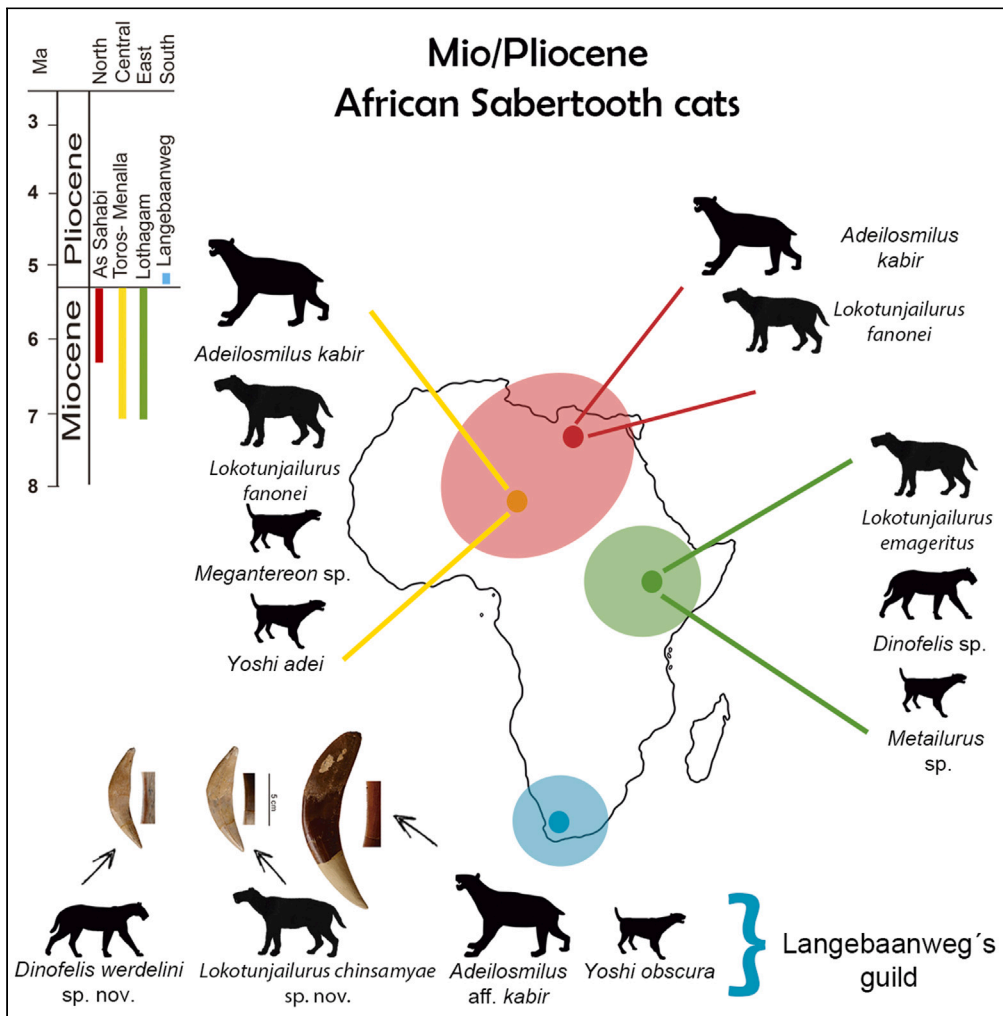


Article

# Langebaanweg’s sabertooth guild reveals an African Pliocene evolutionary hotspot for sabertooths (Carnivora; Felidae)



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**Highlights**  
Langebaanweg’s (LBW) sabertooth cat’s guild includes two new species

*Dinofelis* from LBW is the potential ancestor of Plio-Pleistocene *Dinofelis*

We confirm a Pan-African distribution of *Adeilosmilus* and *Lokotunjailurus*

Comparison with Eurasian felid guild implies open environment at LBW

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## Article

## Langebaanweg's sabertooth guild reveals an African Pliocene evolutionary hotspot for sabertooths (Carnivora; Felidae)

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## SUMMARY

Here, we describe and revise craniodental material from Langebaanweg 'E' Quarry (South Africa, early Pliocene, ~5.2 Ma), which represents one of the largest and best-preserved collections of sabertooth felids from Mio-Pliocene deposits of Africa. Four taxa, including two new species, are recognized: *Lokotunjailurus chinsamyae* sp. nov., *Adeilosmilus* aff. *kabir*, *Yoshi obscura*, and *Dinofelis werdelini* sp. nov. The felid guild composition analyzed herein suggests the presence of a mosaic environment with open components in the region, and shows a potential relationship with that of Yuanmou, suggesting a similar environment and/or dispersal route/event. The reassessment of the rich early Pliocene felids from Langebaanweg is a step toward understanding the transition and evolution of the felids in the southern hemisphere during the late Miocene to early Pliocene.

## INTRODUCTION

The Pliocene witnessed global climate change toward a colder environment.<sup>1,2</sup> Late Miocene fauna experienced a significant change in Europe around the Mio-Pliocene boundary, documenting a shift from a more open savannah-like environment to a more closed forest environment.<sup>3</sup> This change contrasts with eastern and southern Africa where, during the Late Miocene, the environment changed to more open, arid grassland or desert, which continued into the Pliocene.<sup>4–9</sup>

Located on the west coast of South Africa (Figure 1), Langebaanweg 'E' Quarry is one of the most important fossil communities to document the Mio-Pliocene environmental change and animal evolution in southern Africa.<sup>10,11</sup> Baard's Quarry and 'E' Quarry comprise part of the Langebaanweg fossil locality and are located ~13–15 km inland from Saldanha Bay on South Africa's west coast (Figure 1).<sup>12</sup> They were commercially exploited as open-cast phosphate mines from 1943 to 1993. Singer and Hooijer<sup>13</sup> reported the first occurrence of Tertiary vertebrate fossils in the area, describing the remains of an elephant's relative from 'Baard's Quarry' which was later back-filled.<sup>14</sup> Fossils from Baard's Quarry are fragmentary and show evidence of rolling. They were thought to originate from a river lag deposit or reworked from deposits below level 2 that may have been contemporaneous. In 1965, mining started at the Varswater mine, 'E' Quarry, 2.5 km west of Baard's Quarry, producing the rich and diverse fossils from Langebaanweg.<sup>11,12,15</sup> Fieldwork at 'E' Quarry began in 1965 and continues until today.

The fossils from 'E' Quarry occur in the Varswater Formation that spans the middle Miocene (Langhian) to early Pliocene (Zandlean).<sup>10,16,17</sup> All the terrestrial carnivoran fossils from 'E' Quarry,<sup>12,18–25</sup> including the new material described herein, come from the Langeberg Quartz Sand Member (LQSM) and Muishond Fontein Pelletal Phosphorite Member (MPPM). They are concentrated within an 'abbreviated' stratigraphic interval of ca 26–30 m above sea level<sup>10, p. 208</sup> and are associated with numerous transgressive-regressive episodes.<sup>10,16,17,26</sup> The LQSM was deposited in a lagoonal and/or estuarine setting protected from wave action but open to the sea.<sup>10,27,28</sup> The MPPM, Beds 3aN and 3aS, was deposited in a shallow embayment sheltered from the open ocean by granitic islands during the early Pliocene transgression.<sup>29</sup> Both beds are inferred as very close in age, with Bed 3aS being slightly older.<sup>11</sup> However, the ages of LQSM and MPPM were estimated by palaeomagnetic data and global sea level reconstructions as  $\sim 5.15 \pm 0.1$  Ma, suggesting that the fossils accumulated at an early stage in the Early Pliocene transgression when the sea level was 30m above present level.<sup>10</sup> Baard's Quarry<sup>12,14</sup> is interpreted as a much more recent deposit (late Pliocene or early Pleistocene).

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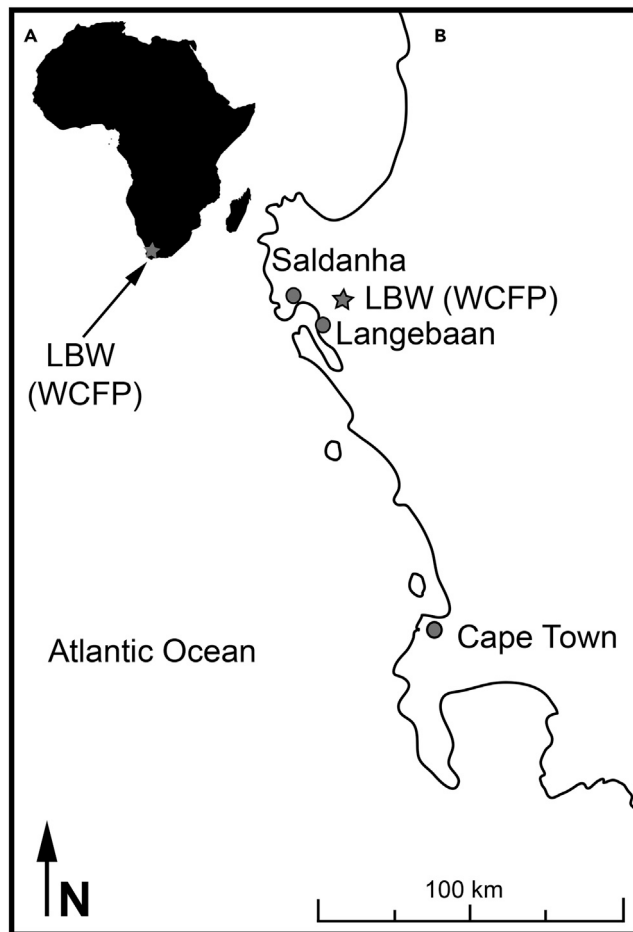
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**Figure 1. Location of the Langebaanweg 'E' Quarry fossil site**

(A) Silhouette of Africa, pointing out the site of Langebaanweg (gray star).

(B) simplified geographic map of the West Coast of South Africa. Modified from Valenciano & Govender (2020b). WCFP, West Coast Fossil Park.

Langebaanweg 'E' Quarry is well-suited because of its temporal position at the Miocene–Pliocene boundary, and its geographic location at the southern tip of Africa.<sup>30</sup> It is extremely fossiliferous, including more than 230 documented species,<sup>15,17</sup> providing key information for the reconstruction of the environment during the Mio-Pliocene in southern Africa, and the evolution and dispersal of animals in this region. The taxonomy, evolution, and diversity of this fauna is therefore very important for a precise reconstruction of the paleoenvironment. Following the initial systematic study led by Hendeby,<sup>27,31–38</sup> continuous taxonomic revision of macro-mammal fossils, including hyaenids,<sup>39</sup> viverrids,<sup>40</sup> mustelids,<sup>23,24</sup> canids,<sup>25</sup> equids,<sup>41</sup> and proboscideans<sup>42</sup> has been undertaken.

Sabertooth cats are also a very important and diverse group at Langebaanweg. Four species of sabertooth, including cf. *Homotherium* sp., *Machairodus* sp., *Dinofelis diastemata*, and *Felis obscura*, were described by Hendeby.<sup>12</sup> Several studies have discussed or mentioned the felid taxa from this fauna, e.g. cf. *Homotherium* sp. Werdelin and Sardella,<sup>43</sup> *Machairodus* sp. Werdelin and Peigné,<sup>44</sup> *Felis obscura* Turner,<sup>45</sup> and *D. diastemata* Werdelin and Lewis,<sup>46</sup> but no systematic comparison or study has focused on any of these species, or the sabertoothed guild as a whole. Recently, knowledge of the Mio-Pleistocene sabertoothed cats has greatly improved,<sup>46–51</sup> enabling a systematic revision of this group from Langebaanweg. The current study presents an update of the dentognathic remains of sabertooth felids from Langebaanweg 'E' Quarry, comprising the classical material<sup>12</sup> and numerous previously unpublished fossils (Table S1). Our main goal is to update our knowledge of these significant felids from Langebaanweg, composed of Miocene and Pliocene genera, to better understand the

taxonomy, paleobiology and ecology of one of the best-preserved and most diverse guilds of saber-tooths from Africa.

## RESULTS

### Systematic paleontology

Order Carnivora Bowdich, 1821.

Family Felidae Fischer, 1817.

Subfamily Machairodontinae Gill, 1872.

Tribe Machairodontini Gill, 1872.

*Lokotunjailurus* Werdelin, 2003.

**Type species:** *Lokotunjailurus emageritus* Werdelin, 2003.

**Included species:** *Lokotunjailurus fanonei* Bonis et al., 2010 and *Lokotunjailurus chinsamyae* sp. nov.

**Chronology and distribution:** Currently known from central, eastern, and southern Africa, late Miocene to earliest Pliocene.

**Amended diagnosis:** Machairodontinae of medium to large size. Very large infraorbital foramen. Alisphenoid canal present. Glenoid fossa antero-posteriorly elongated, and slightly overhung. Mandibular flange absent or very weak, horizontal ramus slender, ascending ramus relatively tall for a machairodont cat. Upper canine moderately laterally compressed, and relatively low-crowned. Serrations present on both anterior and posterior edges. P2 present and often double rooted. Upper carnassial long and slender with highly reduced protocone; p2 can be present; p3 small with single or double root. Lower carnassial long, slender, and low. Metaconid-talonid complex absent.

*Lokotunjailurus chinsamyae* sp. nov.

*Machairodus* sp. p.149, Hendeby, 1974.

*Machairodus* sp. p.248, Turner, 1990.

