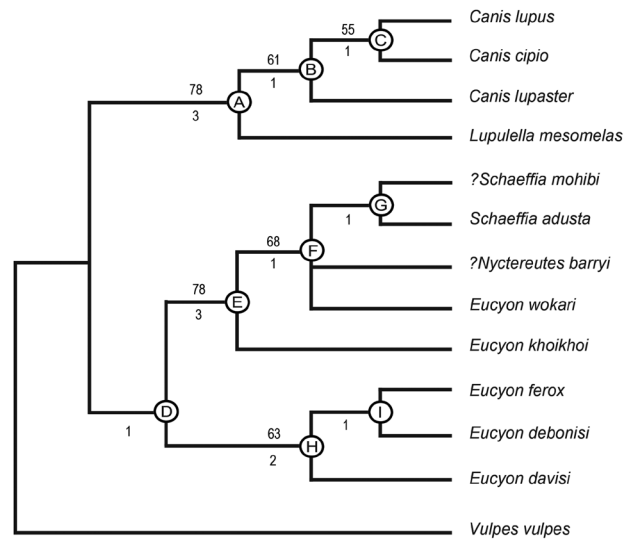
Figure 9. Phylogenetic relationship of *Eucyon khoikhoi*, within selected caninae, based on the strict consensus tree. Length 97 steps, consistency index (CI) = 0.5258, homoplasy index (HI) = 0.4742, and retention index (RI) = 0.5929. The numbers below nodes are Bremer indices, and the numbers above nodes are bootstrap support percentages (only shown if > 50). *Vulpes vulpes* is the outgroup.

