

# New *Eucyon* remains from the Pliocene Aramis Member (Sagantole Formation), Middle Awash Valley (Ethiopia)

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## Abstract

The Aramis Member (Sagantole formation) includes the Gàala Tuff Complex-Daam Aatu Basaltic Tuff interval which has produced a taxonomically diverse vertebrate assemblage including the primitive hominid *Ardipithecus ramidus*. New *Eucyon* remains recovered from this interval come from localities in the Aramis, Sagantole, and Kuseralee catchments. The chronology established for the GATC-DABT interval is 4.4 Ma. These recoveries represent the most abundant available *Eucyon* assemblage of the eastern African Pliocene. Here, *Eucyon* fossils from the Kapsomin and Lemudong'o Late Miocene Kenyan sites are compared with the Aramis representatives, showing comparable morphology although with smaller dimensions. *E. intrepidus*–*E. wokari* nov. sp., might constitute a single lineage, with increasing size and robusticity, and the derivation of some morphological traits mainly on the lower carnassial. *E. wokari* represents a new eastern species of the African Pliocene *Eucyon* lineage.

## Résumé

**Nouveaux restes d'*Eucyon* dans le Membre Aramis pliocène (Formation Sagantole) de la moyenne vallée de l'Awash (Éthiopie).** Le membre Aramis de la formation Sagantole inclut le « Gàlaa Tuff Complex-Daam Aatu Basaltic Tuff interval » qui a livré un ensemble varié de vertébrés, y compris l'hominidé primitif *Ardipithecus ramidus*. De nouveaux restes d'*Eucyon* récoltés dans cet intervalle proviennent de localités des stations d'Aramis, Sagantole et Kuseralee. L'âge de l'intervalle est de 4,4 Ma. Ces découvertes représentent l'échantillon numériquement le plus important du Pliocène d'Afrique de l'Est. Les restes d'*Eucyon* des sites du Miocène supérieur kenyan, Kapsomin et Lemudong'o, sont comparés à ceux d'Aramis, montrant une morphologie comparable, mais une taille plus faible. *E. intrepidus* et *E. wokari* n.sp. pourraient constituer une seule lignée, avec un accroissement de taille et une augmentation de robustesse, ainsi que quelques modifications morphologiques surtout sur la carnassière inférieure. *E. wokari* est une nouvelle espèce orientale dans la lignée des *Eucyon* du Pliocène africain.

**Keywords:** Canidae; *Eucyon*; Mio-Pliocene; Aramis; Middle Awash; Ethiopia

**Mots clés :** Canidae ; *Eucyon* ; Mio-Pliocène ; Aramis ; Aouache moyen ; Éthiopie

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## 1. Introduction

During the last decades, new canid material from the African Mio-Pliocene has increased our knowledge of the evolutionary history of this family. The idea that the first record of canids from eastern Africa was around 4–4.5 Ma was widely accepted until recently [10]. A newly recognized species, *Eucyon intrepidus*, from the Lukeino Formation, Baringo, Kenya [4 (p. 48)] is the first nominate species of *Eucyon* from Africa. Its diagnosis is mainly based on the small size of two upper first molars (BAR 2127'01 and BAR 719'02). Additional material recovered from Lemudong'o, Narok District, Kenya, consists of an upper first molar (KNM-NK41284) and a fragmentary lower first molar (KNM-NK 41285) assigned to this species [3]. This provided new knowledge on the morphology of this small *Eucyon* species. However, the African record of this canid species remains scant.