*Amphimachairodus* sp. B., p. 201, Werdelin, 2006.

'*Machairodus*' sp. p.73, Sardella and Werdelin, 2007.

**Holotype:** SAM-PQL20505, fragmented maxilla, mandible, and anterior part of basicranium of the same individual (Figures 2, 3, and 4).

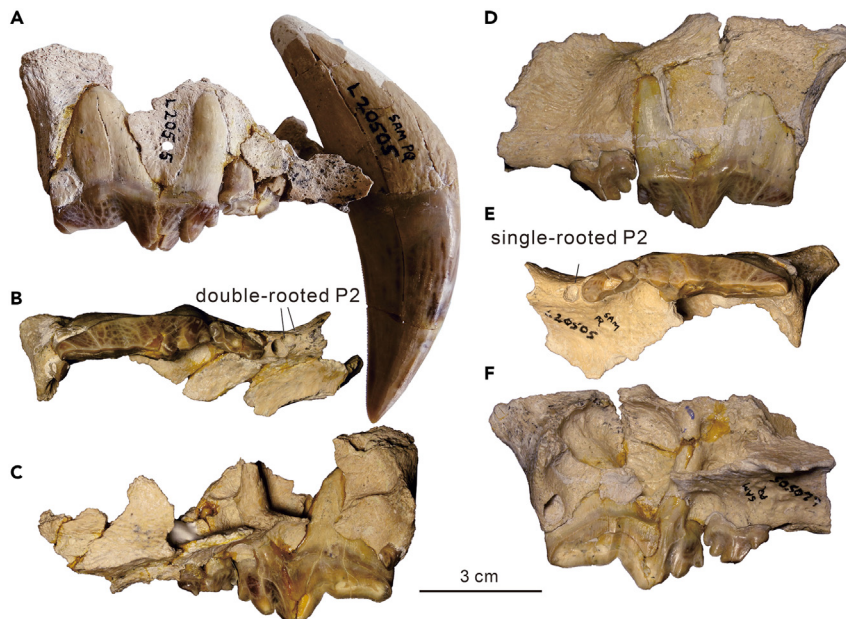
**Etymology:** In honor of Prof. Anusuya Chinsamy, a world renowned South African paleontologist for her contributions to vertebrate paleontology.

**Type locality:** Langebaanweg 'E' Quarry, LQSM, earliest Pliocene (5.2 Ma).

**Assigned material:** SAM-PQL12641, right fragmentary hemimandible with i3-c, and p2-3 alveoli, and fragmentary p4-m1. SAM-PQL-22193, six thoracic vertebrae, three lumbar vertebrae, two femora, two tibiae, the left fibula, the right astragalus, the left calcaneum and the second, third and fourth metatarsals; and SAM-PQL-52061, complete left calcaneum described in Rabe et al.<sup>52</sup> The large size, and its relatively high femur greater trochanter indicate a large felid affinity. Moreover, its morphology does not fit with *Amphimachairodus* (and presumably *Adeilosmilus*), but is closer to *Lokotunjailurus*, as has been discussed in Rabe et al.,<sup>52</sup> and here assigned to *L. chinsamyae* sp. nov.

**Chronology and distribution:** Known from the type locality Langebaanweg, 'E' Quarry (LQSM), South Africa, early Pliocene (5.2 Ma).

**Diagnosis:** Medium-sized machairodontine similar to a large jaguar. Mandibular flange indistinct. Symphysis very robust. Upper canine relatively robust and low-crowned, with clear serration. P2 double or single



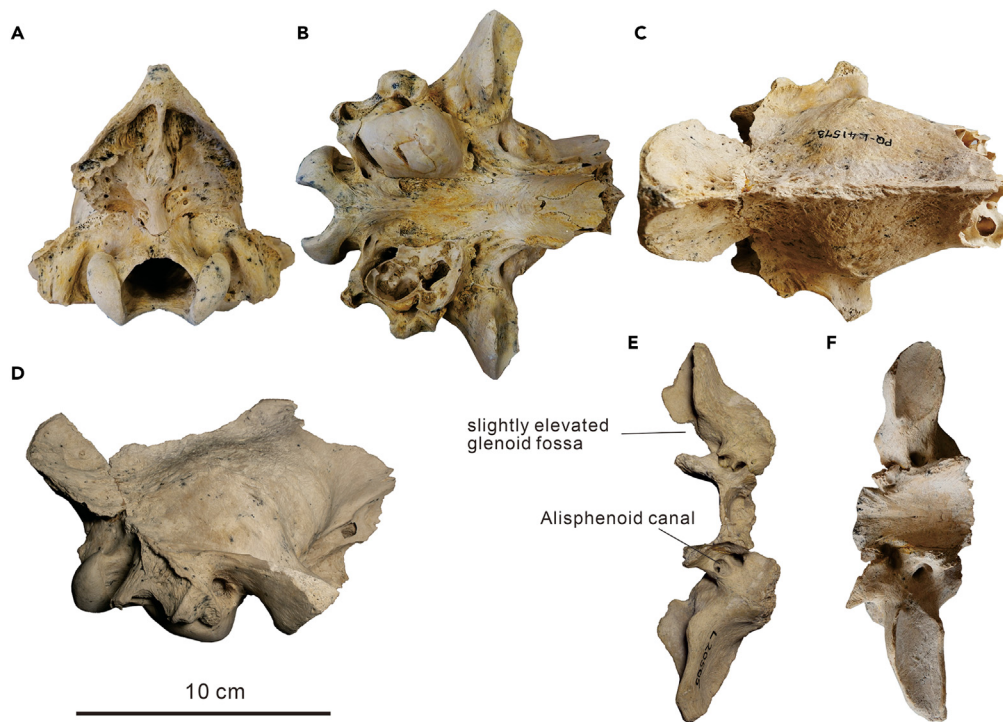
**Figure 2.** The holotype of *Lokotunjailurus chinsamyae* sp. nov., SAM-PQL20505 from Langebaanweg 'E' Quarry (A–C) Left maxillary with C, P3–P4. (A) Buccal, (B) Occusal, and (C) Lingual views. (D–F) Right maxillary with P3–4. (D) Buccal, (E) Occlusal, and (F) lingual views. Scale bar equals 3 cm.

rooted. P3 less than 1/2 length of P4. P4 with large preparastyle. p2 present and single-rooted. p3 relatively large and double rooted. m1 slender.

**Differential diagnosis:** Differs from type species, *L. emageritus*, by having slightly stronger mandibular flange, less posteriorly extended angular process and less posterior inclined coronoid process, retaining of the p2, and less reduced p3; differs from *L. fanonei* by having smaller size, longer C–P3 diastema, slightly smaller upper canine, retaining of the p2, less posteriorly extended angular process; differs from *Machairodus* and *Amphimachairodus* by smaller size, especially upper canine, presence of double rooted P2, proportionally smaller p3/P3 (compared with P4/m1), slenderer P4; differs from *Homotherium* by presence of P2, proportionally larger p3/P3 (compared with P4/m1), weaker mandibula flange, and non-ventrally extended glenoid fossa, and presence of the alisphenoid canal.

**Remarks:** The specimens SAM-PQL20505 and SAM-PQL12641 were described in Hendery (1974)<sup>12</sup> as *Machairodus* sp. (Figures 2, 4, and 5; Tables 1 and 2). The maxilla is incomplete but the dentition is well preserved. The canine is relatively low crowned for a machairodontine. There is strong serration in both keels of the canine. P2 is present on both sides, but on the left side it is single rooted whereas on the right side it is double rooted. The P3 is slender, with a mesial accessory cusp located slightly medial to the main cusp. The distal cingulum is cusp-like. The P4 is very slender and elongated. The preparastyle is large and in line with the main axis of the tooth. The protocone is highly reduced (more than that of *Amphimachairodus*, and similar to the state of early *Homotherium*), and located at or slightly distal to the parastyle/paracone notch. The mandible has a complete horizontal ramus, but the dentition is broken. The symphysis is very thick. The mandible flange is small. There are two mental foramina. The anterior one is larger. The lower dentition is poorly preserved, but p2 is present, and the p3 is very small.

There is a small fragment of the basicranium of SAM-PQL20505 not described by him (Figures 3E and 3F). It preserves several very important anatomical traits that are included here. The glenoid slightly overhangs the basicranium. It is distinctly antero-posteriorly elongated and faces more ventrally. The oval foramen is located medial to the glenoid fossa. A short alisphenoid canal is present.



**Figure 3. Basicranial material of sabertoothed cats from Langebaanweg**

(A–D) Braincase of *Dinofelis werdelini* sp. nov. SAM-PQL41573, posterior, ventral, dorsal and lateral views; (E and F) glenoid and basicranial fragment of *Lokotunjailurus chinsamyae* sp. nov. SAM-PQL20505, anterior and ventral views. Note on the presence of elevated glenoid fossa and alisphenoid canal in *Lokotunjailurus chinsamyae* sp. nov., neither of which is present in *Dinofelis werdelini* sp. nov. Scale bar equals 10 cm.

*Adeilosmilus* aff. *kabir*

cf. *Machairodus*, p.149, Hende, 1974

cf. *Homotherium* sp., p.158, Hende, 1974.

*Amphimachairodus* sp. indet., p. 125, Werdelin and Sardella, 2006.

*Amphimachairodus* sp. A., p. 201, Werdelin, 2006.

**Material:** SAM-PQL11846, a broken left upper canine from LQSM (Figure 5C), and SAM-PQL6386, a mandibular fragment retaining the symphysis to the p3 part from MPPM (Figures 4F and 4G).

**Remarks:** The upper canine was initially described in Hende (1974).<sup>12</sup> It is very large, and the last third of the crown including the tip is missing and restored. The upper canine has distinct serration in both keels. The enamel is clearly more extended on its distal side. The mandibular fragment has a moderately sized flange, an antero-posteriorly narrow symphysis. The mesial border seems to be vertical. Two large mental foramina are present and located between the canine and the p3. The p2 is not present.

“Metallurini”

*Dinofelis* Zdansky, 1924.

*Dinofelis werdelini* sp. nov.

*D. diastemata*, p.169, Hende, 1974.

*Dinofelis barlowi*, p.250, Turner, 1990.



**Figure 4. Mandibular fragments of *Lokotunjailurus chinsamyae* sp. nov and *Adeilosmilus* aff. *kabir* from Langebaanweg 'E' Quarry**

*Lokotunjailurus chinsamyae* sp. nov (A–E). (A–C) SAM-PQL-12641, dorsal, lateral and anterior views; (D and E) SAM-PQL-20505, lateral and dorsal views; *Adeilosmilus* aff. *kabir* (F and G) SAM-PQL-6386, lateral and dorsal views. Scale bar equals 5 cm.

*D.* cf. *D. diastemata*, p.237, Werdelin et Lewis, 2001.

*Dinofelis* sp., p. 201, Werdelin, 2006.

**Holotype:** SAM-PQL-47523, fragmented maxilla (Figures 6A–6G).

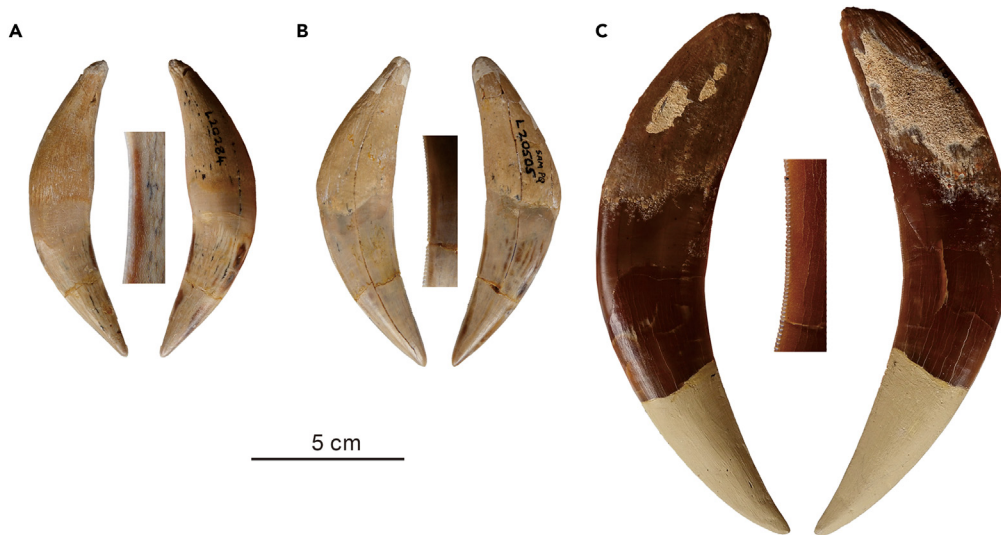
**Paratype:** SAM-PQL-20284, a pair of nearly complete mandibles, with associated upper canine, Langebaanweg 'E' Quarry, LQSM (Figures 7A–7D).

**Etymology:** In honor of Prof. Lars Werdelin, who has made great contributions to African Palaeontology, and the systematics and evolution of Carnivora, especially *Dinofelis*.

**Type locality:** Langebaanweg 'E' Quarry.

**Assigned materials:** SAM-PQL-20995, a partial mandible with complete toothrow from LQSM; SAM-PQL-20685, a nearly complete mandible, and associated lower canine, m1 and upper canines from LQSM; SAM-PQL-41573 braincase of a cranium, unknown member; SAM-PQL-51591, a partial mandible with complete toothrow, from LQSM; SAM-PQL-50128, a maxilla fragment with P4 and m1 from MPPM; SAM-PQL-20702, a single upper canine, unknown member; SAM-PQL-12237, a mandibular fragment with p4 and m1, unknown member; SAM-PQL-41054, pair of partial mandibles of a juvenile individual, with dp3 and dp4, from MPPM; SAM-PQL-41726, a partial mandible of a juvenile individual, with dp3 and dp4, from MPPM.