et al., 2014b) (Fig. 10). These three forms are clearly differentiated from *Vulpes riffautae* Bonis *et al.*, 2007, considered as the oldest canid in Africa. *Eucyon intrepidus* is smaller and has slenderer M1 and m1 than *Eucyon khoikhoi*, although the smallest fossils of Langebaanweg overlap with the largest teeth of this species, as is the case of one of the M1 from Lukeino (Figs 11, 12). The M1 morphology of the holotype of *E. intrepidus* differs from *Eucyon davisi* from North America (Tedford *et al.*, 2009) by the strength of the parastyle and the most pronounced individualization of the hypocone, a character shared with *E. khoikhoi* and with the M1 described by Howell & García (2007) as *Eucyon* aff. *intrepidus* from Lemudong'o. An incomplete m1 from Lemudong'o, with a broken paraconid but a well-preserved talonid, shows a morphology similar to *E. khoikhoi* with a weak internal connection between the entoconid and hypoconid, and the presence of a small distal depression (hypoconulid shelf), separated from the rest of the talonid valley and closed by a hypoconulid. The m1 from Amba East Vertebrate Locality 1, classified as *Eucyon* sp., shows the same morphological features of the Lemudong'o m1. Thus, the canids of these three localities can be determined as *E. intrepidus*, a smaller-sized species than *E. khoikhoi* (Figs 11, 12), but having the same morphological dental pattern, more derived than *E. davisi*. Unfortunately, the scarcity of fossils attributed to *E. intrepidus* and
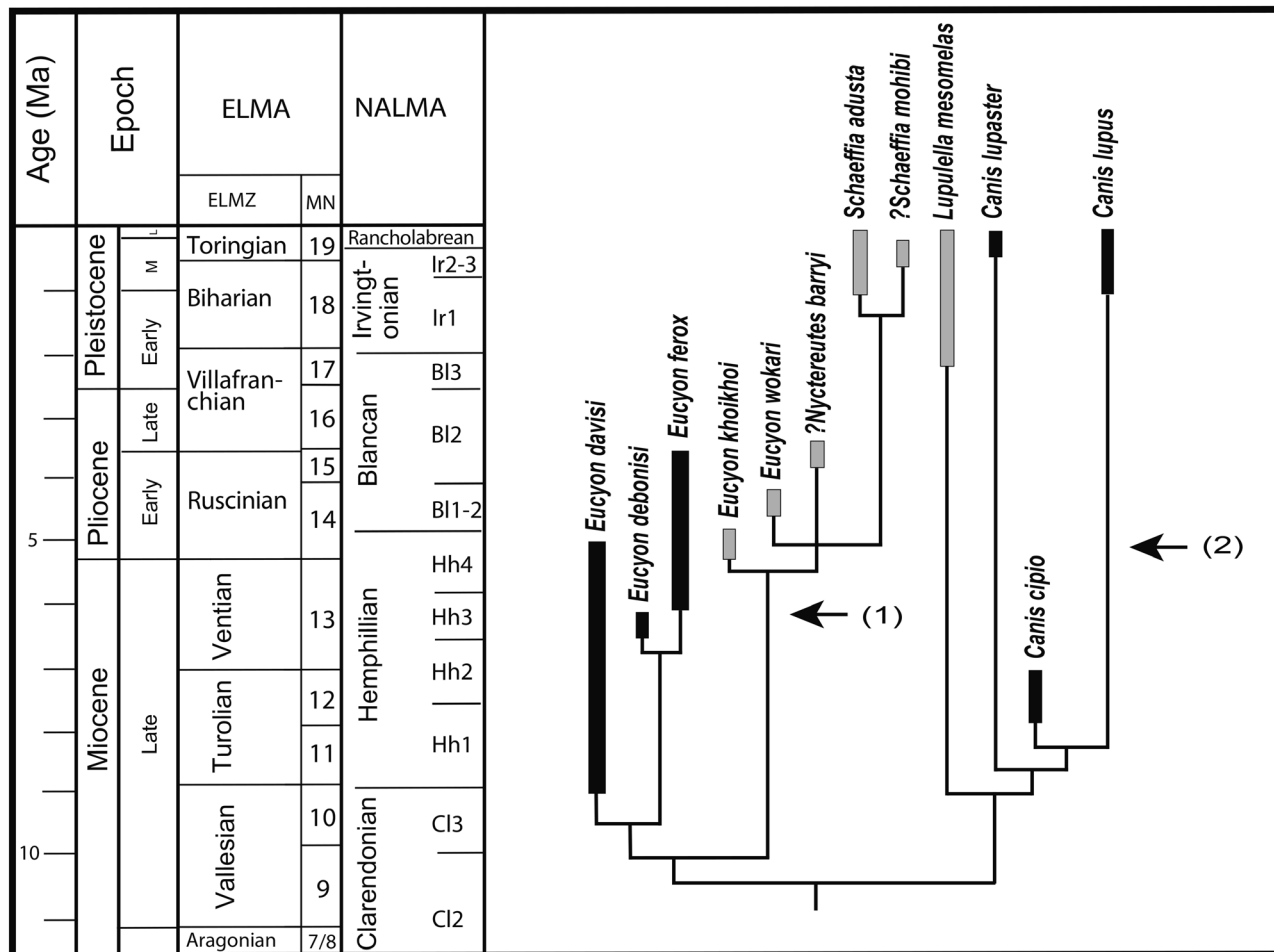
Figure 10. Biochronological range chart of *Eucyon* species and selected Caninae taxa based on our phylogenetic hypothesis. Data source in Crusafont (1950), Pons-Moyà & Crusafont (1978), Tedford & Qiu (1996), Montoya *et al.* (2009) and Tedford *et al.* (2009). Events: (1) African first canini (*Eucyon intrepidus*, based on Morales *et al.*, 2005; (2) The most ancient North American *Canis* representing by *Canis lepophagus* according Tedford *et al.* (2009), after the inclusion of *Canis ferox* into *Eucyon*. Taxa in grey came from Africa and in black from Eurasia and North America. North American land mammal age (NALMA) based on Tedford *et al.* (2004), Albright *et al.* (2008) and Hilgen *et al.* (2012); European Mammal Neogene Units (MN) based on Hilgen *et al.* (2012) and Morales *et al.* (2013). Abbreviations: ELMA, European land mammal ages; NALMA, North American land mammal ages (units defined by immigrant taxa); E, early, M, middle; L, late.

its dispersion in three different localities prevent its inclusion in our phylogenetic analysis.

The differences between *E. khoikhoi* and the clade comprised by *Eucyon* from North America (*Eucyon davisi*, *Eucyon ferox*) and Europe (*Eucyon debonisi* from Venta del Moro) (Fig. 9, clade H; Supporting Information, Table S4) indicate that the South African species has a more robust dentition (P4–M2 and p4) with relatively more elongated second molars (M2 and m2) (Figs 11, 12). These characters not only distinguish *E. khoikhoi* from *E. davisi*, but also from some of the living Canini species from the African continent, including *Lupulella* Hilzheimer, 1906 and *Canis*, with the exception of the side-striped jackal *Schaeffia adusta* Hilzheimer, 1906.