The published indications regarding the Lukeino Formation and Lemudong'o Late Miocene Kenyan sites considerably deepen the initial immigration of *Eucyon* into Africa, implying an expansion from Eurasia earlier than previously thought. Younger, about mid-Pliocene age occurrences of several canid taxa, including *Canis* sp., are reported from Laetoli (Tanzania) [1] and South Turkwell (Turkana, northern Kenya) [9]. In the latter instance, gnathic and several postcranial parts definitely attest to the genus *Canis* (*Canis* sp. nov. A of the authors, pp. 1176) at 3.5 Ma. In the former instance, incomplete cranio-dental and various postcranial remains are attributed to aff. *Canis brevirostris* (Ewer) by Barry [1 (pp. 237–240)], with a size comparable to extant *Nyctereutes*. This material exhibits features found within the morphometric range of *Eucyon* [6] and at a substantially younger mid-Pliocene age than the previously discussed Kenyan localities. The Langebaanweg (South Africa) cf. *Eucyon* [2,7] might represent a separate form with more robust upper molars (Morales, personal communication). At 4.4 Ma, the *Eucyon* finds from the Aramis Member therefore play an important role in characterizing the evolution and spread of canids in Africa during the Mio-Pliocene.

## 2. Geology and location of the canid remains

The Ethiopian rift system comprises the Afar Depression, the Main Ethiopian Rift, and a wide rifted zone located in the Southwest of the country. The Central Awash Complex is a domelike horst located in the southwestern Afar rift and includes the Sagantole Formation with alluvial and volcanic sediments, tephra and

basaltic lavas exposed. One of the Sagantole Members, Aramis, includes a thin stratigraphic interval between the Gāala Tuff Complex and the Daam Aatu Basaltic Tuff (GATC-DABT). This effectively isochronous, largely terrestrial unit has produced a taxonomically extensive vertebrate assemblage including the primitive hominid *Ardipithecus ramidus* [5,11].

The base of the Aramis Member is defined by the Gāala (camel) Tuff Complex (MA92-12), a 0.5–2-m thick, crystal-vitric tuff. The GATC variably overlies conglomerates and/or brown to orange silty clays of the underlying Haradaso Member. The Daam Aatu (baboon) Basaltic Tuff (MA92-38B) crops out a few centimetres to ~5 m above the GATC. The DABT ranges in thickness from a few centimetres to ~1 m. It is a poorly consolidated tuff composed chiefly of bedded and laminated dark grey basaltic glass lapilli and scoria in its lower third (~15–20 cm). This tuff was deposited subaerially on a remarkably flat landscape and was not reworked. Wolde-Gabriel et al. [12] reported  $^{40}\text{Ar}/^{39}\text{Ar}$  results and uniform chemical data on glass from different outcrops of the DABT. The DABT occurs in close association with the GATC along the eastern half of the Central Awash Complex. The chronology established for the GATC-DABT is 4.4 Ma [5].

The carnivore assemblage within the GATC-DABT interval comprises at least 14 species, Canidae (one species), Felidae (five species), Viverridae (one species), Herpestidae (at least three species), Hyaenidae (two species), Ursidae (one species), Mustelidae (one species). The canid remains are described below as *Eucyon wokari* nov. sp., a new, small to medium size *Eucyon* species. These finds come from the Aramis member (Sagantole Fm.) (GATC-DABT) from vertebrate paleontology localities: ARA-VP-1, -16, -17 and KUS-VP-2; and belong to a minimum of three different individuals. These remains are of special relevance given the scarce evidence of *Eucyon* at African sites during the Early Pliocene.

## 3. Description of the new species

### 3.1. Systematic paleontology

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Infraorder CYNIDEA Flower, 1869

Family CANIDAE, Gray, 1821

Subfamily CANINAE Fischer von Waldheim, 1817

Genus *Eucyon*, Tedford and Qiu, 1996

*Eucyon wokari* sp. nov.