**Chronology and distribution:** Known from the type locality, Langebaanweg 'E' Quarry (LQSM and MPPM), South Africa, early Pliocene (5.2 Ma).



**Figure 5. Upper canine of sabertoothed cat from Langebaanweg 'E' Quarry**

(A) *Dinofelis werdelini* sp. nov., SAM-PQL20284;

(B) *Lokotunjailurus chinsamyae* sp. nov., SAM-PQL20505; (C) *Adeilosmilus* aff. *kabir*, SAM-PQL11846. Scale bar equals 5 cm.

**Diagnosis:** Medium *Dinofelis*, similar to a large jaguar. Mandibular flange indistinct, but with clear mental ridge; mandibular symphysis high, and corpus deep; mastoid process enlarged; Upper canine robust; cheek teeth relatively small; P2 absent; P3 with large anterior accessory cusp and distinct postero-lingual convexity. P4 with variable preparastyle.

**Differential diagnosis:** Differs from all the African *Dinofelis*, by having proportionally smaller cheek teeth, less reduced anterior premolars, more robust upper canine, and higher mandibular symphysis; differs further from *Dinofelis petteri*, *Dinofelis aronoki* and *Dinofelis piveteaui* by having longer rostrum, less elongated P4 without strong reduction of the protocone; differs further *D. barlowi* by having smaller size, less reduced P4 protocone; differs further from *D. piveteaui* by having smaller incisor, without V-shaped accessory cusps in I1 and I2; from *D. diastemata* by having slightly more robust upper canine, wider mastoid processes with distinctly more ventrally extended anterior branch, and deeper mandible; from *Dinofelis cristata* by having a distinctly smaller body size, shorter rostrum, more distinct angle between the anterior and ventral borders of symphysis, higher but antero-posteriorly narrower coronoid process, more distinct anterior and posterior ridges of the upper canine, more robust P4 protocone, and less reduced p3; differs from *Dinofelis palaeoconca* by having slightly larger size, longer rostrum, more ventrally extended anterior branch of the mastoid process, deeper mandibular corpus; from *Metailurus* by having distinctly larger and deeper mandibular corpus, more distinct P3 anterior accessory cusp, absence of the m1 metaconid-talonid complex; from "*Metailurus*" *ultimus* by larger size, more ventrally extended anterior branch of mastoid, deeper mandibular corpus, stronger postero-lingual convexity of the P3; from *Paramachaerodus* by having distinct larger size, more ventrally extended anterior branch of mastoid, deeper mandibular corpus, more distinct P3 anterior accessory cusp; differs from *Adelphailurus* and *Yoshi* by having much larger size, lower-crowned cheek teeth, presence of distinct P3 anterior accessory cuspid, and absence of the m1 metaconid-entoconid complex.

**Remarks:** The specimens SAM-PQL-20284, SAM-PQL-20685, SAM-PQL-20702, SAM-PQL-12237 were described in Hendey<sup>12</sup> as *D. diastemata*. The maxilla SAM-PQL-47523 was selected as the holotype because the upper dentition of felids is often more diagnostic (Figures 6A–6G). It preserves complete dentition from I1 to M1. The incisor row is only very weakly procumbent. The incisors are small, especially the I1 and I2, with both having two distinct posterior accessory cusps. I3 is distinctly larger than the I1 and I2 and has a distinct medial accessory cusp. The canine is broken. P3 has a strong anterior accessory cusp, and a weak additional cusplet behind it. The posterolingual corner is convex, and the posterior cingulum is well developed and laterally extended. The P4 has a strongly undulated buccal border.



**Table 1. Measurements and ratios of the upper dentition of sabertoothed cats in this study**

Taxon	<i>Dinofelis werdelini</i>							<i>?Dinofelis werdelini</i>	<i>Yoshi obscura</i>	<i>Lokotunjailurus chinsamyae</i>	
	L20284	L47523 L	L47523 R	L20685 L	L20685 R	L50128	L20702	L2674	L10100	L20505 L	L20505 R
CL	20.17	18.69	17.55	17.88			20.84	18.61			23.23
CW	13.24	14.53	10.52	10.73			13.25	9.01			11.22
CH	50.04		41.96	42.58			37.30				49.40
CW/L	0.66	0.78	0.60	0.60			0.64	0.48			0.48
CH/L	2.48		2.39	2.38			1.79				2.13
P3L	19.80	20.83						19.35	14.00	15.55	
P3W	11.63	11.97						9.04	6.30	6.84	
P3W/L	0.59	0.58						0.47	0.45	0.44	
P4L	33.45	33.29			30.49				23.80	37.71	37.19
P4W	17.82	17.03			14.38			14.18	12.20	12.37	13.25
P4BW	11.92	12.33			9.84			9.74		10.69	10.85
P4W/L	0.53	0.51			0.47				0.51	0.33	0.36
P4BW/L	0.36	0.37			0.32					0.28	0.29
M1L		5.62						4.23	5.60		4.48
M1W		10.05						9.04	7.40		6.26
M1W/L		1.79						2.14	1.32		1.40
CL/P4L		0.56							0.55		0.63
P3L/P4L	0.59	0.63							0.59	0.41	
M1W/P4L		0.30							0.31		0.17
LT		87.52							59.65		88.16
LDP		9.80						5.20	6.39	7.39	7.61
LDP/LT		0.11							0.11		0.09

The preparastyle is large, and oriented in a strong angle with the parastyle. The protocone is not reduced and is located at the level between the parastyle and paracone. The M1 is small, transversely shortened.

The maxillary fragment SAM-PQL-50128 (Figures 6H and 6I) has P4 and M1 preserved. There is only an indistinct preparastyle present, and the buccal border is less undulating. M1 is similar/same as that of SAM-PQL-47523.

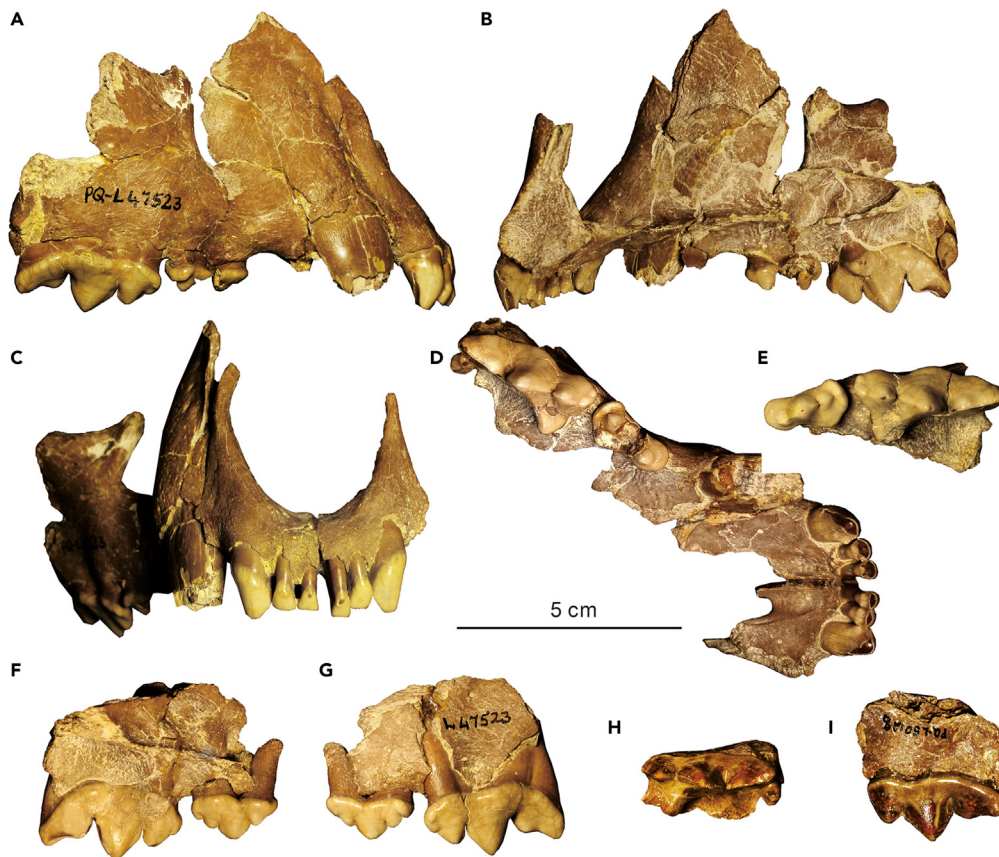
The braincase SAM-PQL-41573 (Figures 3A–3D) has a well-developed sagittal crest and its widest point is at the level of the glenoid. The occipital plane is posteriorly inclined. In lateral view, both mastoid and paroccipital processes are well developed. The mastoid process is distinctly anteroventrally extended and does not cover the ventral border of the auditory bulla. The anterior branch of the mastoid extends to a similar level as the posterior branch, and the posterior branch is strongly posteriorly inclined. The paroccipital process is posteriorly extended and is detached from the bulla. The auditory bulla is inflated and has its highest point at its anterior part. In the ventral view, the glenoid fossa does not overhang the basicranium, and is not antero-posteriorly elongated. It faces more anteriorly than that of *Lokotunjailurus* (Figures 3E and 3F). The oval foramen is located medial to the glenoid fossa and was partially covered by a bone bridge. The auditory bulla is enlarged. The medial border is nearly straight. The opening of the stylomastoid foramen and hyoid fossa share a common opening. The mastoid is laterally expanded, located at the buccal side of the common opening mentioned above. The paroccipital process is located slightly medial to this opening. The posterior lacerated foramen is rather narrow and separated from the hypoglossal foramen. In posterior view, the nuchal crest is wide, robust, and well developed dorsally. The muscle scar in the occipital plane is strongly developed, especially near the edge of the lambdoidal crest.

**Table 2. Measurements and ratios of the lower dentition of sabertoothed cats in this study**

Taxon	<i>Dinofelis werdelini</i>									<i>Lokotunjailurus chinsamyae</i>		
	catalog	L20995	L20284	L20284	L51591	L12237	L20685	L41054 L	L41054 R	L41726	L12641	L-20505
cL		15.20	15.79	16.41			12.92					
cW		9.92	10.56	12.07			11.43					
cH		23.77	25.25	20.58			22.29					
cW/L		0.65	0.67	0.74			0.89					
cH/L		1.56	1.60	1.25			1.73					
p3L	14.03	14.54	13.99	15.25							12.30	
p3W	6.47	7.22	7.41	8.84							5.50	
p3W/L	0.46	0.50	0.53	0.58							0.45	
p4L	20.09	22.38	22.45	22.64	20.47	20.60					20.00	
p4W	9.35	9.25	9.95	10.67	8.81	8.70					9.50	
p4W/L	0.47	0.41	0.44	0.47	0.43	0.42					0.48	
m1L	22.70	23.78	23.78	25.63	23.87	23.00					28.00	29.00
m1W	10.70	11.59	10.66	12.77	10.22	10.20					11.00	11.20
m1W/L	0.47	0.49	0.45	0.50	0.43	0.44					0.39	0.39
dcL										8.81		
dcW										3.71		
dp3L							13.59	13.45	12.68			
dp3W							4.33	4.39	4.70			
dp4L							17.83	17.81	18.80			
dp4W							7.23	7.86	6.19			
c/m1		0.64	0.66	0.64		0.56						
p3/m1	0.62	0.61	0.59	0.60							0.44	
p4/m1	0.89	0.94	0.94	0.88	0.86	0.90					0.71	
LT	89.49	98.71	97.93	101.10		86.26					111.83	
LDP	26.04	25.15	24.16	26.27		20.51					25.34	
LM	55.90	59.42	59.12	61.33		56.48					66.05	
H1	32.15	44.13	39.90	40.44		36.01					38.92	
W1	19.98	26.25	24.10	23.95		20.96					31.56	
H2	29.10	31.82	32.52	32.02		25.23					34.09	
H3		37.53	38.70	37.27		32.88					37.01	39.14
W3		17.87	18.53	24.63		16.47					17.84	17.58
LDP/LT	0.47	0.42	0.41	0.43		0.36					0.38	
H1/H3		1.18	1.03	1.09		1.10					1.05	
m1L/H3		0.63	0.61	0.69		0.70					0.76	0.74

There are several mandibles with well-preserved dentition (SAM-PQL-20284, SAM-PQL-20685, SAM-PQL-20995, SAM-PQL-51591), but unfortunately none of them are complete. The horizontal ramus is generally deep, especially in the region of the symphysis. The coronid process is large, and the angular process is ventrally extended. There are a variable number of mental foramina. The lower canine is large, with a sharp distal keel. The c-p3 diastema is elongated. The p3 is much lower crowned than the p4. The mesial border of the p4 and the m1 is posteriorly inclined. The m1 is robust, without a metaconid-talonid complex.