Other African fossil forms included in the phylogenetic analysis, like *Eucyon wokari* from the Early Pliocene of Aramis Member (4.4 Mya), Sagantole Fm, in the Middle Awash Valley, Ethiopia (García, 2008), ?*Nyctereutes barryi* from the Early/ Late Pliocene of the Upper Laetoli Bed (3.7–3.4 Mya) (Su & Harrison, 2007; Werdelin & Dehghani 2011) and *Lupulella mohibi* from the Middle Pleistocene of Oulad Hamida 1 Quarry (0.5 Mya) (Geraads, 2011), are grouped with *E. khoikhoi* and *Schaeffia adusta* (Fig. 9, clade E; Supporting Information, Table S4), although the relationships between the species in the group are not resolved. This African clade is characterized by a paraoccipital process fused with the bulla in most of its length, long M2 in relation with
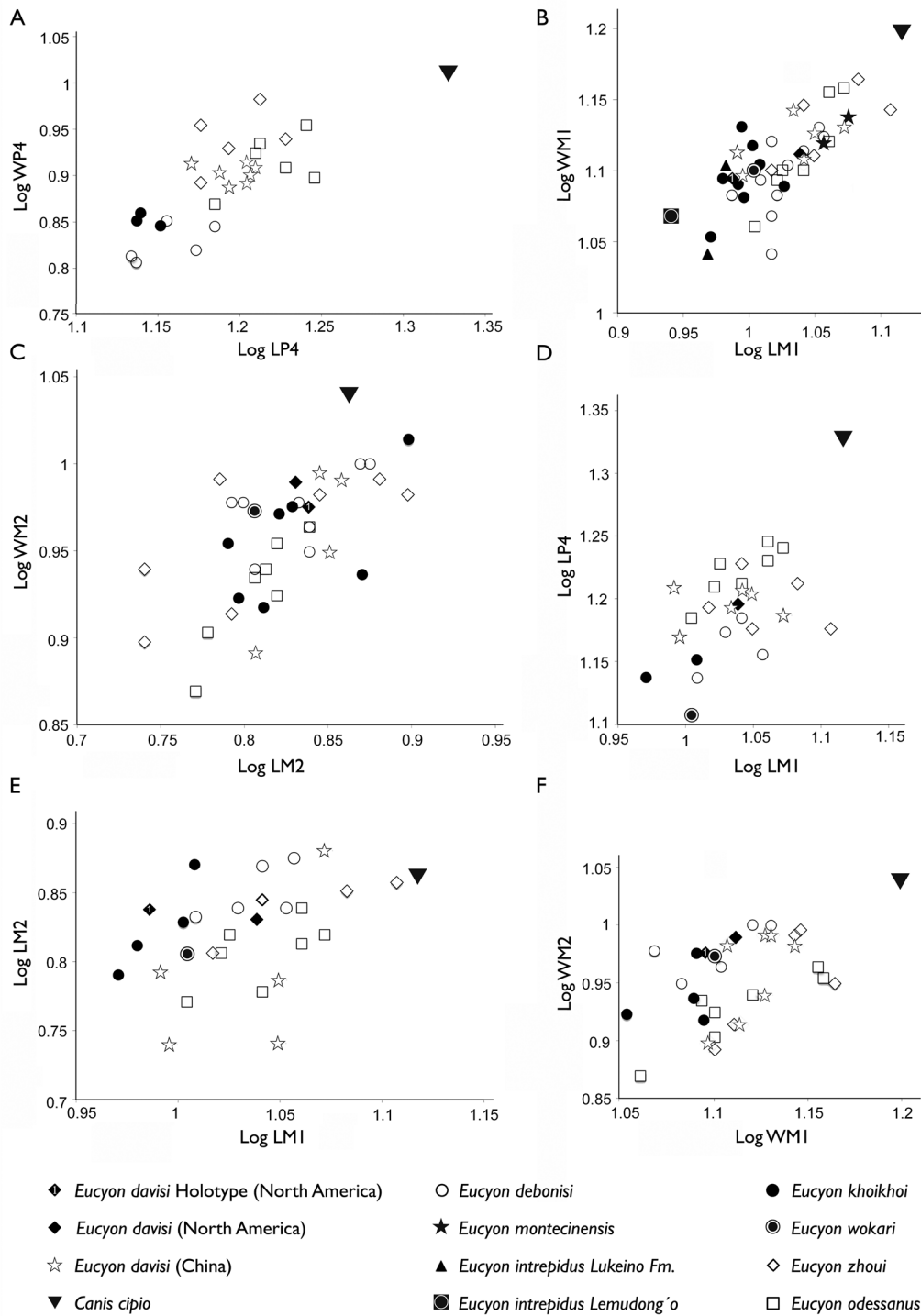
Figure 11. Bivariate plot comparing the upper dentition of *Eucyon khoikhoi*, with other *Eucyon* spp. from North America, Europe, and Africa. A, P4; B, M1; C, M2; D, lengths of M1 and P4; E, lengths of M1 and M2; F, widths of M1 and M2. Abbreviations: L, length; W, width. Sources: Tedford & Qiu (1996) and Tedford *et al.