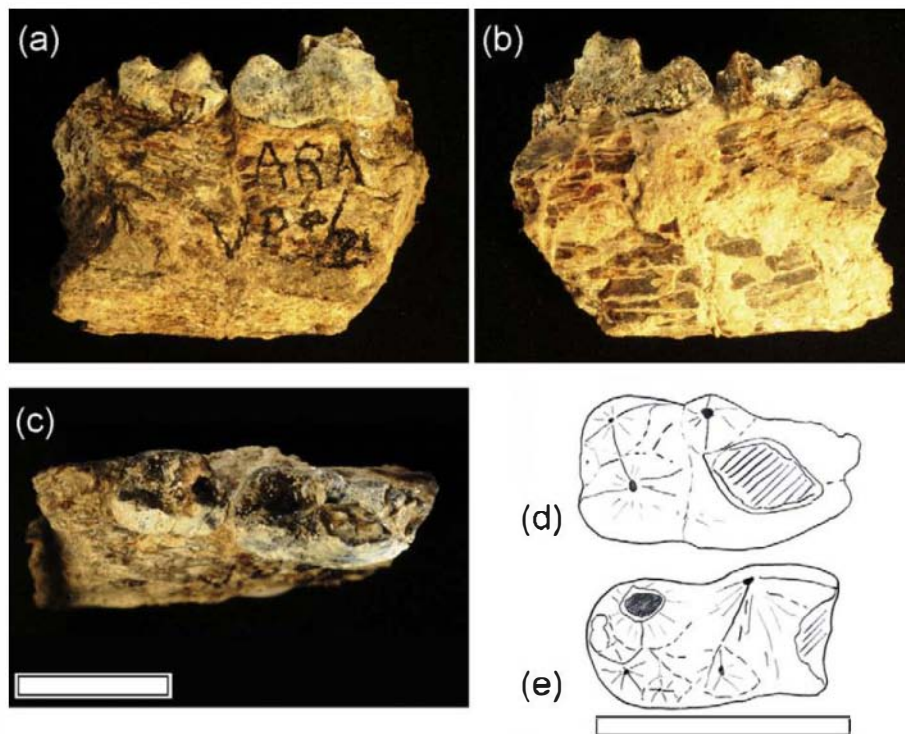


Fig. 1. Buccal (a), lingual (b) and occlusal (c): ARA-VP-6/21 right mandible fragment with m1–m2 of *Eucyon wokari*; (d): ARA-VP-6/21 right m1 (Aramis, Ethiopia); (e): KNM-NK-41285 left m1 of *E. intrepidus* (Lemudong'o, Kenya).

Fig. 1. Vues buccale (a), linguale (b) et occlusale (c): ARA-VP-6/21, fragment de la mandibule droite avec m1–m2 de *E. wokari*; (d): m1 droite: ARA-VP-6/21 (Aramis, Éthiopie); (e): m1 gauche: KNM-NK-41285 de *E. intrepidus* (Lemudong'o, Kenya).

**Type specimen:** right mandible fragment with M<sub>1</sub>–M<sub>2</sub> (ARA 6/21; Fig. 1).

**Measurements** (in millimetres). Holotype (ARA VP6/21): greatest length of m1 = 13.6; greatest breadth of m1 = 6; greatest length of m2 = 7.8; greatest breadth of m2 = 5.4; greatest length of molars (m1–m2) = 21.4.

**Other material:** right m2 (KUS VP-2/73) and left m2 (KUS VP-2/198) (Fig. 2); maxillary fragment (KUS VP-1/197; Fig. 3) with P4–M2; left upper C (ARA VP-1/2112); left (talón) of M1 (ARA1/137); left half of a femur –distal– (ARA 6/22); right half of a humerus –distal– (ARA 1/89); left proximal second metacarpal (ARA-VP-1/322).

**Derivatio nominis:** this canid is the size of a jackal and *wokari* is the name of the jackal in the local Afar language. The holotype and all other material is housed at the Ethiopian National Museum (Addis Ababa, Ethiopia).

**Locality:** Aramis and Kuseralee.

**Horizon and associations:** all the *Eucyon* specimens were located in the GATC-DABT interval. The chronology established for the GATC-DABT interval, from where the canid remains were recovered, is 4.4 Ma [5].

**Differential**

*E. monticiniensis* and *E. davisi* in a subtriangular outline

of the M1 compared with the quadrangular one observed in the Eurasian species. When compared to *E. intrepidus*, the m1 of *E. wokari* presents a more robust metaconid. It also shows a more robust talonid with additional differences: a more massive and pyramidal-shaped hypoconid. It presents a well-marked oblique crest, a posterior protoconid cristid oriented postero-buccally (parallel to the buccal margin), and an internal cristid that joins a simple metaconid. A tiny and very low hypoconulid can be distinguished, isolated from the other two cusps, resulting on a posterior open valley.