The juvenile mandible SAM-PQL-41054 (Figures 7M and 7N) has the deciduous dp3 and dp4 in place, and the permanent canine and m1 in an initial stage of eruption. The m1 morphology is the same as other specimens of the m1 in Langebaanweg and supports its assignment to this taxon. The high symphysis is already



**Figure 6. Maxillary fragments of *Dinofelis werdelini* sp. nov. from Langebaanweg 'E' Quarry**

(A–G) Holotype: SAM-PQL-47523, (A–D) lateral, medial, anterior and ventral views of right side, (E–G) occlusal, medial and lateral views of left side; (H and I) SAM-PQL-50128, occlusal and lateral views. Scale bar equals 5 cm.

developed. The dp3 has sharp main cuspid and anterior and posterior accessory cuspids, and a cusp-like posterior cingulid. The dp4 has well developed metaconid and talonid. Its lingual border is strongly concave. The juvenile mandible SAM-PQL-41726 (Figures 7O and 7P) belongs to a slightly younger individual than SAM-PQL-41054, with both the canine and m1 unerupted. The overall morphology is similar, but the posterior cingulid of the dp3 in SAM-PQL-41726 is less developed.

?*D. werdelini*.

*D. diastemata*, p.169, HendeY, 1974.

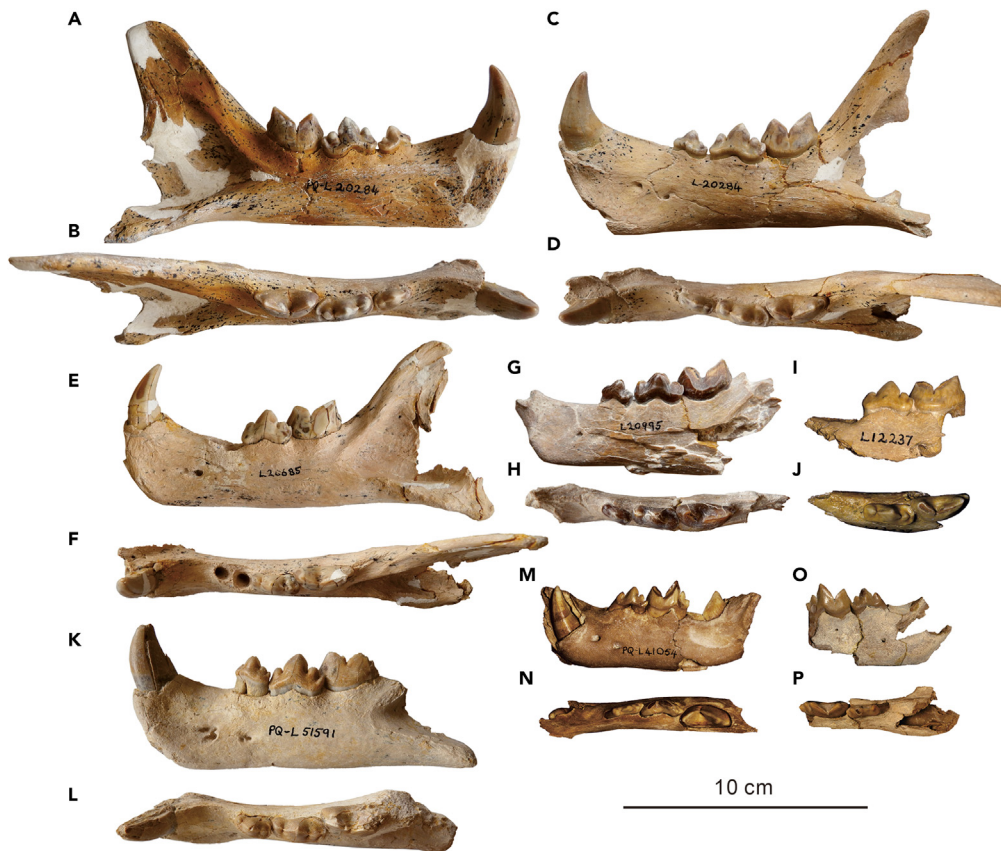
**Material:** SAM-PQL-2674, a fragmented maxilla with canine, and fragments of maxilla with P3–M1, from MPPM.

**Remarks:** This material was initially described and figured as *D. diastemata* by HendeY.<sup>12</sup> Its P3 is similar to the P3 of SAM-PQL-47523, with a distinct anterior accessory cusp, but its P4 buccal border is much less undulating, and the protocone is distinctly smaller. The canine of this individual is much narrower, and differs from the other canine assigned to *D. werdelini*. It is unclear whether this individual represents another species or a variant of *D. werdelini*.

Yoshi Spaasov et Gerrads, 2014.

*Yoshi obscura* (HendeY, 1974)

*Felis obscura*, p.164, HendeY, 1974.



**Figure 7. Mandibles of *Dinofelis werdelini* sp. nov. from Langebaanweg 'E' Quarry**

(A–D) paratype: SAM-PQL-20284.

(E and F) SAM-PQL-20685.

(G and H) SAM-PQL-20995.

(I and J) SAM-PQL-12237.

(K and L) SAM-PQL-51591.

(M and N) juvenile, SAM-PQL-41054.

(O and P) juvenile, SAM-PQL-41726. All lateral and dorsal views. Scale bar equals 10 cm.

*Adelphailurus obscura*, p.250, Turner, 1999.

?*Megantereon obscura*, p.43, Morales et al., 2005.

*Metailurus obscurus*, p. 201, Werdelin, 2006.

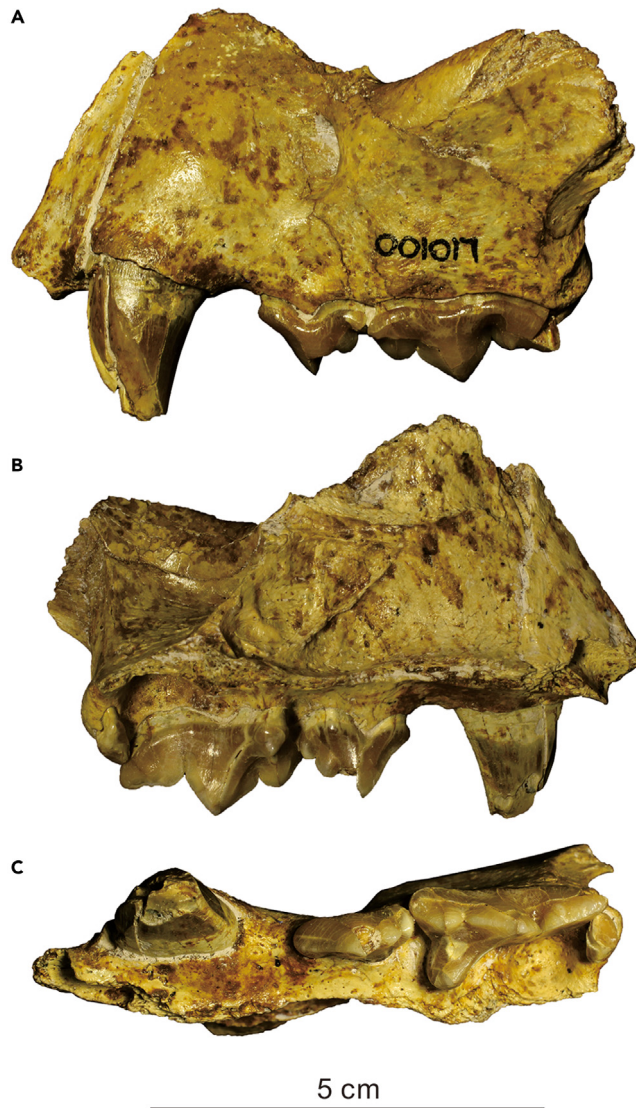
*Metailurus obscurus*, p.646, Werdelin et Peigné, 2010.

**Holotype:** SAM-PQL10100 from Langebaanweg 'E' Quarry, MPPM (Figure 8).

**Chronology and distribution:** Known from the type locality, South Africa, earliest Pliocene.

**Emended diagnosis:** Small metailurine, size of a female leopard. Infraorbital foramen moderate in size. Small canine. Short C-P3 diastema. P3 high crowned without anterior accessory cusp. P4 slender, with large protocone, without distinct preparastyle. M1 small, button-like and transversely short.

**Differential diagnosis:** Differs from all other machairodonts except *Yoshi* spp. in having smaller size and straight P4 buccal border; differs from all other species of *Yoshi* by having less high crowned P3, and reduction of the M1 inner lobe.



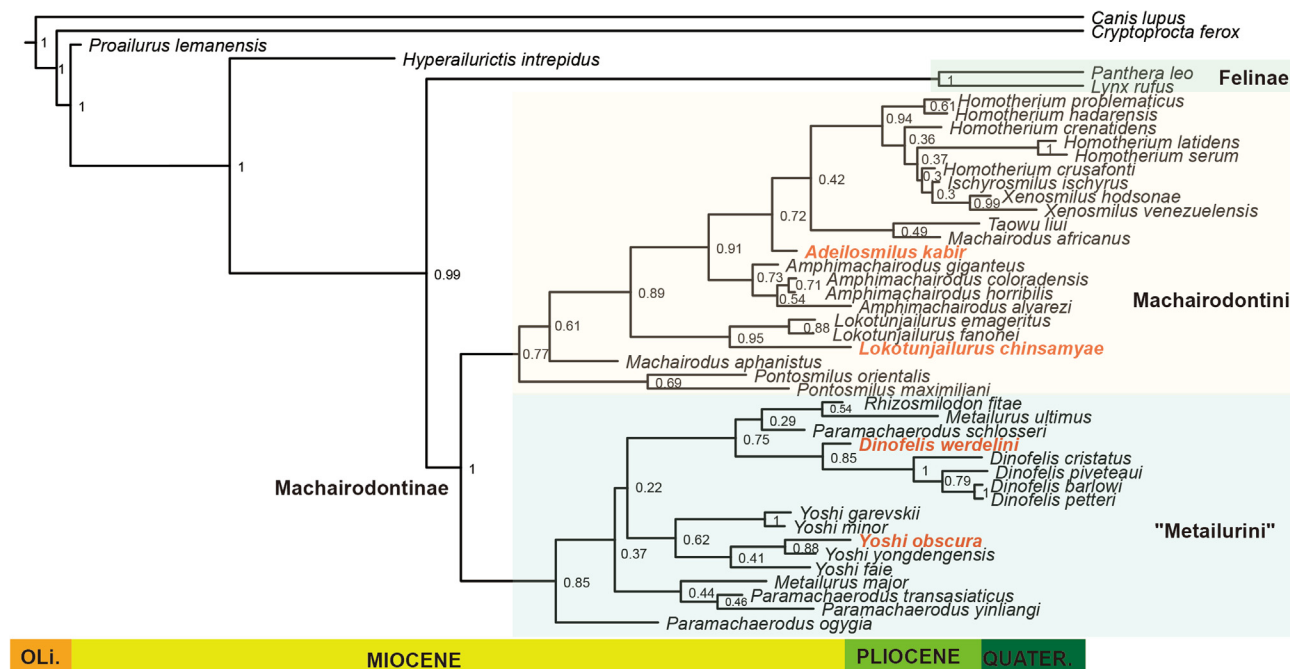
**Figure 8. Holotype of *Yoshi obscura*, SAM-PQL10100, from Langebaanweg 'E' Quarry**  
(A) Buccal, (B) lingual and (C) Occlusal views. Scale bar equals 5 cm.

**Remarks:** The maxillary fragments contain complete dentition from the upper canine to the M1. The infraorbital foramen is not enlarged and located at the level of the P3. The upper canine is moderately robust with a posterior keel. There is no P2. The P3 is slender without a mesial accessory cusp but the distal accessory and cingulum are well developed. The P4 is also slender with a straight buccal border, and no preparastyle. The protocone is large and located mesial to the parastyle/paracone notch. The M1 is transversely shortened.

## DISCUSSION

### Phylogenetic analysis

The evolutionary position of Langebaanweg felids has been previously discussed, but never tested by phylogenetic analysis.<sup>12,30,43</sup> Our detailed description of both old and new materials enables such an analysis for the first time. We use the matrix and the character descriptions and states from the recent work on sabertooth phylogeny by Jiangzuo et al.,<sup>53</sup> and added three newly revised taxa here (appendix nexus file, Table S2). The coding of *Adeilosmilus* is still based on previous material, as the specimens from Langebaanweg did not introduce new knowledge.



**Figure 9. Bayes inferences tree using tip-dating methods and constraints on Felidae and Machairodontinae**

The position of the four sabertooth from Langebaanweg are in bold. The outgroup is *Canis lupus*. Numbers in the nodes represent the posterior probability. It was implemented using the software MrBayes 3.2.7 (<https://nbisweden.github.io/MrBayes/download.html>).

The overall topology of the phylogeny (Figure 9) is very close to the one in Jiangzuo et al.<sup>53</sup> The smaller Langebaanweg Machairodontini is supported as a member of *Lokotunjailurus*, sister to the two previously known species. The new species *D. werdelini* is supported as the earliest definitively defined species of *Dinofelis*. *Y. obscura* is sister to recently described *Yoshi yongdengensis*. These two species have similar size and share the derived trait of transversely shortening of the M1 compared with other species of this genus.

### The affinity of two machairodontini

The tribe Machairodontini flourished during the Late Miocene, with numerous species from Africa to North America.<sup>54</sup> The two most common genera are *Machairodus* and *Amphimachairodus*.<sup>54,55</sup> *Amphimachairodus* was viewed as invalid as the species within this genus shows a continuous evolution from *Machairodus aphanistus*,<sup>56–58</sup> but a recent paper suggest there is significant ecological change from *Machairodus* to *Amphimachairodus*, and *Amphimachairodus* evolved early in the border of the Tibetan Plateau,<sup>59</sup> therefore *Amphimachairodus* is accepted as a valid genus in this study.