* (2009) for *E. davisi* from North America and China and *E. zhoui* from China; Crusafont (1950) for *C. cipio*; Montoya *et al.* (2009) for *E. debonisi*; Rook (1992, 1993) for *E. monticinensis* and *E. odessanus*; Morales *et al.* (2005) for *E. intrepidus* from Lukeino Fm; Howell & García (2007) for *E. intrepidus* from Lemudong´o; García (2008) for *E. wokari*; and this work for *E. khoikhoi*.
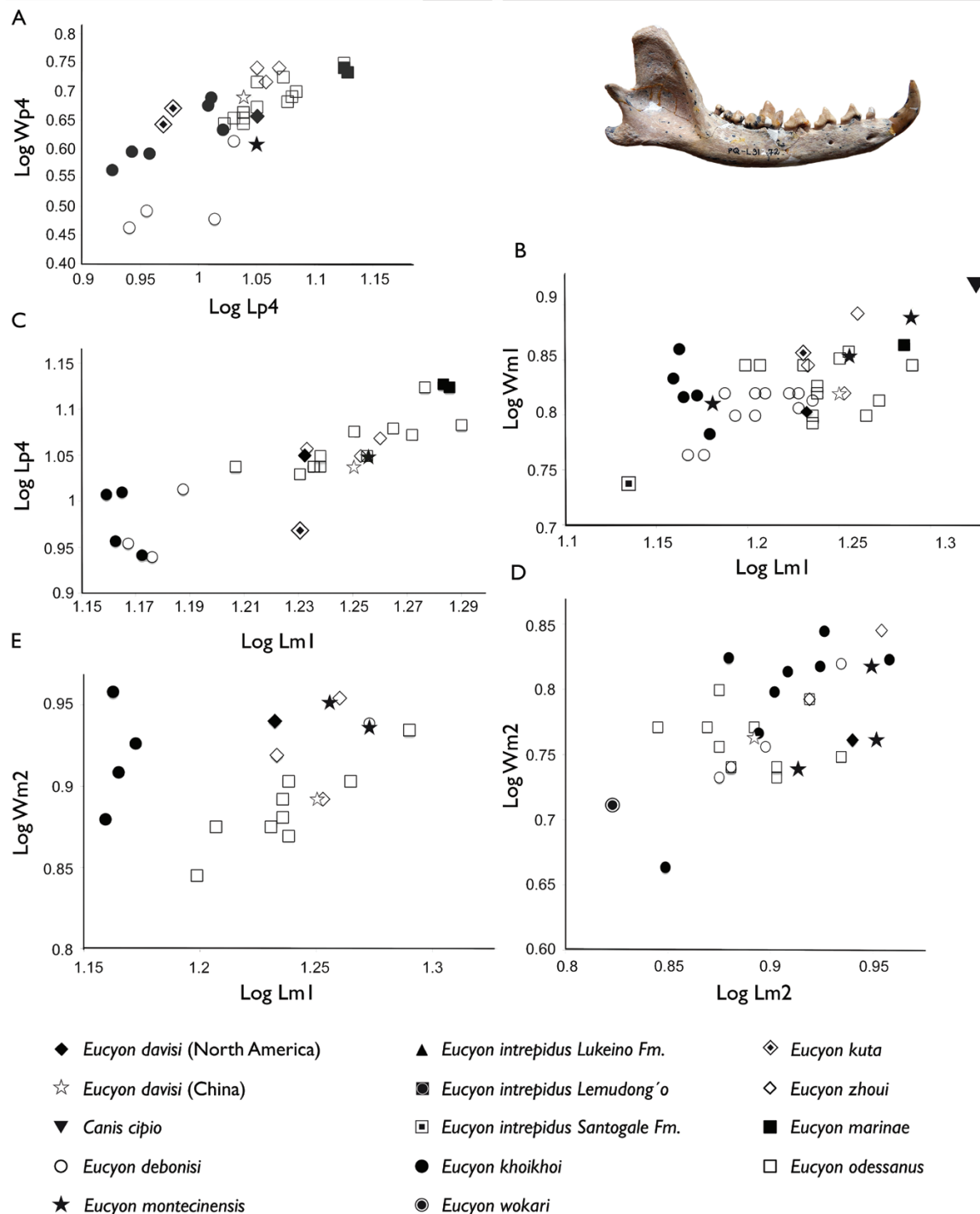
Figure 12. Bivariate plot comparing the lower dentition of *Eucyon khoikhoi*, with other *Eucyon* spp. from North America, Europe, and Africa. A, p4; B, m1; C, lengths of m1 and p4; D, m2; E, lengths of m1 and width m2. Abbreviations: L, length; W, width. Sources: Tedford & Qiu (1996) and Tedford *et al.* (2009) for *E. davisi* from North America and China and *E. zhoui* from China; Pons-Moyà & Crusafont (1978) for *C. cipio*; Montoya *et al.* (2009) for *E. debonisi*; Rook (1992, 1993) for *E. monticinensis* and *E. odessanus*; Morales *et al.* (2005) for *E. intrepidus* Haile-Selassie & Howell (2009) for *E. intrepidus* from Santogale Fm; García (2008) for *E. wokari*; Werdelin *et al.* (2014b) for *E. kuta*; Spassov and Rook (2006) for *E. marinae*; and this work for *E. khoikhoi*.