### 3.2. Description of the dental material assigned to *Eucyon*

Maxillary fragment (KUS-VP-1/197) with P4–M2; right mandible fragment with M1–M2 (ARA-VP-6/21); right m2 (KUS-VP-2/73); left m2 (KUS-VP-2/198); left C<sup>0</sup> (ARA-VP-1/2112); left (talón) of M1 (ARA-VP-1/137). On the basis of the locality where the remains were found and additional dental criteria, a minimum number of three adult individuals was calculated; one each from Aramis VP-1, -6 and Kuseralee VP-2.

The morphology and size of the dentition is mostly comparable to the samples attributed to the genus *Eucyon*



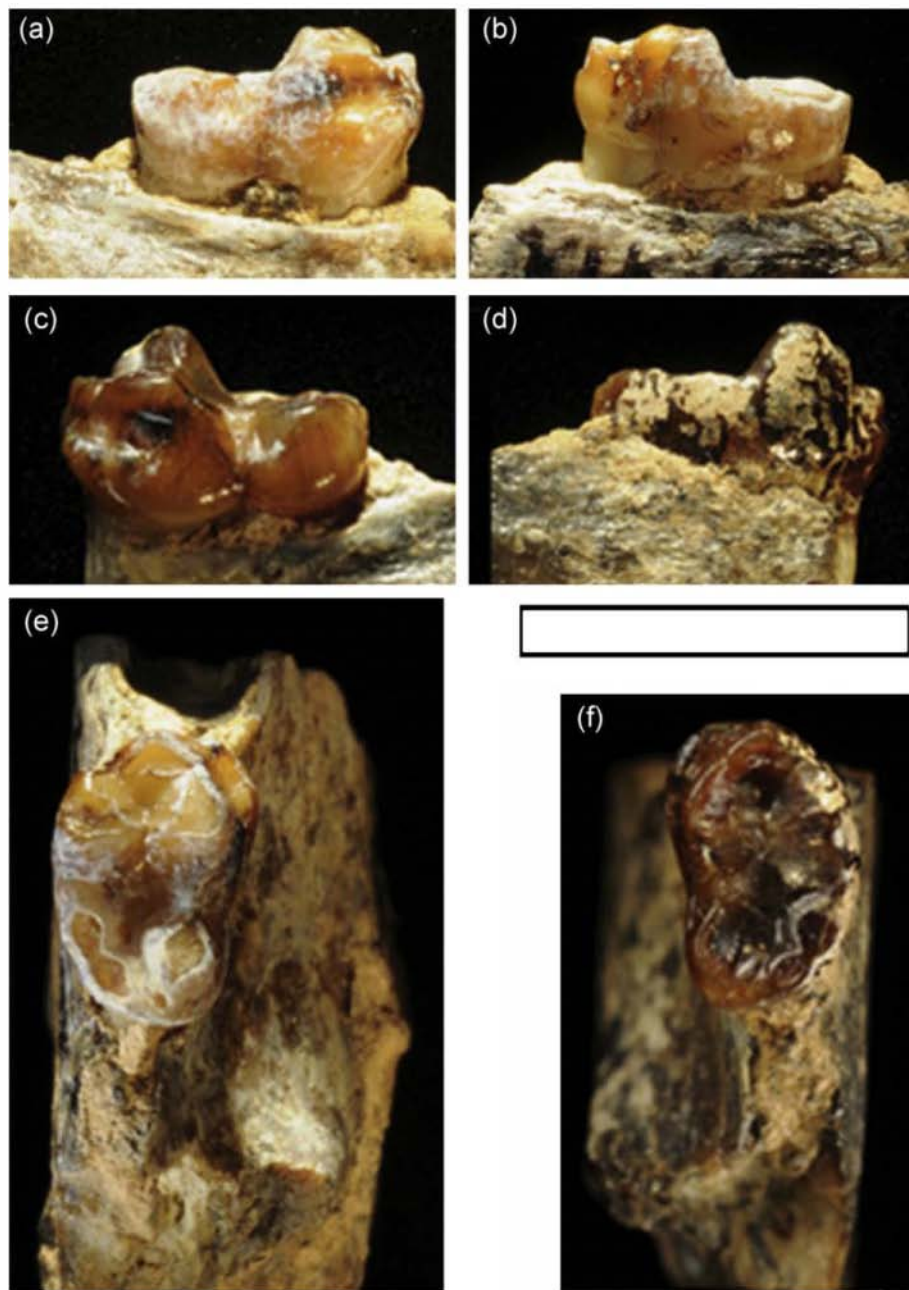


Fig. 2. KUS-VP2/73 (right m2): labial (a), lingual (b); KUS-VP2/198 (left m2): labial (c), lingual (d); (e): KUS-VP2/73; (f): KUS-VP2/198 (both occlusal). Scale bar 1 cm.

Fig. 2. KUS-VP2/73, (m2 droite): vues labiale (a), linguale (b); KUS-VP2/198 (m2 gauche): vues labiale (c), linguale (d); (e): KUS-VP2/73; (f): KUS-VP2/198 (toutes deux en vue occlusale). Barre d'échelle 1 cm.

[8]. A comparison of dimensions in such samples and the Aramis dental material is presented in Table 1.