In Africa, two distinct body sizes are recognised for machairodont felids, the larger one, referred to *Machairodus* or *Amphimachairodus*, and recently *Adeilosmilus*, and the smaller *Lokotunjailurus*.<sup>49,60</sup> *Lokotunjailurus* is previously known only from Central and East Africa.<sup>44,49,60</sup>

*Machairodus kabir*, the large machairodont, was established based on mandible and humerus material from the Late Miocene hominid locality of TM 266, Toros-Menalla, Chad.<sup>60</sup> Later, a complete mandible and a partial cranium preserving the braincase and surrounding parts, from Sahabi of Libya were assigned to this species and generically changed to *Amphimachairodus*.<sup>61</sup> A lower canine of an indeterminate sabertooth has been found in the early Pliocene of West Africa (Tobène fauna, Senegal) and could be related to this lineage.<sup>62</sup> Recently, a phylogenetic analysis supported this species belonging to its own genus *Adeilosmilus*.<sup>63</sup> Our new analyses also support this view (Figure 9). This species has a large body size and dentition. It is characterized by a derived dentition comprising a more reduced p3 and p4 compared with those of *Amphimachairodus*. The p3 is no more than half of the m1 length, and p4/m1 length ratio is smaller than 0.75.<sup>56,60,61,64–67</sup> This genus is intermediate between *Amphimachairodus* and the more derived Plio-Pleistocene *Homotherium*. The glenoid fossa from the partial cranium from Sahabi is distinctly

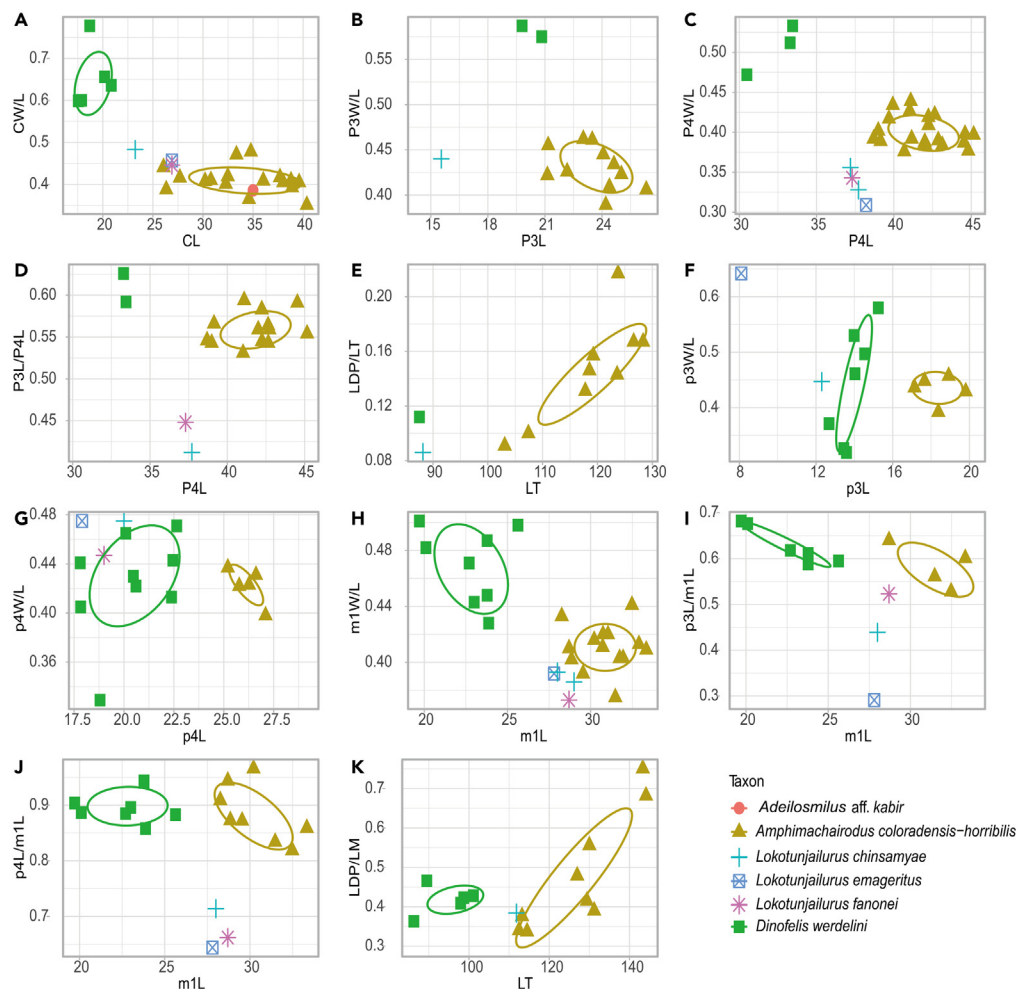
antero-posteriorly wide and overhangs the basicranial region, similar to *Homotherium* and is more derived than *Amphimachairodus*.

*L. emageritus* was established based on a partial skeleton from Lothagam, Nawata Formation, Kenya.<sup>49</sup> This species is characterized by highly derived dentition comprising a P4 with a large preparastyle, and a very reduced protocone. The lower premolars are reduced and similar to *Adeilosmilus kabir*. The mandible is slender, without a distinct mandibular flange, and the coronoid process is well developed, larger than that of *Amphimachairodus*. *L. fanonei* was later identified from Toros Menalla, Chad.<sup>50</sup> The maxilla suggests that P2 is present and double-rooted, in contrast to its highly reduced premolars. This genus shows an interesting combination of derived dentition, and conservative mandibular (weak flange, large coronoid process), and dental traits (retaining of the double rooted P2). The Sahabi mandible assigned to *Dinofelis* sp. by Rook and Sardella<sup>68</sup> has a reduced and double-rooted p3. This specimen fits *L. fanonei* in morphology and probably represents the same species.

At Langebaanweg ('E' Quarry), South Africa, two Machairodontini species have been identified at the genus level. Hendey<sup>12</sup> assigned the smaller one to *Machairodus* sp., and the larger one to cf. *Homotherium* sp. A detailed analysis of the canine, together with some postcranial bones, especially the astragalus and calcaneum, supported that this species should be better assigned to *Amphimachairodus*.<sup>43</sup> This material does not provide clues for a more specific taxonomic assignment. The new mandibular fragment SAM-PQL-6386 (Figures 4F and 4G) probably represents this species. It is slightly larger than that of *Lokotunjailurus* from the same locality, and more importantly, has a more expanded symphysis, with a distinct mandibular flange, which is absent in *Lokotunjailurus*. The mandibular heights of SAM-PQL-6386 behind the canine and in front of p3 are similar to those of the small individuals of *Amphimachairodus coloradensis* and *Amphimachairodus horribilis*. The p3 is much smaller than any individuals of *A. coloradensis-horribilis*, suggesting a reduction of this tooth. This is characteristic of *Ad. kabir* from Toros-Menalla, Chad<sup>60</sup> and Sahabi, Libya,<sup>61</sup> which has a distinctly larger overall size and stronger mandibular flange. We suggest that the large machairodont from Langebaanweg represents a species with the closest affinity to *Ad. kabir* and is herein ascribed to *Adeilosmilus* aff. *kabir*.

The potential presence of species belonging to or closely related to *Lokotunjailurus* in Langebaanweg has recently been proposed based on postcranial bone morphology and limb proportions.<sup>52</sup> This is in accordance with our study on craniodental material. The original and the new material of *Machairodus* sp. from Langebaanweg is represented by several fragments of a skull, and a partial mandible (Figures 2 and 3E, 3F, 4A–4E, 5B, and 10 [as *L. chinsamya* sp. nov.]). Sardella and Werdelin<sup>61</sup> suggested that this species is close to *Lokotunjailurus* in many aspects but differs in many other aspects. We agree with this view. The *Machairodus* sp. material from Langebaanweg shows characteristic traits of *Lokotunjailurus* such as a relatively low and robust canine with distinct serration, reduction in size of the anterior premolars, P4 elongated with straight buccal border, large preparastyle, long metacone, and a very reduced protocone. This combination is not seen in other machairodonts except *Lokotunjailurus*. *Amphimachairodus* spp. are generally large, with larger mandibular flange, higher and narrower upper canine, proportionally larger anterior premolars, undulating P4 buccal border, with larger protocone but shorter metacone.<sup>56,57,64,65,69</sup> *Homotherium* spp. and *Ischyrosmilus-Xenosmilus* are also generally larger, with larger mandibular flange and distinctly deeper mandibular corpus, higher and narrower upper canine, proportionally smaller anterior premolars, more reduced P4 preparastyle, and protocone.<sup>63</sup> *Machairodus* spp. have proportionally larger anterior premolars, undulating P4 buccal border, with smaller and angled preparastyle, distinctly larger protocone, and shorter metacone. The material from Langebaanweg therefore should be assigned to *Lokotunjailurus*. It differs from both known species as indicated in the differential diagnosis, and merits a new species name, *L. chinsamya*. Our phylogenetic analysis (Figure 9) points to *L. chinsamya* as the sister group of the two known species of the genus (*L. emageritus* and *L. fanonei*).

The material from Langebaanweg provides many important craniodental traits for this bizarre machairodont. The P2 is present and double rooted on one side, as in *L. fanonei*, suggesting this trait is not a variation in the latter species, but probably common to the genus. The p2 is also present, which seems to be lost in *L. fanonei*. We list this trait in diagnosis, but note that this tooth could be variably present in some species, e.g., *Paramachaerodus ogygia*.<sup>48</sup> The glenoid fossa is derived in morphology, being antero-posteriorly widened, and faces ventrally, like in *Homotherium*, but only slightly overhangs the basicranium, similar to *Amphimachairodus*. Especially interesting is the presence of the alisphenoid canal. This structure is absent in all living felids and derived machairodonts, e.g., *Homotherium*, *Smilodon*, *Megantereon*, and



**Figure 10. Comparative measurements and ratios of Machairodontini from Langebaanweg 'E' Quarry and other Neogene sites compared to the similar-sized metalurine *Dinofelis werdelini* from Langebaanweg 'E' Quarry** (A) C length vs width/length ratio; (B) P3 length vs width/length ratio; (C) P4 length vs width/length ratio; (D) P4 length vs P3/P4 length ratio; (E) upper tooth row (C-P4) length vs (C-P3) diastema/tooth row length ratio; (F) p3 length vs width/length ratio; (G) p4 length vs width/length ratio; (H) m1 length vs width/length ratio; (I) m1 length vs p3/m1 length ratio; (J) m1 length vs p4/m1 length ratio; (K) lower tooth row (c-m1) length versus (c-p3) diastema/tooth row length ratio. Biplot measurements/ratios were made using ggplot2 (<https://cran.r-project.org/web/packages/ggplot2/index.html>) of R (<https://www.r-project.org/>).

all metalurine, but present in more primitive species, e. g. *Proailurus*, *Hyperailurictis*.<sup>54,70–73</sup> It is generally absent in *Amphimachairodus*,<sup>64</sup> though occasionally is remnant in some individuals.<sup>57</sup> The situation in *M. aphanistus* is not mentioned by Antón et al.,<sup>47</sup> but it is present in North American *Nimravides* (Q. Jiangzuo, personal observation).

In summary, *Lokotunjailurus* shows a mosaic of craniodental traits, with highly derived cheek tooth morphology, and glenoid fossa, but retaining primitive mandibular morphology (no or very weak mandibular flange, large coronoid process), and being conservative in retaining P2, p2 (sometime species), and alisphenoid canal. This combination precludes a judgment of its position within Machairodontini, but it is likely to be a unique lineage, converging with *Amphimachairodus-Homotherium* lineage in dental traits. *Lokotunjailurus* was described as having an appendicular skeleton relatively slender, lacking extreme machairodont features, which reveals it as a cursorial felid.<sup>49,74</sup> Thus, three species of *Lokotunjailurus* roamed Africa during the late Miocene and early Pliocene. During the Late Miocene *L. emageritus* occurred in East Africa (Lothagam, Kenya),<sup>49</sup> and *L. fanonei* in Central and North Africa (Toros Menalla, Chad and probably in Sahabi, Lybia)<sup>50,68</sup> and at the beginning of



the Pliocene *L. chinsamya* lived in the South of the continent (Langebaanweg). This confirms the high mobility of this taxon as a Pan-African sabertooth felid.

The postcranial bones described by Rabe et al.<sup>52</sup> show similarity to *L. emageritus*, and are here assigned to *L. chinsamya*. The size of the postcranial is slightly larger than the corresponding bone of *L. emageritus* (e.g., tibia), but such degree of differences does not support a distinct body size discrepancy of the two species. It is interesting to note that the maxilla and mandible of *L. chinsamya* are only slightly larger than those of *D. werdelini* (see Figure 10), but the postcranial bones are distinctly larger, suggesting the different body plane of these machairodonts.