P4 and M1, m1 relatively robust and m2 relatively long. The morphology of the m1 of *E. wokari* differs from *E. khoikhoi* by the greater development of the transverse cristid, which closely links the hypoconid with the entoconid as occurs in the living jackals *s.l.* (García, 2008; Tedford *et al.*, 2009). The Ethiopian species has a robust m2 and a long M2 in relation to P4 like *E. khoikhoi*; thus, the association of an advanced morphology in the m1 talonid with the large size of the second molars links *E. wokari* close to the side-striped jackal *S. adusta*. The canid from Laetoli, ?*Nyctereutes barryi*, is another component of this group, previously determined by Barry (1987) as New Genus aff. *Canis brevirostris* Ewer, 1956, suggesting a close relationship with *Nyctereutes donnezani* Depéret, 1890, in particular with the material described from Layna (Spain) by Soria & Aguirre (1976). Werdelin & Dehghani (2011) revised this form, proposing a new species ?*Nyctereutes barryi* with dental morphology intermediate between that of *N. donnezani* and *Nyctereutes tingi* Tedford & Qiu, 1991, but maintaining the same doubts about the generic attribution of Barry (1987). Werdelin & Dehghani (2011) noted that ?*N. barryi*, as well as *N. tingii*, lack the subangular lobe of the mandibular ramus trait typical of more derived species of *Nyctereutes*. Finally, *Lupulella mohibi* from the Middle Pleistocene of Morocco has a clearly hypocarnivorous dentition, which resembles that of some *Nyctereutes* species, but neither the skull nor the mandible correspond to that of the modern species of this genus (Geraads, 2011), in our tree are nested with *Schaeffia adusta*, and because of the low node support, we provisionally assigned it as ?*Schaeffia mohibi* (Figs 9, 10).