### 3.2.1. Upper teeth

KUS-VP-1/197 is a left maxillary fragment that preserves the posterior portion of a third premolar, a broken carnassial with missing protocone and damaged blade, a well preserved upper first and second molar (partially worn), and a broken alveolous of an M3 (Fig. 3).

The M1 of KUS-VP-1/197 is robust, with larger dimensions than the small *E. intrepidus*. It falls within the smallest *E. davisi* (one individual), but is still smaller than all the Eurasian species (Table 1 and Fig. 4).

The Lukeino (BAR 212'01) and Lemudong'o (KNM-NK 41284) M1s present an almost identical pattern, for what the original attribution *E. aff. intrepidus* [3] should be now considered as *E. intrepidus*.

The M1 of KUS-VP-1/197 (Fig. 3) has a subtriangular shape, a slightly incurved distal crown border,

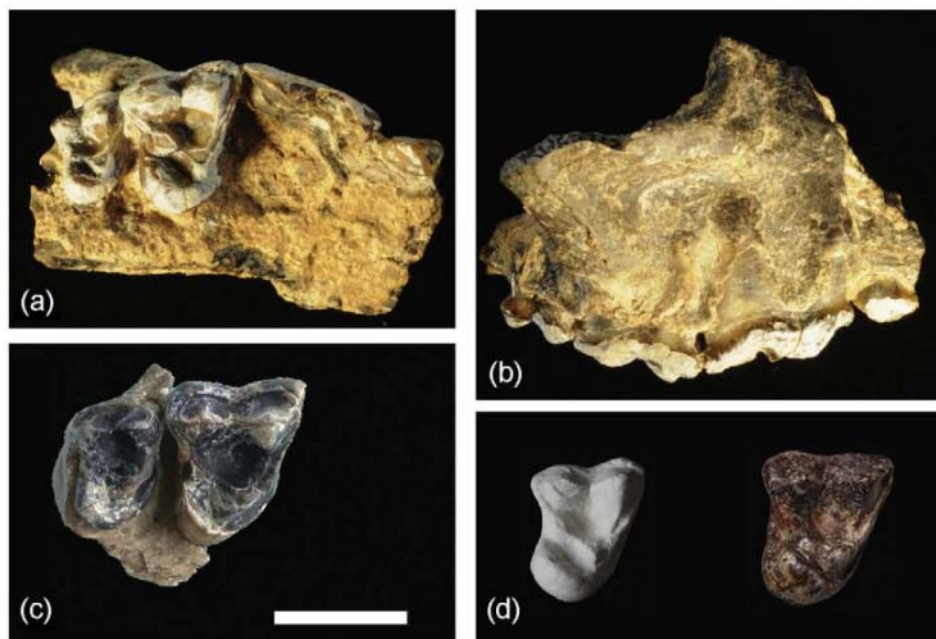


Fig. 3. Occlusal (a) and buccal (b): KUS-VP-1/197 left maxillary fragment of *Eucyon* from Aramis, with a partial P3, a broken P4, M1, M2 and alveolus of M3; (c): UCMP 545 left maxillary fragment with M1–M2 of *E. davisi* (holotype) from Rattlesnake; (d): right M1 of *E. intrepidus* from (right) Lukeino (BAR 212'01 holotype) and (left) Lemudong'o (KNM-NK 41284). Scale bar 1 cm.