### The affinity of two metalurine

Several small to medium-sized sabertoothed genera, assigned to metalurine, were known from the Late Miocene in the Old and New World. *Metailurus* was established on a well-preserved skull from Baode, northern China.<sup>66</sup> The type species *Metailurus major* is of medium size, with moderately developed upper canine, high-domed cranium, and wide forehead. A smaller species, *M. minor* was also found in Baode.<sup>66</sup> This small species is probably similar or identical to "*Machairodus*" *parvulus* from Pikermi,<sup>75</sup> but as Spassov and Geraads<sup>51</sup> suggested, the type of latter species is too poorly preserved, and the species should be treated as *nomen dubium*. This species is craniodentally different from *M. major*, and was erected as a separate genus *Yoshi* by Spassov and Geraads.<sup>51</sup> *Paramachaerodus* is another medium-sized sabertooth, with a similar body size to that of *Metailurus*.<sup>48</sup> This genus is thought to be or close to the ancestor of the Plio-Pleistocene *Smilodon* and *Megantereon*, and was referred to Smilodontini.<sup>54</sup> The overall morphology, however, is not significantly different from *Metailurus*, with a lower cranium and narrower forehead. Some authors support separating the Vallesian species *P. ogygia* to a separate genus *Promegantereon*,<sup>48,76</sup> whereas some other authors support the two genera are indistinguishable.<sup>77</sup> *Dinofelis* is the largest and most widely spread member of the metalurines. It was first established based on a skull from the Quaternary site of Mianchi, Henan, central China, as *Dinofelis abeli*.<sup>66</sup> Several new species were later recognized from Africa, Europe, and North America see a review by.<sup>46</sup> The North American medium-sized sabertoothed cats are represented by *Adelphailurus kansensis* and *Pratifelis martini*.<sup>78</sup> The validation of the former genus is generally accepted, whereas the latter is largely omitted by most authors. Turner and Antón<sup>54</sup> assigned *Adelphailurus* to metalurini, whereas Martin<sup>79</sup> hypothesized this genus evolved from North American *Pseudaelurus* (now viewed as the distinct genus *Hyperailurictis*).<sup>80</sup> *Adelphailurus* is generally similar to *Metailurus* but differs in two important traits: the presence of the P2, and the lack of the anterior accessory cusp in the P3. The m1 talonid of *Pratifelis* is well-developed, unlike any other metalurine, and its position is unclear. Two genera were known from the Late Miocene (Turolian) of Spain, *Stenailurus*<sup>81</sup> and *Fortunictis*.<sup>82</sup> Both genera were assigned to metalurini by Salesa et al.<sup>48</sup> *Stenailurus* is peculiar in having the P2, whereas *Fortunictis* is generally not mentioned by most authors.

The medium-sized sabertoothed cat from Langebaanweg (Figures 6 and 7) shows affinity to *Dinofelis*, *Paramachaerodus*, and *Metailurus*. It is distinctly larger than *Yoshi* and *Adelphailurus*, in addition to many traits (e.g. presence of enlarged P3 anterior accessory cusp, which is absent or very weak in *Yoshi* and *Adelphailurus*). The Langebaanweg medium-sized sabertoothed cat was first assigned to *D. diastemata* by Hendedy.<sup>12</sup> Hendedy<sup>12</sup> compared this material to *D. barlowi*, *D. piveteaui* and *D. diastemata*, and concluded that the Langebaanweg material is closer to the latter; we agree. Hendedy,<sup>12</sup> however, did not give a direct comparison of the Langebaanweg material to *D. diastemata*, nor the Asian species *D. cristata*. Turner<sup>45</sup> assigned the Langebaanweg material to *D. barlowi* without clear evidence. Werdelin and Lewis<sup>46</sup> suggested that the Langebaanweg material is metrically different from *D. barlowi* and does not likely belong to this species. The general morphology of this Langebaanweg felid is close to that of *D. diastemata*, but Werdelin and Lewis<sup>46</sup> realized that this similarity is represented by primitive traits, which provides little information in inferring its phylogenetic relationships.

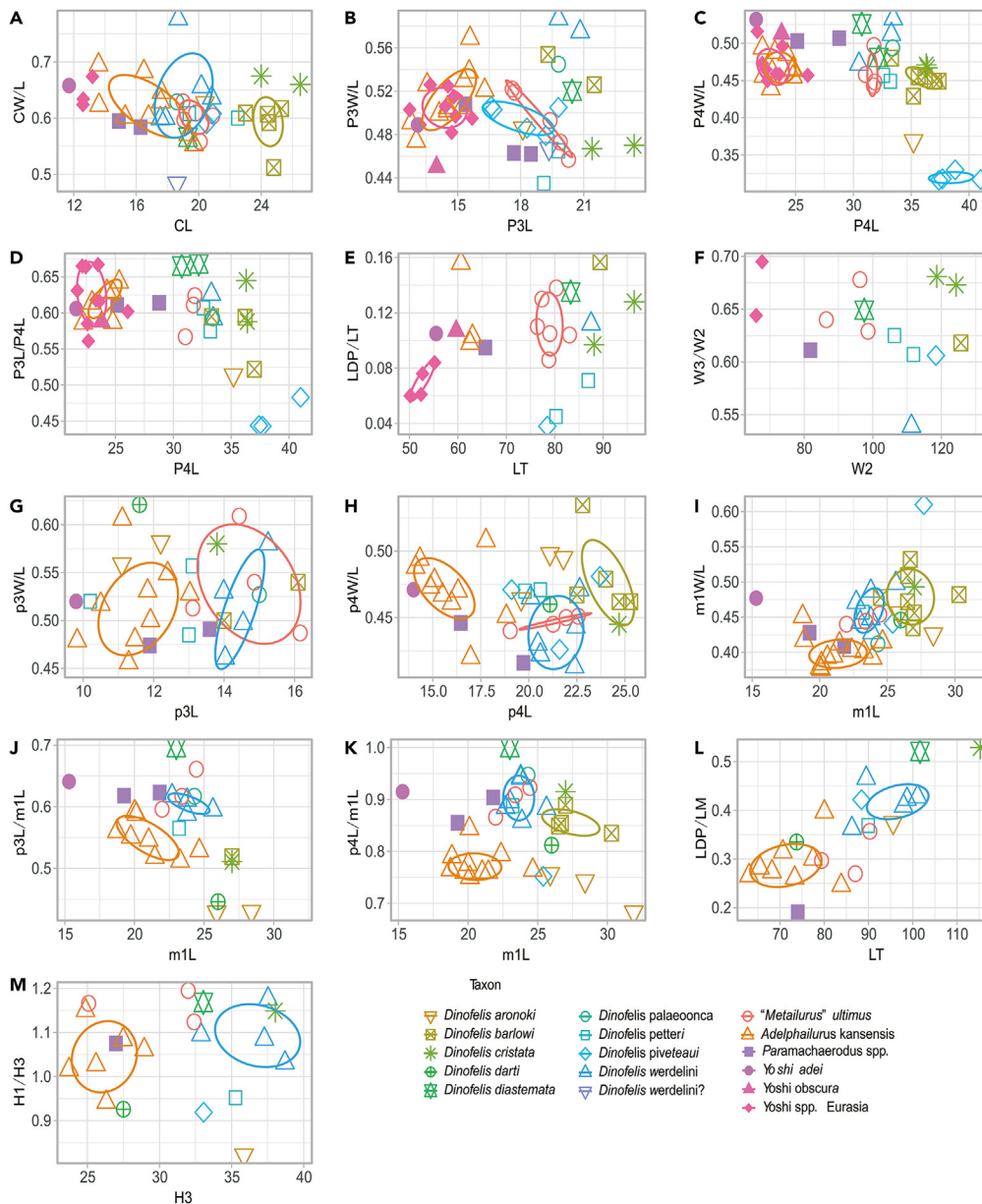
The new maxillary material (Figure 6) provides important information for this machairodont. The unique P3, P4 morphology is unlike any known species of *Dinofelis*. It is close to *D. diastemata* in general proportion, and protocone size, but the preparastyle seems to be stronger, and the P4 buccal contour has more undulations. All other species of *Dinofelis*, including Asian *D. cristata*, have a more reduced protocone. The other African species of *Dinofelis* have more reduced P3, without a strong postero-lingual convexity, and less developed preparastyle. The incisors of the maxilla are enlarged and more arched in arrangement compared with two Asian species of *Dinofelis*, and comparable to that of other African *Dinofelis*. The

mandible of the Langebaanweg machairodont is mainly characterized by its well-developed symphysis and deep corpus. All other species of African *Dinofelis* have a shallow symphysis, with the height of the mandible behind the canine being lower than that behind the m1. In contrast, for all specimens from Langebaanweg, the opposite is true (Figure 11M). In this aspect, the Langebaanweg machairodont resembles Eurasian *D. diastemata* and *D. cristata*, with a high symphysis. Both Eurasian species, however, have a rather elongated c-p3 diastema, with LDP/LT ratio of mandible clearly higher than that of Langebaanweg machairodont and other African species (see Figure 11L but see 11e that the differences in the DP/LT ratio of the maxilla are not distinct). The mandibles of the two Eurasian species are also not as deep. The lower dentition generally shows fewer differences, and the Langebaanweg machairodont has unreduced p3 compared with most other species of *Dinofelis*. The upper canine is more robust than any other species, other than *D. cristata*, and overlaps with *D. barlowi*. The dental sizes place the Langebaanweg machairodont among the smallest *Dinofelis*, however, the toothrow length (C-P4 and c-m1 length) is only distinctly smaller than that of *D. cristata*, similar to that of *D. diastemata* and *D. barlowi*, and slightly larger than that of *D. petteri* and *D. piveteaui*. This suggests that *Dinofelis* largely retained a similar body size, but the derived African species developed proportionally larger cheek teeth, reaching its peak in *D. aronoki-piveteaui*. The North American species *D. palaeonca* is the smallest *Dinofelis*, except for a recently discovered mandible from North Africa.<sup>83</sup> This species has a very short rostrum, and conservative dental traits, and seems to be a unique lineage of *Dinofelis*. The braincase (Figure 3D) shows a clear *Dinofelis* affinity, e.g., the glenoid fossa is not antero-posteriorly widened and not overhung, and the alisphenoid canal is totally absent. The mastoid process is well developed, especially its anterior branch, which reaches a level more than that in *D. diastemata* and *D. palaeonca*.

Apart from *Dinofelis*, the Langebaanweg machairodont also shows some similarities to *Metailurus* and *Paramachaerodus*. Both genera are distinctly smaller, and generally have a shorter rostrum, but the dentitions are similar. In both *M. major* and *P. transasiaticus*, the P3 has distinct postero-lingual convexity, and P4 has undulating buccal border. The lower p3 and p4 are also similar, especially the p4 lateral view.<sup>66,77</sup> However, both *M. major* and *P. transasiaticus* have m1 metaconid-talonid complex and have a somewhat trapezoid occlusal shape (buccal border not smooth). *Dinofelis*, therefore, probably originated from either of these two genera, but the Langebaanweg machairodont is already too derived to be placed in these two genera. A new species, *Metailurus ultimus* was named by Li<sup>84</sup> from the Mazegou Formation of the Yushe Basin, Late Pliocene. Two unpublished crania of this species from Shanxi housed in AMNH, suggest the cranium of this species is low and the forehead is narrow. This contrasts with that of *Metailurus*, but better fits with *Dinofelis* as assigned by Turner and Antón.<sup>54</sup> This species shows greater similarity to the Langebaanweg machairodont, in the m1 morphology. We add the metric data of this species to our analysis, and it can be seen that the Langebaanweg machairodont is larger and has a longer rostrum (Figure 11). Moreover, the incisors of these taxa are also smaller and less arched in the arrangement as seen in the Langebaanweg machairodont (Figure 12). A mandible and several other fragments of *Dinofelis* were reported from the Middle Awash by Haile-Selassie and Howell.<sup>85</sup> This taxon, which is slightly earlier than Langebaanweg, shows an overlap in dental size with that of the Langebaanweg felid (Figure 10), but the c-p3 diastema is shorter, and the corpus depth (behind the m1, 24.4 mm) is distinctly smaller than that of the South African one (behind the m1, 32.88–38.70 mm) (Figures 6 and 7). The *Dinofelis* from the Middle Awash seems to better fit the trait of *Metailurus* or *Paramachaerodus* and is distinct from the Langebaanweg felid.

In summary, the Langebaanweg machairodont should be assigned to *Dinofelis*, but is different from all known species of this genus, and is erected as a new species, that we named *D. werdelini* sp. nov. (Figures 6, 7 and 9). In general, our analyses support the view of Werdelin and Lewis,<sup>46</sup> that this species is closer to *D. diastemata* in morphology, but such similarity does not necessarily support a close phylogenetic relationship. *D. diastemata* seems to share a longer c-p3 diastema, and a similar mandibular morphology with the larger and more derived *D. cristata*. The younger African species seem to share the further reduction of both the anterior premolars, and P4 protocone. *D. petteri*, *D. aronoki* and *D. piveteaui* also share the shortening of the rostrum, and highly elongated P4. *D. werdelini* shares the enlarged and slightly arched incisors with the younger African species.

