A new species of *Plesiogulo* (Mustelidae: Carnivora) from the Late Miocene of Africa

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A new species of *Plesiogulo* (*Plesiogulo botori* sp. nov.) is described from 5.5–6.0 Ma deposits in East Africa. This new fossil material comes from two localities: Lemudong’o in southern Kenya, and Adu Dora, in the Afar Depression of Ethiopia. The new mustelid species is considerably smaller than those of *P. crassa*. However, Harrison (1981) has since reported that *P. crassa* falls within the range of variation observed in *P. minor*. *Plesiogulo crassa* has also been identified from Cherevichn, near Odessa on the Black Sea in the Ukraine. Korotkevich & Semenov (1975) referred 45-3106 (snout with teeth), 45-3271 and 45-3272 (associated crania, mandible and teeth), and 45-3107 (right and left mandible with dentition) from the MN-12 of Cherevichn to *P. crassa*. These specimens are housed at the Ukrainian Academy of Sciences, Kiev. *P. crassa* is also known from cranial and jaw remains from Paveodar (Irysh River, west Siberia). The remains were originally attributed by Orlov (1941) to *P. brachygnathus*, and subsequently assigned to *P. crassa* by Kurtén (1970). They are housed in the collections of the Paleontological Institute of the Russian Academy of Sciences (Moscow).

In Europe, *Plesiogulo monspessulanus* was named by Viret (1939) for a right mandible fragment with p3–m1. This was the only specimen recovered from the Montpellier red sands but the species has since been recognized from a geographically wide range of sites. Teilhard de Chardin (1945) referred a Yushé mandible from China (Licent Collection 14.046) to a new taxon, *P. b. major*. Kurtén (1970) elevated this subspecies to full species rank and argued that *P. major* is differentiated from *P. monspessulanus* by its retention of the m1 metaconid (although he did question the taxonomic significance of this trait). Hendey (1978) and Alcala et al. (1994) also noted the similarities between

INTRODUCTION

The large mustelid *Plesiogulo* (Zdansky, 1924) was first described from the late Miocene or early Pliocene of China (Schlosser 1903). Species of this genus have since been identified from late Miocene and early Pliocene deposits in Asia, Europe, North America and South Africa, and was clearly geographically widespread. Five species are well characterized (Harrison 1981). Though there are distinct morphological differences between these taxa, in terms of size alone three are small (*P. crassa*, *P. praecociden*, and *P. marshalli*) and two are large (*P. lindsayi* and *P. monspes-

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these two species and suggested that P. major is synonymous with P. monspessulanus. Hendey (1978) referred three dental specimens from Langebaanweg, South Africa, to P. monspessulanus, presenting the first evidence for Plesiogulo in Africa. Alcalá et al. (1994) referred three isolated teeth from the upper MN-13 locality of Las Casiones (Teruel Basin, Spain) to P. monspessulanus. From another site in Spain, the MN-13 locality of Venta del Moro, Morales (1984) identified an isolated P4 fragment as being large and like P. monspessulanus. This species has a large geographic range covering China, Europe, and South Africa.

From North America, P. marshalli (Hibbard 1934) is represented by a number of craniodental and postcranial remains from ten late Hemphillian sites (see Harrison 1981). Other specimens of Plesiogulo from four late Hemphillian North American localities have been referred to a new species, P. lindsayi, a species the size of P. monspessulanus (Harrison 1981).

Plesiogulo was previously unknown in eastern Africa. The new fossil material presented here comes from two late Miocene eastern African localities: Lemudong’o in southern Kenya (Ambrose et al. 2003) and Adu Dora, in the Afar Depression of Ethiopia (WoldeGabriel et al. 2001). This is the earliest occurrence of Plesiogulo in Africa, and the first evidence of this genus in eastern Africa, although Plesiogulo praecocidens has been preliminarily reported to be present in late Miocene deposits in the Tugen Hills of Kenya (Morales et al. 2004, abstract). The two sites that have yielded remains of the new Plesiogulo species are more than 1000 km apart demonstrating a fairly wide geographic range for this taxon. The faunal assemblages associated with Plesiogulo botori sp. nov. suggest a closed/woodland habitat at both sites (Ambrose et al. 2003; WoldeGabriel et al. 2001). This is unlike the habitats of the Chinese species, which are believed to have lived in open country (Kurtén 1970).


**SYSTEMATICS**

Carnivora Bowdich, 1821  
Mustelidae Fischer, 1817  
Mellivorinae Gill, 1872  
Gulonini Webb, 1969  
Plesiogulo Zdansky, 1924

**Plesiogulo botori sp. nov., Fig. 1**

*Holotype.* KNM-NK 41420, an associated partial maxillary dentition including left P3–M1, right P4–M1, partial right zygomatic process and fragment of right temporal bone preserving the glenoid cavity recovered from the Narok locality, Lemudong’o, Kenya (Fig. 1a; all measurements are given in Table 1) housed in the National Museums of Kenya, Nairobi.