Fig. 3. Vues occlusale (a) et buccale (b) : KUS-VP-1/197 : fragment de maxillaire gauche de *Eucyon* en provenance d'Aramis, avec une P3 partielle, une P4 cassée, M1, M2 et une alvéole de M3; (c) : UCMP 545 : fragment de maxillaire gauche, avec M1–M2 de *E. davisi* (holotype) en provenance de Rattlesnake; (d) : M1 droite de *E. intrepidus* en provenance de Lukeino, pour la droite (BAR 212'01 holotype) et de Lemudong'o (KNM-NK 41284) pour la gauche. Barre d'échelle 1 cm.

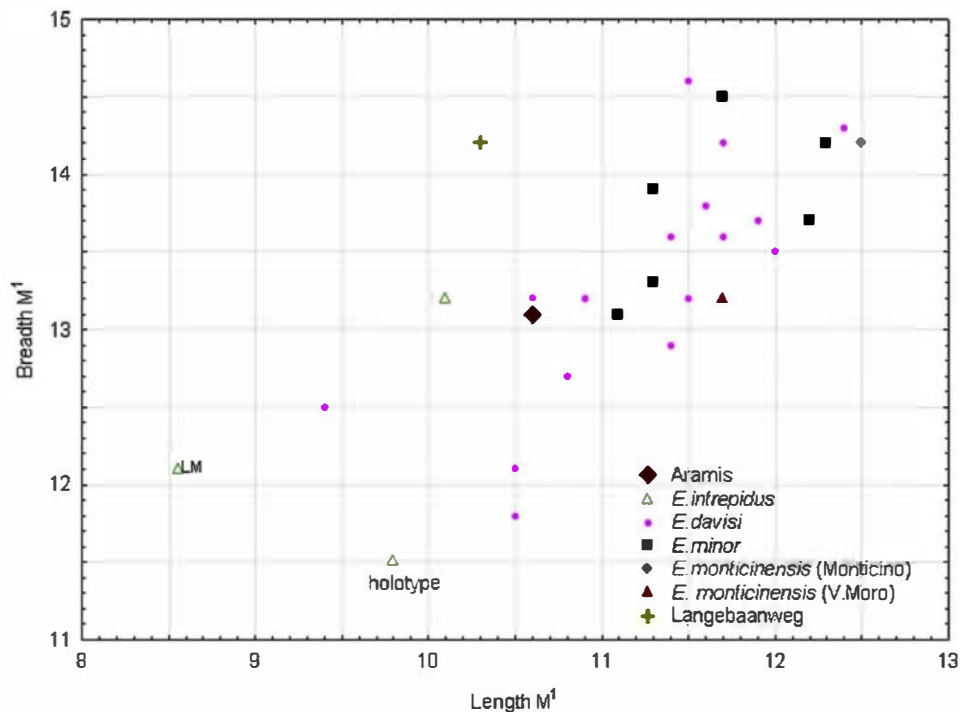


Fig. 4. Plot of length/breadth relationship of upper M1 of *Eucyon* species. Data for *E. intrepidus* (Lukeino) are from [4], for *E. aff. intrepidus* (Lemudong'o) from [3], for *E. monticinensis* (Brisighella and Venta del Moro) after [6], for *E. davisi* and *E. odessanus* are from [7], for *E. minor* are from [8] and for Langebaanweg are from [1]. All reported measurements are in millimetres.