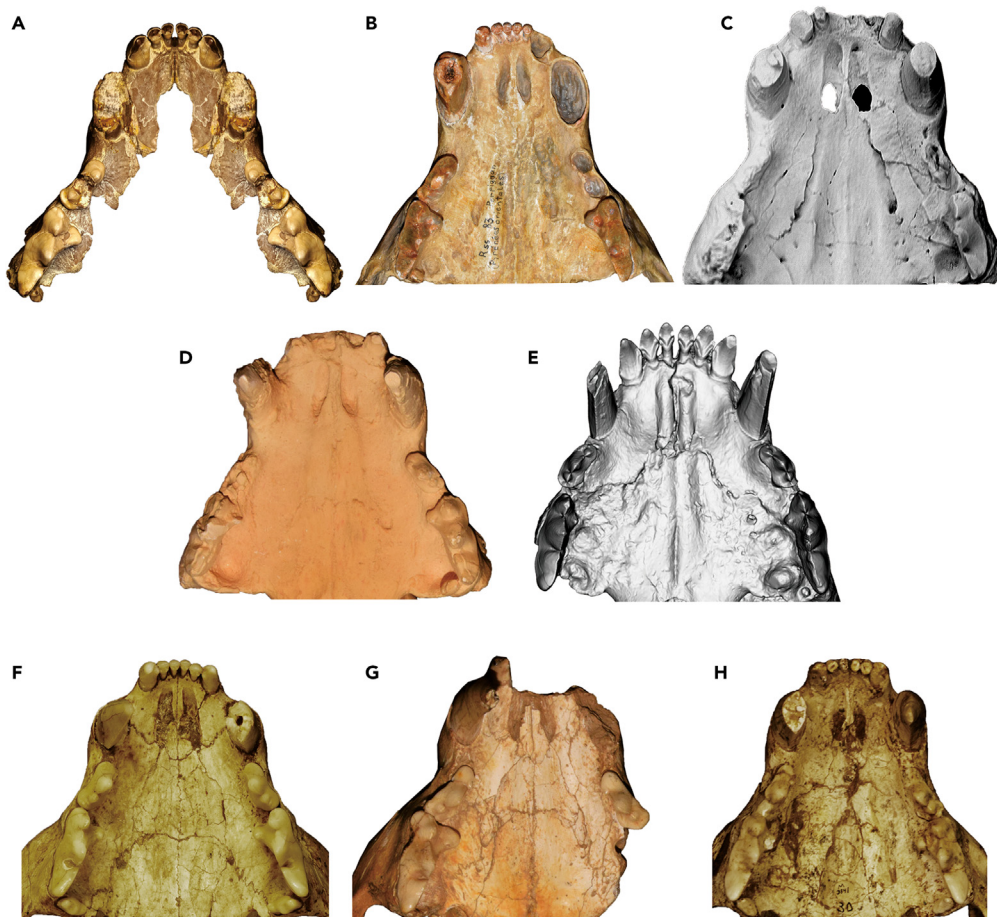
The smaller sabertoothed cat from Langebaanweg (Figure 8), only known by a fragmentary maxilla, has had a controversial systematic position since its description. It was first assigned to *Felis obscura* sensu lato by Hensley.<sup>12</sup> This is probably because of its relatively small canine, which is broken and has an unclear crown height. Hensley<sup>12</sup> thought the species may be correlated with *Sivapanthera* because of its small snout. The



**Figure 11. Comparative measurements and ratios of metalurine from Langebaanweg 'E' Quarry and other selected metalurine**

(A) C length vs width/length ratio; (B) P3 length vs width/length ratio; (C) P4 length vs width/length ratio; (D) P4 length vs P3/P4 length ratio; (E) upper tooth row (C-P4) length vs (C-P3) diastema/tooth row length ratio; (F) width of rostrum across P4/M1 vs width ratio of rostrum across C and across P4/M1; (G) p3 length vs width/length ratio; (H) p4 length vs width/length ratio; (I) m1 length vs width/length ratio; (J) m1 length vs p3/m1 length ratio; (K) m1 length vs p4/m1 length ratio; (L) lower tooth row (c-m1) length vs (c-p3) diastema/tooth row length ratio; (M) mandibular height behind the m1 vs mandibular height ratio behind C/behind m1. Biplot measurements/ratios were made using ggplot2 (<https://cran.r-project.org/web/packages/ggplot2/index.html>) of R (<https://www.r-project.org/>).

P2, however, is absent in this species, which is more common with Machairodontinae. In fact, the posterior ridge of the canine is clearly present, a key trait that distinguishes Machairodontinae from Felinae. Turner et al.<sup>86</sup> assigned this species to the North American genus *Adelphailurus* without stating their evidence. Morales et al.<sup>87</sup> recognized the machairodontine affinity of this species and hypothesized it could be correlated with *Megantereon*. However, *Megantereon* is a more derived genus, with much larger canine, and smaller P4 protocone. The loss of the P2 is also not unique to *Megantereon* among machairodontine.



**Figure 12. Comparison of maxilla of *Dinofelis* and related taxa**

(A) *Dinofelis werdelini* sp. nov. SAM-PQL-47523, right side mirrored; (B) *Dinofelis diastemata*, Perpignan, cast; (C) *Dinofelis cristata*, Siwaliks (photos courtesy of L. Werdelin); (D) *Dinofelis barlowi* UCMP88766, cast, Bolt's Farm; (E) *Dinofelis piveteaui* Ka 61, Kromdraai, from MorphoSource. A; (F) *Yoshi minor* PMU M3835, Baode (photos courtesy of X. Wang); (G) *Paramachaerodus transasiaticus* IVPP V20106, Shilei, Linxia Basin; (H) *Metailurus major* PMU M3841, Baode (photos courtesy of X. Wang). Adjust to the same size to show the different dental proportion.

Finally, Werdelin and Peigné<sup>44</sup> assigned this species to *Metailurus*, but did not mention the trait for this assignment.

Metrically, the body size of "*Felis*" *obscura* is closest to that of *Yoshi* spp., within its variation range, though near the upper boundary, and is distinctly smaller than *Metailurus*, *Paramachaerodus*, and *Dinofelis* (Figure 11). Morphologically, "*Felis*" *obscura* is also closest to *Yoshi*. The shared traits include the relatively high-crowned P3 (judging from the preserved part), without an anterior accessory cusp, P4 with a slender blade, no or weakly undulating buccal border, and relatively large protocone. The anterior accessory cusp of the P3 is present in most sabertooths, including derived *Paramachaerodus* (*Pa. transasiaticus*), *M. major*, and Machairodontini. Notably, the North American *Adelphailurus* also lacks this accessory cusp (probably the reason why Turner et al. assigned "*Felis*" *obscura* to this genus). *Yoshi* generally lacks this accessory cusp, but in some cases, it is present but very small and less defined. The P4 of *Paramachaerodus* and *Metailurus* shows a distinctly undulating buccal border,<sup>48,66,77</sup> which is very weak or absent in "*Felis*" *obscura* and *Yoshi*. However, there are two differences between "*Felis*" *obscura* and *Yoshi*. Most importantly, the M1 of "*Felis*" *obscura* is button-like and transversely short. In *Yoshi*, the M1 is invariably transversely elongated, and there is weak buccal concavity between the connected paracone and metacone. The morphology in the latter case represents the primitive stage seen in *Pseudaelurus-Hyperailurictis*. Another difference is the relatively longer C-P3 diastema. A very small-sized sabertoothed cat, *Tchadailurus adei* was erected from TM 112, Toros Menalla,

Chad, ~7 Ma.<sup>88</sup> Bonis et al.<sup>88</sup> noticed the similarity of their new genus to *Yoshi* and stated that *Tchadailurus* is different from *Yoshi* in smaller size, proportionally higher canine, and longer diastema. In other aspects, this genus is much like *Yoshi* and unlike other metailurine, in having a high crowned P3, without an anterior accessory cusp and a transversely elongated M1. This genus is very close, if not identical, to *Yoshi*. "*Felis*" *obscura* is also close to this species in general morphology mentioned above, and in addition, having long C-P3 diastema.

In brief, "*Felis*" *obscura* is close to both *Yoshi* and *Tchadailurus*, and these two genera are closer to each other than to "*Felis*" *obscura*. This, therefore, implies two hypotheses of classification. The first one, is to include "*Felis*" *obscura* and *T. adei* in the genus *Yoshi*. This implies that the first two represent unique members of the genus with elongated C-P3 diastema, and *Y. obscura* an independently reduced M1 inner lobe. The second one, validates the distinct genus *Tchadailurus*, and that "*Felis*" *obscura* should be viewed as a distinct genus too. In order to not oversplit in genera taxonomy, and that the material is incomplete, we adopt the first classification, which includes both "*Felis*" *obscura* and *T. adei* in *Yoshi*. Thus, *Y. obscura* emerges so far as the youngest known and most unique species of the genus. Our phylogenetic analysis (Figure 9) confirms its assignation in the genus *Yoshi*, and it emerges as the sister taxon of *Y. yongdengensis* from the latest Miocene of China.<sup>53</sup>

### Unique combination of felid guild and its palaeoecological implications

Among the six species of Felidae at Langebaanweg 'E' Quarry, two of them are small to medium felids (*Felis*-like and *Caracal*-like forms; under study) and four are sabertooths. Among them, there are two Machairodontini (*Adeilosmilus* aff. *kabir*, *L. chinsamyae* sp. nov.), and two metailurine (*D. werdelini* sp. nov., *Y. obscura*). The two Machairodontini species are larger than the two metailurine species, but *Lokotunjailurus* is probably only slightly larger than *Dinofelis*. Even though the postcranial bones from this locality have not been studied in detail (e.g., Hendeby, 1974<sup>12</sup>; Rabe et al.<sup>52</sup>), it is generally thought that Machairodontini are more adapted to open environments, as most known members of this tribe have certain cursorial adaptation.<sup>54,89</sup> The known species of metailurine shows no<sup>46</sup> or only moderate<sup>90</sup> cursorial adaptation. The composition of different tribes of machairodonts in the fauna, therefore, gives some clues about the paleoenvironment. Overall, the guild of sabertooths from Langebaanweg 'E' Quarry is composed of typical Miocene Machairodontini (*Adeilosmilus*, *Lokotunjailurus*) and metailurine (*Yoshi*), which represent one of the last records of these genera in the fossil record, as well as one of the earliest well-known Pliocene records of *Dinofelis*. Previously, significant differences between the carnivoran faunas of the MPPM and LQSM have been highlighted,<sup>12,15,17,20–22,30,33,91</sup> and interpreted as because of temporal differences and faunal replacement. More specifically, Hendeby,<sup>12</sup> Werdelin, and Sardella,<sup>43</sup> pointed out the differential occurrence of *Amphimachairodus*, *Lokotunjailurus* and *Dinofelis* (determined as *Homotherium*, *Amphimachairodus* and *Machairodus*) in LQSM, and *Yoshi* (determined as *Felis* and *Metailurus*) in MPPM. The updated distribution of these taxa in the members of 'E' Quarry indicate that *Lokotunjailurus* occurred in LQSM (NMI = 2), *Ad. Aff. Kabir* and *Dinofelis* in both members (NMI of *Adeilosmilus* = 1 in both members; NMI of *Dinofelis* = 5 in both members), and *Yoshi* in MPPM (NMI = 1). The re-study of plenty of new fossils of mustelids, canids and sabertooths from the site<sup>23–25,52</sup> suggests that the previously observed differences may be produced by sedimentation (estuarine/marine/fluvial deposition) or sampling biases, instead of temporal replacement of the carnivoran guild.<sup>23–25</sup> Moreover, this is supported by a same relative dating of both members (~5.15 ± 0.1 Ma) by sedimentological, petrographical and geochemical evidence.<sup>10,92,93</sup>

We compared the felid guild of Langebaanweg with six other well-established Late Miocene faunas: Lothagam in eastern Africa,<sup>49</sup> Toros Menalla in central Africa,<sup>50,60,88,94</sup> Samos-Pikermi in Greece,<sup>95</sup> Las Casiones in Spain,<sup>96</sup> Baode in northern China,<sup>66</sup> and Yuanmou in southern China,<sup>97</sup> as well as seven faunas from the Pliocene and early Pleistocene of Africa: Laetoli bed Upper Unit in Tanzania (3.7–4.46 Ma),<sup>98–100</sup> OMO Shungura in Ethiopia (2.91–2.53 Ma),<sup>44,101</sup> Limeworks Makapansgat in South Africa (3–2.6 Ma),<sup>102</sup> Malapa in South Africa (1.98Ma),<sup>103,104</sup> Cooper's Cave System (1–0.6 Ma) in South Africa,<sup>105</sup> Swartkrans Member 1 in South Africa (1.8–1.36 Ma),<sup>106,107</sup> and Koobi for a, Okote member in Kenya (1.5 Ma).<sup>108,109</sup> The body sizes of these felids (which play a key role in their ecology), were classified into six grades based on cranial and P4 length (Table S3). Our multivariate analyses (hierarchical cluster and principal component analyses) based on taxonomic composition (five basic measurements: number