All the species grouped in clade E (Fig. 9) have hypocarnivorous dentition to a greater or lesser degree, as occurs in *Nyctereutes* species. None of the mandibles of *E. khoikhoi*, ?*N. barryi*, ?*S. mohibi* and *S. adusta* present the characteristic morphology of *Nyctereutes*, not even incipient. Nevertheless, some African species, such as *Nyctereutes terblanchei* Broom, 1948 (see also Ficcarelli *et al.*, 1984) and *Nyctereutes lockwoodi* Geraads *et al.*, 2010, possess mandibular characteristics that could be correlated with the species of *Nyctereutes* from the Pliocene of Europe. Alternatively, Reynolds (2012) has discussed in depth the presence of *Nyctereutes* in African fauna, concluding that it is not present on this continent. Thus, this hypocarnivore clade (Fig. 9, clade E) is more closely related to *Eucyon* species than to the clade of *Lupulella–Canis*, which is important support to consider for the independent generic status of the extant *Schaeffia adusta*, that Van den Brink (1973) and Zrzavý & Řičankova (2004) have proposed. More recently, the segregation of *S. adusta* from the

species of the *Canis* group has been suggested in other molecular works (Atickem *et al.*, 2017; Viranta *et al.*, 2017; Taron *et al.*, 2021), but not taxonomically formalized. Our phylogenetic analysis clearly shows the separation of *E. khoikhoi* from the group formed by *Lupulella–Canis* (Fig. 9, clade A); characterized by a patent hypercarnivorous tendency of the dentition, especially by the elongation of the carnassial teeth with respect to the molar dentition, and an m1 with a transverse cristid and reduced hypoconulid shelf (Supporting Information, Table S4). The inclusion in this group of the controversial *Canis cipio* – from the older geological levels of Concud, Spain (7.9–7.0 Mya) (Crusafont, 1950; Pons-Moyà & Crusafont, 1978; Rook, 1993, 2009; Tedford *et al.*, 2009) – morphologically is not surprising, being more derived than the basal forms of the *Canis* group considered here as *Lupulella mesomelas* and *Canis lupaster* (Figs 9, 10). Several traits, such as the relative elongation of the P4 compared with M2, the P4 protocone mesially positioned and reduced, and the elongated and derived m1 – presence of a transverse cristid, absence of pre-entoconid, and both reduced metaconid and hypoconulid shelf – support its position in our phylogeny. Consequently, our analysis refutes the inclusion of *C. cipio* within the *Eucyon* species group, as recently has been proposed in Rook (2009) and Bartolini Lucenti & Rook (2020). It does not solve the enigma of the presence of such a derived *Canis* species in geological levels prior to the arrival of the first *Eucyon* on the Old World – with *Eucyon debonisi* from the Venta del Moro site, Spain dated 6.22 Mya (Montoya *et al.*, 2009; Gibert *et al.*, 2013; Morales *et al.*, 2013) (Fig. 10). This problem has been exacerbated with the re-assignation of *Canis ferox* as *Eucyon ferox*, also proposed by Bartolini Lucenti & Rook (2020) – which is supported in our analysis – and that places the oldest North American record of *Canis* ca. 5 Mya with *Canis lepophagus* Johnston, 1938 from the beginning of the Pliocene (Tedford *et al.*, 2009). Consequently, if we accept the generic determination of *Canis cipio*, the separation of *Canis* from *Lupulella mesomelas* would be placed at least between 7.9 and 7.0 Mya, a hardly assimilable hypothesis. The robustness of the clade formed by *Lupulella mesomelas*, *Canis lupaster* and *Canis lupus* is strongly supported in most of the molecular analyses that have included these three taxa (e.g. Atickem *et al.*, 2017; Viranta *et al.*, 2017).

Eucyon kuta from the Woranso-Mille Area, 3.82– 3.57 Mya, as noted by Werdelin *et al.* (2014b), could represent the most modern and largest species of *Eucyon* recorded in Africa. It is known by two hemi-mandibles. The p2 and p3 are more robust than those of *E. khoikhoi*. This Ethiopian canid has a relatively longer m1 than the South African taxon (Fig. 12B). These characteristics support their separation from

the *E. khoikhoi* clade, it could probably be included closer to the African Pliocene hypercarnivore group (*Lupulella*), which certainly needs to be reviewed.