Fig. 4. Relations longueur-largeur de la M1 supérieure de l'espèce *Eucyon*. Les données pour *E. intrepidus* (Lukeino) proviennent de [4], pour *E. aff. intrepidus* (Lemudong'o) de [3], pour *E. monticinensis* (Brisighella and Venta del Moro) d'après [6], pour *E. davisi* et *E. odessanus* de [7], pour *E. minor* de [8] et pour Langebaanweg de [1]. Toutes les mesures reportées sont indiquées en millimètres.

Table 1

Comparison of upper dental dimensions in *Eucyon*.

Tableau 1

Comparaison entre les dimensions des dents supérieures d'*Eucyon*.

|                     | <i>E. wokari</i> nov. sp.<br>(Aramis) KUS VP1/197 | <i>E. aff. intrepidus</i><br>(Lemudong'o)<br>KNM NK 41284 | <i>E. intrepidus</i><br>(Lukeino) BAR<br>2127'01 | <i>E. intrepidus</i> (Lukeino)<br>BAR 719'02 | <i>E. monticinus</i><br>(Brisighella)<br>BRS24/12 | <i>E. monticinus</i> (Venta del<br>Moró) ILM VM1-VM5 | <i>E. davisi</i><br>(average) |
|---------------------|---|---|--|--|---|--|-------------------------------|
| <i>P4</i>           |   |   |  |  |   |  |                               |
| Length              | 12.8  |   |  |  |   | 16.7   | 16.4                          |
| <i>M1</i>           |   |   |  |  |   |  |                               |
| Width               | 12.6  | 8.06  | 9.3  | 9.6  | 13.7  | 12.7   | 12.8                          |
| Length              | 10.1  | 11.6  | 11   | 12.7   | 12  | 11.2   | 10.8                          |
| <i>M2</i>           |   |   |  |  |   |  |                               |
| Width               | 9.4   |   |  |  |   | 9.2  | 9.1                           |
| Length              | 6.3   |   |  |  |   | 6.8  | 6.9                           |
| Length <i>P4-M2</i> | 27.2  |   |  |  |   |  |                               |
| Length <i>M1-M2</i> | 16.3  |   |  |  |   |  |                               |

Data for *E. intrepidus* (Lukeino) are from [2], for *E. aff. intrepidus* (Lemudong'o) from [3], Measurements of *E. monticinus* after [12] and *E. davisi* are from [6]; all reported measurements are in millimetres.

a well-developed buccal cingulum, and a distinct parastyle. Paracone and metacone are subequal, not very high, and pyramidal. The well-developed protocone and metaconule join in the middle, creating one continuous wear facet connected mesially to the parastyle and distally to the buccal cingulum. An anterior cingulum is present, and a postero-lingual cingulum is stronger and is as high as the protocone (looking like an hypocone). A deep fissure, open mesio-distally, separates this hypocone-like elevation from the area formed by the trigon cusps and connected by crests.

The M2 of KUS-VP-1/197 (Fig. 3) follows the same subtriangular outline as the M1, with subequal paracone and metacone and evident buccal cingulum. No parastyle is observed. The protoconid is well developed and is joined to a tiny but distinguishable metaconule. The postero-lingual cingulum is large. In general the M2 shows a very similar morphology to the M1.

No M2s have been recorded from Lukeino or Lemudong'o, and this molar is also absent from the published material from Langebaanweg. Its morphology remains unknown for *E. intrepidus* and for the African record.

The Aramis specimen differs from *E. davisi* in displaying a subtriangular outline rather than the quadrangular shape seen in the North American *Eucyon*.

### 3.2.2. Lower teeth

ARA-VP-6/21 is a right mandible fragment with m1-m2, and the mesial part of the alveolus of an m3 (Fig. 1). Them1 is incomplete, lacking part of the mesio-lingual (paraconid) portion of the trigonid. It shows scant wear. In order to compare this fossil with *E. intrepidus*, we have used the specimen described from Lemudong'o (KNM-NK 41825) [3] because no m1 was found at the type locality (Lukeino). The mesiolingual portion of the trigonid is also missing in this m1, but the rest is well preserved, and the wear stage between both molars is similar.