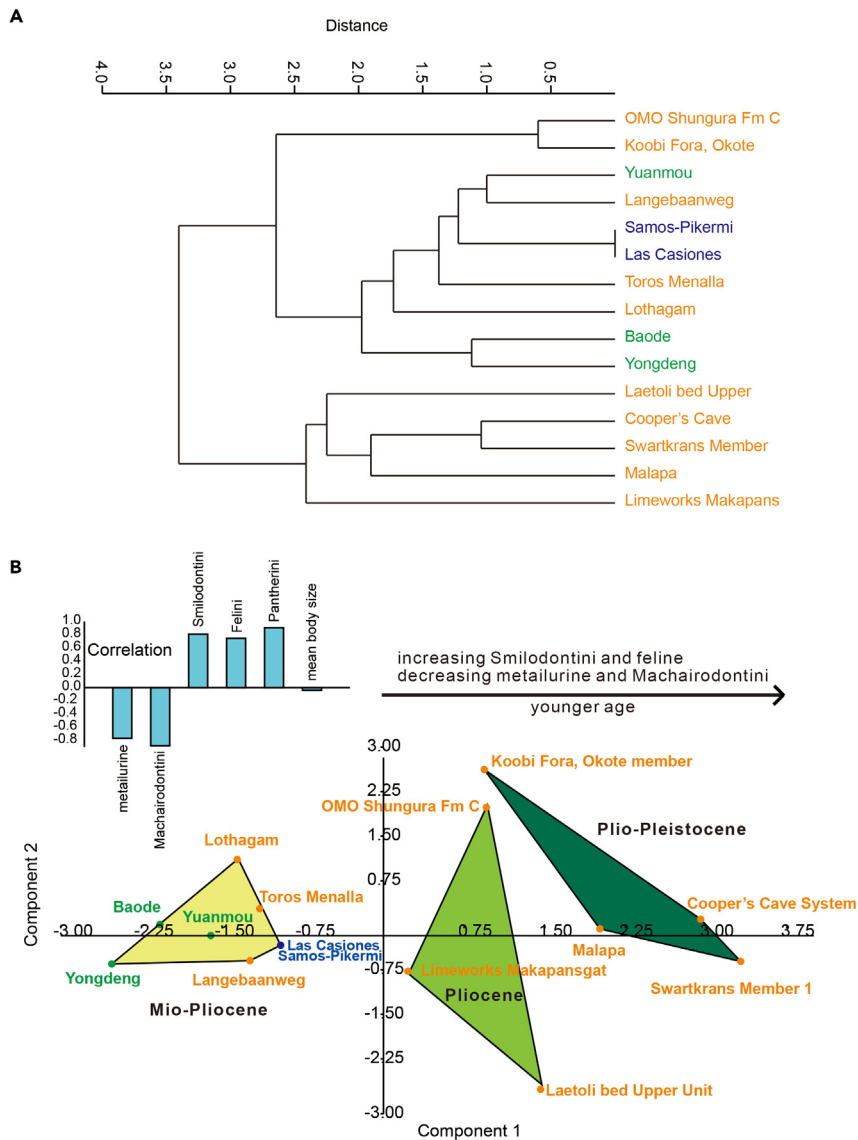
of Machairodontini, metailurine, Smilodontini, Felini and Pantherini) and mean body size (averaged for grade, see [Table S3](#) for details, and the highlight rows are used in cluster and PCA analyses), suggest that the Late Miocene faunas have an assemblage of felids comprising both Machairodontini and metailurine. The metailurine are generally more diverse, as they have a smaller body size and occupy a lower position in the ecosystem. In terms of Machairodontini proportion Langebaanweg has a relatively high value, only lower than that of Toros Menalla and Yuanmou, suggesting the environment was at least partially open. The presence of *Lokotunjailurus*, a relatively cursorial Machairodontini<sup>74</sup> also support this hypothesis. The number of *Dinofelis* (metailurine) specimens at Langebaanweg exceeds that of other felids, suggesting the forest environment is most likely present, revealing a complex environment with a mosaic of ecosystems in Langebaanweg. Isotopic analyses of the herbivorous fossil fauna from Langebaanweg<sup>10</sup> suggest a Mediterranean climate, consisting in an open C3-dominated ecosystem where C4 grasses had not yet extended. Additional evidence from the site such as pollen and the occurrence of grazing taxa<sup>10,17,111,112</sup> indicate an open subtropical C3 vegetation, with a weighty contribution by sclerophytic fynbos pointing to a cooler and more seasonal climate than in the Miocene.

In terms of mean body size grade, it is interesting that among the Mio-Pliocene sites, African felid guilds generally have a large body size compared with those in Eurasia ([Table S3](#)). This is because of its generally higher Machairodontini proportions, and larger body size (*Dinofelis*) among metailurines. In general, the large-bodied carnivores are more abundant in an open environment, as seen in the modern eastern African savanna. The body size grade therefore supports that the African environment is generally open during the Late Miocene.

Comparisons of the evolution of the felid guild from the Miocene-Pliocene to the Plio-Pleistocene in southern Africa ([Figure 13](#)) are intricate due to the c. 3 million years<sup>113</sup> of information hiatus between Langebaanweg and the Cradle of Humankind fossils (northern part of South Africa), where multiple taxa of sabertooth cats have been found. The proportionally higher composition of Machairodontini, including *Lokotunjailurus*, and larger body size metailurines (*D. werdelini*) in Langebaanweg, contrasts with the increase in proportions of both Smilodontini e.g., *Megantereon* spp., and felines (*Acinonyx*, *Caracal*, *Leptailurus*, *Panthera* spp., and *Felis*) in the Cradle of Humankind fossil record during the late Pliocene (e.g., Limeworks Makapansgat, 3–2.6 Ma) and Pleistocene (e.g., Malapa, 1.98 Ma; Swartkrans Member 1, 1.8–1.36Ma; Cooper's Cave System, 1–0.6 Ma). Overall, the Pliocene and Pleistocene African localities are not closely nested with the Mio-Pliocene localities. In contrast, in PCA plots, the faunas from different ages are clearly located close to each other, and in PC1 from the most negative to the most positive values, the age tends to be younger. This suggests that the felid guild is more chronological than geographic and supports a high dispersal ability of this group.

Of interest, Langebaanweg shows the same felid composition to Yuanmou, a middle Late Miocene fauna from Yunnan Province, southern China. In hierarchical cluster and PCA analyses ([Figure 13](#)), Langebaanweg is close to Yuanmou in both analyses. A recent study of Yuanmou felids<sup>97</sup> reveals that these felids are unique in many respects, and one new form *Longchuansmilus*, potentially has a close relationship with *Lokotunjailurus*. This suggests that the environment of the two regions could be similar, but also suggests the presence of a potential dispersal route between these two remote areas, though current evidence is insufficient to give a more comprehensive analysis.

During the Mio-Pliocene boundary, most sabertoothed cats in Eurasia went extinct, and during the Pliocene, new forms of machairodonts appeared.<sup>54,114</sup> This is not the case in Africa. Most Pliocene machairodonts in Africa evolved directly from their late Miocene ancestors, including *Dinofelis* spp., and *Ad. kabir-Homotherium*. As already mentioned, Africa experienced a more continuous change to more open and arid grassland or desert since the late Miocene which continued into the Pliocene, in contrast to Eurasia. Our analysis shows that the African late Miocene-early Pliocene felid guild structure already showed adaptation to open environments compared with Eurasia, where there is no distinct disruption in environmental change. Eurasia experienced a profound environmental change during this boundary, and as a result, most saber-toothed cats, together with many other carnivores, e.g., very diversified hyena guild, went extinct. The continuous aridification throughout the Mio-Pliocene, with the spread of



**Figure 13. Felid guild composition (species number) and mean body size of selected faunas from Eurasia and Africa**

(A) Hierarchical cluster (Euclidean distance).

(B) PCA scoring plot. Localities in orange are from Africa, in green from Asia and in blue from Europe. Those analyses were performed using software PAST 4.0.3 (<https://past.en.lo4d.com/windows>).

open environments, could be an important trigger on the bipedalism of hominids,<sup>115,116</sup> and the saber-tooth guild in Langebaanweg and its environmental and paleobiogeographic implications provide background for future discussion on hominid origination and evolution.

### Limitations of the study

In this study, we have not compared our specimens with many African sabertooths from other localities, e.g., *Adeilosmilus*, *Lokotunjailrus*, in person, so our coding on these species is based on literature. The material for some species, especially *Adeilosmilus* aff. *kabir*, is too poor to give a good evaluation on its affinity, so more material will be needed to clarify this large sabertooth cat.

## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
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  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.107212>.

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## AUTHOR CONTRIBUTIONS

A.V. developed the initial concept for the research. Q.J., C.R., and A.V. performed data collection. Q.J. and A.V. performed analysis and wrote the first draft of the manuscript. C.R., J.A., and R.G. assisted and reviewed the manuscript. Q.J., C.R., J.A., R.G., and A.V. read and contributed to the final draft.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a gender minority in their field of research. One or more of the authors of this paper self-identifies as a member of the LGBTQIA+ community.

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## STAR★METHODS

### KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Phylogenetic character matrix	Modified from Jiangzuo et al. <sup>63</sup>	NA
Software and algorithms	Mrbayes 3.2.7 <sup>117,118</sup> ggplot2 3.3.5 <sup>119</sup> in R 4.0.5 <sup>120</sup> PAST 4.03 <sup>121</sup>	NA

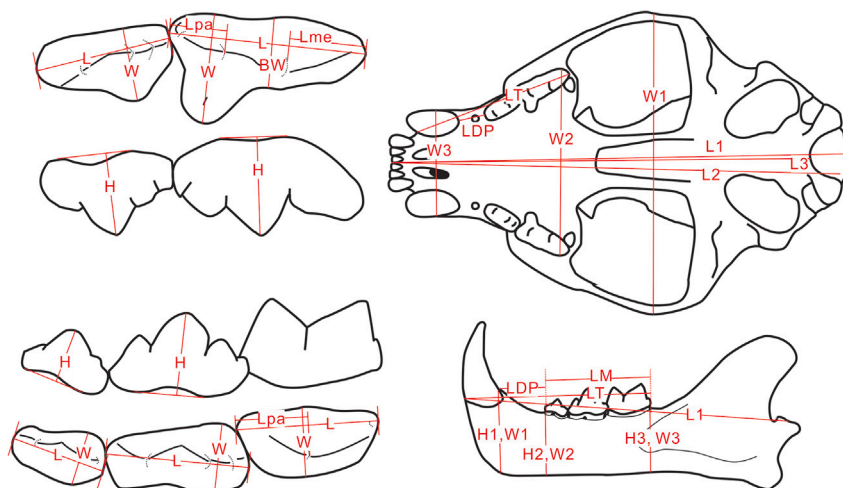
### RESOURCE AVAILABILITY

#### Lead contact

Alberto Valenciano; [albvalen@ucm.es](mailto:albvalen@ucm.es).

#### Materials availability

The material discussed in this study is housed at the Iziko South African Museum. Only craniodental material was studied. The used measurements are shown in below figure. The comparative material includes original fossils of *Metailurus* spp. housed in the AMNH, IVPP and HM, *Paramachaerodus* spp. housed in the IVPP and HM, *Yoshi* spp., housed in the AMNH, IVPP and HM, *Rhizosmilodon fitae* housed in the UF, *Amphimachairodus* spp. from the collections of AMNH, IVPP and HM, *Nimravides* spp. from the AMNH and UF, as well as *Homotherium* spp., and *Xenosmilus hodsonae* from the AMNH, UF, IVPP, HM.



**Craniodental measurement for felids. H1-3 and W1-3 in the mandible represent the mandibular height and width behind the canine, before the p3 and behind the m1**

#### Institutional abbreviations

AMNH FM fossil mammal collection of American Museum of Natural History, New York, USA

AMNH F:AM Frick fossil mammal collection of American Museum of Natural History, New York, USA

AMNH M mammalian collection of American Museum of Natural History, New York, USA

HM Hezheng Paleozoological Museum, Hezheng, China

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

IOZ Institute of Zoology, Chinese Academy of Sciences, Beijing, China

SAM-PQL Quaternary Palaeontology (Langebaanweg), Iziko South African Museum, Cape Town, South Africa

UCMP University of California Museum of Paleontology, Berkeley, California, USA

UF Florida Museum of Natural History at University of Florida, Gainesville, Florida, USA

USNM Smithsonian National Museum of Natural History, Washington DC, USA

#### Other Abbreviations

AW anterior width of the M1 and M2

BW blade width of the P4 (width across the paracone posterior to the protocone)

H height

Hh2 Hemphillian2, late Early Hemphillian North American Land Mammal 'Age' (NALMA)

Hh3 Hemphillian3, Late Hemphillian NALMA

Hh4 Hemphillian4, Latest Hemphillian NALMA

L length

LP diastema between the upper canine and the P3 or lower canine and the p3.

LT toothrow length from anterior border of C (c) alveolus to the posterior border of the P4 (m1) alveolus

M/m upper/lower molar

ML metacone length

P/p upper/lower premolar

PL paracone length

W width

WC width of the rostrum at the canine

WP4 width of the rostrum at the posterior of the P4

The dentognathic measurements used in this study are presented in [Figure 14](#) and the values and interpretations are given in [Tables 1](#) and [2](#).

#### Data and code availability

Data

- Data have been deposited at text and supplementary material

Code

- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request

#### EXPERIMENTAL MODEL AND SUBJECT DETAILS

We do not have experimental model and subject.

#### METHOD DETAILS

The phylogenetic analysis using the tip-dating Bayes Inference method (fossilized birth-death model)<sup>122</sup> was implemented using software MrBayes 3.2.7 (<https://nbisweden.github.io/MrBayes/download.html>).<sup>117,118</sup> 10 million generations of two runs, each with run 4 chains were performed. Constraints on Felidae and Machairodontinae were set, since the characters used in the matrix are especially designed for Machairodontinae. See the details setting in appendix nexus file.

### QUANTIFICATION AND STATISTICAL ANALYSIS

The principal component analysis (PCA) and hierarchical cluster of the felid guild analyses were performed using software PAST 4.0.3 (<https://past.en.lo4d.com/windows>),<sup>121</sup> and the biplot measurements/ratios were made using ggplot2 (<https://cran.r-project.org/web/packages/ggplot2/index.html>)<sup>119</sup> of R (<https://www.r-project.org/>).<sup>120</sup>