<div align="center">PALAEOBIOLOGICAL ASPECTS</div>

Postcranial remains of *Eucyon* are rare, with the exception of the articulated skeleton F:AM 63010 of *E. davisi* figured, but not described, by Tedford *et al.* (2009), some large bones of the recently considered member of this genus *E. ferox*, also figured in the former work, some long bones of *E. montecinensis* described in Rook, (1992) and a few tarsals from *E. debonisi* described by Montoya *et al.* (2009). *Eucyon* was the earliest members of the subfamily Caninae to show, undoubtedly, the modern neck morphology associated with the presence of the nuchal ligament, and developed proportionally longer forelimbs than any of its earlier relatives, probably reflecting an adaptation to drier, more open environments and wider foraging areas (Wang *et al.*, 2008). Although we cannot demonstrate the presence of the attachment of the nuchal ligament in the axis of *Eucyon khoikhoi*, its resemblance with those of the living jackals, points to its presence. This canid possesses a comparable skeleton to that of *E. montecinensis* and *E. davisi*, but with some minor differences in the long-bone proportions. Compared with the known dimension of the maximum length of the radius, *E. khoikhoi* (134.94 and 124.11 mm) and, in lesser degree, *E. monticinensis* (120.43 mm), have a relatively elongated radius to those of the primitive *E. davisi* (114.6 mm) (Tedford *et al.*, 2009) (Supporting Information, Table S2). The length of the Mc III is comparable among the three species. The South African species also differs to the type species and the Italian one in the slenderer tibia. Based on the known dentognathic and postcranial remains of *Eucyon* spp., we have calculated their body mass and compared them with some living canini and vulpini (Supporting Information, Table S5). The new canid from Langebaanweg has a body mass estimation of 8.944 kg (5.187–12.547 kg), which is bigger than the East African *E. intrepidus*, but similar to others from Africa, like *E. kuta*, and the European *E. monticinensis* and *E. debonisi*. Our body mass inferences indicate that *E. khoikhoi* is smaller than the Eurasian Late Pliocene *E. marinae*, *E. odessanus* and *E. zhoui*, and is much smaller than the North American *E. ferox* [23.5 kg following Bartolini Lucenti & Rook (2020)]. Thus, the body mass of *E. khoikhoi* is analogous to the females of *L. mesomelas*, and similar to the average for the species *Canis aureus*. The overall morphology of the skull, dentition and postcranial skeleton of *E. khoikhoi* suggests that it may have had a comparable role in the ecosystem to those of the living African jackals, more specifically, like the side-striped jackal (*Schaeffia adusta*), which possesses the most hypocarnivorous/omnivorous scavenger diet of these jackals (Ewer, 1956, 1973; Van Valkenburgh & Koepfli, 1993; Nowak, 2005).

<div align="center">CONCLUSION</div>

The description of the unpublished material of Canidae from Langebaanweg, (South Africa) allows us to define a new species: *Eucyon khoikhoi*. This new species contributes substantially to the knowledge of the initial Canidae radiation in Africa, for the quality of the sample that includes cranial, dentognathic and postcranial bones from a site close to the Mio-Pliocene boundary and close to the first records of this family in the Old-World continents. The differences with respect to the type species *Eucyon davisi*, the oldest and better-known species *Eucyon ferox* (North America) and *Eucyon debonisi* (western Europe) are clear, and indicate that the South African species has a more robust dentition, with more elongated second molars. Our phylogenetic analysis shows that *E. khoikhoi* is the most basal canini of an African clade composed of *E. wokari* + ?*Nyctereutes barryi* + ?*Schaeffia mohibi* + *Schaeffia adusta* (extant side-striped jackal). We also suggest that the Late Miocene *Eucyon intrepidus* from East Africa could belong to the same clade, and the Middle Pliocene *Eucyon kuta* could represent a different member, being more closely related with the *Lupulella* group.

her assistance with the etymology of the new species. We also thanks the editor M. Christenhusz, and two anonymous reviewers for their useful comments and suggestions, which significantly improved the original manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Postcranial measurements used in this work. A, B, atlas: A, ventral; B, cranial views. C, D, axis: C, lateral; D, ventral views. E, F, cervical vertebrae (C3–7): E, lateral; F, cranial views. G, H, caudal vertebra: G, lateral; and H, dorsal views. I–K, humerus: I, cranial; J, lateral; K, proximal views. L–O: radius: L, proximal; M, distal; N, cranial; O, medial views. P, Q, ulna: P, cranial; Q, medial views. R, scapula, ventral view; S, T: metacarpals: S, lateral; T, dorsal views. U, V, first phalanges: U, dorsal; V, proximal views. W, X, second phalanges: W, dorsal; X, proximal views. Y, Z, ungual phalange: Y, lateral; Z, proximal views. Aa, Ab, pyramidal: Aa, lateral; Ab, dorsal views. Ac, Ad, magnum: Ac, medial; Ad, dorsal views. Ae, Af, ectocuneiform: Ae, medial; Af, proximal views. Ag, Ah, tibia: Ag, cranial; Ah, lateral views. Meaning of the measurements: atlas: 1, maximum width; 2, lateromedial width of the cranial articular processes; 3, craniocaudal length of the vertebral body; 4, lateromedial width of the caudal articular processes; 5, dorsoventral height; 6, width of the wing. Axis: 1, length of the vertebral body; 2, maximum dorsoventral height; 3, lateromedial width of the articular process; 4, lateromedial width of the transverse processes; 5, height of the spinous process; 6, length of the spinous process. Cervical vertebrae (C3–7): 1, length vertebral body; 2, lateromedial width of the transverse processes; 3, maximum height. Caudal vertebrae: 1, length vertebral body; 2, lateromedial width of the transverse processes. Humerus: 1, maximum total length; 2, craniocaudal length of the proximal epiphysis; 3, lateromedial width of the proximal epiphysis; 4, proximodistal height of the humerus head; 5, lateromedial width of the diaphyseal shaft measured at the last third of the bone, where the lateral crest of m. anconeus finish; 6, craniocaudal width of the previous measurement (5); 7, height of the medial epicondyle; 8, maximum lateromedial width of the distal epiphysis; 9, lateromedial