The m1 of ARA-VP-6/21 has a salient protoconid with the usual steep, sub-vertical distal slope to the talonid. There is a distinct but low buccal cingulum at the base of the protoconid. The buccal side of the protoconid expands, showing a well-rounded profile that differs from *E. intrepidus* from Lemudong'o, in which it drops vertically. The metaconid is distinct, enlarged, and disto-lingually offset from the back of the protoconid. The talonid is broad and bears a marginal hypoconid, and a larger, very robust, more posterior, and simple marginally placed entoconid (differing from *E. intrepidus* from Lemudong'o). These cusps are connected by a tiny cristid. The posterior-most part of



the talonid basin is simple (minute hypoconulid) and is placed apart from the entoconid and hypoconid. In *E. intrepidus*, the talonid presents a small hypoconulid constricted by the entoconid and hypoconid, closing the molar posteriorly. The lingual outline of the talonid is almost straight (differing from Lemudong'o, which is slightly convex) and the buccal outline is slightly incurved between the protoconid and hypoconid (but does not show any constriction evident in the Lemudong'o specimen).

The m2 of ARA-VP-6/21 is also scarcely worn, and presents a strong labial cingulum, a double entoconid, and a high protoconid (Fig. 2).

Two more m2s have been recovered from the Aramis Member: KUS-VP-2/198 is a left m2 and KUS-VP-2/73 is a right m2. Both specimens present a considerable wear stage and show a similar morphological pattern that could include them within the same individual. The pattern observed in these two molars is identical to the one on place (ARA-VP-6/21). Second lower molars are not represented in any of the sites with *E. intrepidus*, so comparisons with this species are not possible.

#### 4. Comparisons and discussion

The M1 of *E. monticinis* [6] is not only more robust and quadrangular-shaped than any African representatives, but also presents a very straight buccal side, rather than rounded, with a constriction dividing paracone and metacone. *E. minor* also presents larger dimensions, with subequal protocone and metacone and very pronounced parastyle [7], differing from the African forms.

*E. wokari* differs from *E. intrepidus* (Kapsomin and Lemudong'o) by its larger dimensions in all molars which are still smaller than the Eurasian species and *E. davisii*. Furthermore, the M1 shows a paracone subequal to metacone, and smaller relative heights of the buccal cusps (which are higher and sharper in *E. intrepidus*, especially in the paracone). The differences with *E. intrepidus* from Lemudong'o lie in the lower carnassial, related not only with the distinct robustness, but with some specific traits observed in the talonid. Together, these indicate that a different species of *Eucyon* was present in the Pliocene of Ethiopia.

The *Eucyon* remains identified in GATC-DABT comprise at least three individuals, described here as a new species, based mainly on differences detected on the lower carnassial, and on intermediate dimensions between the larger Eurasian *Eucyon* species and the small *E. intrepidus*. Generally, the molars of the Aramis canid are more heavily built, and all cusps are more robust, which brings the idea of a robusticity increase

during the Mio-Pliocene. Differences in the upper first molar within this proposed African lineage are less evident, although the two *E. intrepidus* (coming from different Late Miocene sites) present a pattern which is somewhat different than the Aramis one, especially in the high, sharp and unequal metacone and paracone, compared to the subequal, low cusped condition observed in *E. wokari*.

Morphological differences are even clearer in the lower carnassial, when comparing the Aramis fossil and *E. intrepidus* from Lemudong'o. All cusps show a more robust pattern in *E. wokari*, but also display a different talonid pattern from its likely forerunner Miocene species.

The remains from Aramis represent, up to date, the most abundant *Eucyon* assemblage of the East African Pliocene. *E. wokari* might represent a new eastern African chronospecies of this canid lineage that inhabited during the Pliocene and further morphological analyses will considerably improve our knowledge of this group. The Langebaanweg (South Africa) cf. *Eucyon* (Hendey 1974, Rook, 1993) might represent a separate form, although deeper analyses are needed to understand the full pattern of *Eucyon* relationships and its evolution in Africa.

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