length of the trochlea–capitulum; 10, craniocaudal height of the trochlea–capitulum; 11, craniocaudal width of the lateral epicondyle including the capitulum. Radius: 1, total length; 2 (lateromedial); 3, (craniocaudal) widths of the proximal epiphysis; 4, (lateromedial); 5, (craniocaudal) widths of the middle point of the diaphysis; 6, (lateromedial); 7, (craniocaudal) widths of the distal epiphysis. Ulna: 1, maximum total length; 2, maximum lateromedial width; 3, maximum craniocaudal width of the olecranon tuber; 4, proximodistal height of the proximal epiphysis of the ulna, measured from the proximal edge of the olecranon to the distal edge of the radial notch; 5, proximodistal height of the trochlear notch; 6, proximodistal height of the olecranon; 7, lateromedial width of the radial notch, comprising both medial and lateral coronoid processes; 8 (lateromedial), 9 (craniocaudal) widths of the middle point of the diaphysis. Scapula: 1, craniocaudal length of ventral angles comprising the glenoid fossa and supraglenoid tubercle. Metacarpal: 1, (dorsopalmar), 2, (lateromedial) widths of the proximal epiphysis; 3, total length; 4, (dorsopalmar), 5, (lateromedial) widths of the middle point of the diaphysis; 6, (dorsopalmar), 7, (lateromedial) widths of the distal epiphysis. First–second phalanges: 1, total length; 2, lateromedial width of the proximal epiphysis; 3, lateromedial width of the distal epiphysis; 4, dorsopalmar height of the proximal epiphysis. Ungual phalanges: 1, total length; 2, lateromedial width of the proximal epiphysis; 3, maximum dorsopalmar height. Pyramidal: 1, maximum length; 2, maximum dorsopalmar width; 3, proximodistal height. Magnum: 1, maximum proximodistal width; 2, maximum dorsopalmar length; 3, lateromedial width of the palmar area; 4, lateromedial width of the dorsal area. Ectocuneiform: 1, maximum length; 2, craniocaudal length of the distal facet; 3, maximum width; 4, maximum height. Tibia: 1, lateromedial, 2, craniocaudal widths of the middle point of the shaft.

Data S1. Character–taxon matrix in nexus format.

Table S1. Location of *Eucyon khoikhoi* from Langebaanweg, including units, beds and horizons.

Table S2. Postcranial measurements (in mm) of the new specimens of *Eucyon khoikhoi* from Langebaanweg and *Eucyon monticinensis* from Brishiguela. Meaning of the measurements explained in Supporting Information, Figure S1.

Table S3. Descriptions of characters used in the phylogenetic analysis performed in this work.

Table S4. Synapomorphies for selected nodes (see Fig. 9), as indicated by character numbers followed by character states within parentheses. Italics denote ambiguous synapomorphies.

Table S5. Estimations on body mass of *Eucyon* spp. in kg, compared with living canini and vulpini. Abbreviations: F, females; L, length; M, males. Source: Van Valkenburgh (1990); Rook (1992, 1993); Anyonge (1993); Tedford & Qiu (1996); Spassov & Rook (2006); Haile-Selassie & Howell (2009); Montoya *et al.* (2009); Sillero-Zubiri (2009); Tedford *et al.* (2009); Figueirido *et al.* (2011); Werdelin *et al.* (2014b).