*Paratype.* ADD-VP-1/10, left M1 (Fig. 1b), from the Adu Dora locality of the Middle Awash, Afar Depression, Ethiopia.

*Horizon.* All the specimens referred to *Plesiogulo botori* were collected from deposits radiometrically dated to between 5.54 ± 0.17 and 6 Ma.

*Etymology.* ‘botor’ means ‘old’ in the Masai language, spoken by the people living near Lemudong’o, Kenya, where the type specimen was found.

*Diagnosis.* A species possibly larger than all known species of *Plesiogulo* and at the higher end of the range of variation seen in *P. lindsayi* from North America. The P3 and P4 are longer and wider compared to *P. monspessulanus* and the M1 is longer.

*Plesiogulo botori* differs from *P. lindsayi* in the lack of an anterior cingulum on P4. The M1 internal lobe of *P botori* is expanded relative to the external lobe, compared to the condition in *P. monspessulanus* and *P. lindsayi*. The M1 protocone of *P. botori* is tall compared to that of *P. monspessulanus*, and the lingual cingulum is not continuous but rather interrupted mesially.

*Comparative description*  
KNM-NK 41420 comprises associated left P3, right and left P4, M1, partial right zygomatic process and fragment
of right temporal bone. The occlusal morphology and overall crown shape of the P3 is similar to all other species of *Plesiogulo*. However, it is longer and broader than all known P3s of Eurasian *Plesiogulo* and thus similar to the North American *P. lindsayi*. The lingual bulge seen in the P3 of *P. botori* is shared with *P. lindsayi*, but is not present in the Langebaanweg specimen, L40042 (Hendy 1978). The P4 is relatively broad at the protocone level, being comparable to *P. crassa* (= P. minor), *P. marshalli*, and *P. monspessulanus* (= P. major). *Plesiogulo lindsayi* has a relatively low length/breadth ratio of the P4. Even though the presence or absence of labial cingulum on the P4 has not been recorded for most species of *Plesiogulo*, *P. lindsayi* is reported to have labial cingulum (Harrison 1981), which *P. botori* lacks. This cingulum is also present in L40042, which has approximately the same length/breadth ratio (1.47 vs 1.49) as *P. botori*. The P4 protocone is a distinct cusp in almost all *Plesiogulo* species although there seems to be intra- and interspecific variation in its placement relative to the rest of the carnassial.

The protocone height of the M1 in both specimens of *P. botori* is more elevated than seen in the Langebaanweg specimen. Additionally, neither of the three M1s of *P. botori* has the continual cingulum seen in the Las Casiones specimen from Spain, the sole reported M1 of *P. monspessulanus* from the site (Alcalá et al. 1994). The lingual and buccal lobes of the M1 are more equal in mesiodistal length in the Las Casiones specimen than is seen in either of the M1s of *P. botori*. M1 lingual lobe of *P. botori* tends to be proportionately more expanded than in M1s of both *P. monspessulanus* and *P. lindsayi* but less expanded than *P. marshalli*. The median constriction between the two lobes of the M1 is pronounced in almost all specimens of *Plesiogulo*, except that of *P. praecocidens*, which tends to have a more triangular occlusal crown shape. ADD-VP-1/10 is similar to the M1s of KNM-NK 41420 in almost all morphological and metric variables.

The associated right zygomatic process and right glenoid cavity of KNM NK 41420 preserve typical Mustelidae morphology but are not taxonomically informative at the species level.

**DISCUSSION**

*Plesiogulo botori* was compared to the five commonly recognized species of *Plesiogulo* with upper dentition. The three relatively smaller species (*P. crassa*, *P. praecocidens*, and *P. marshalli*) are distinct from *P. botori* primarily in size though numerous other characters also differentiate them. These species have similar overall M1 crown morphology, in that the buccal lobe is not expanded, giving the M1 a more triangular occlusal appearance. The M1 of *P. botori* is also more triangular in overall shape than the other larger *Plesiogulo* species (*P. monspessulanus* and *P. lindsayi*) in that the buccal lobe is relatively more reduced in mesiodistal length relative to the expanded lingual lobe. The lingual and buccal lobes of the M1 of *P. lindsayi*, for example, are sub-equal, giving the molar a more rectangular appearance to this tooth rather than a more triangular appearance as in *P. botori*.

*Plesiogulo crassa* has a relatively narrower P3, even though the P4 is of approximately the same relative length/breadth ratio as *P. botori*. *Plesiogulo marshalli* has approximately the same length/breadth ratio as *P. botori* but lacks the lingual bulge on P3 and has a less distinct P4 protocone. The M1 internal lobe of *P. marshalli* is also more expanded (internal lobe length/minimum length) than that of the M1 of *P. botori* or any of the other species of *Plesiogulo*. *Plesiogulo praecocidens* lacks a median constriction completely, even though its buccal lobe, relative to the lingual lobe, is considerably more narrow than in *P. botori* or any of the other species of *Plesiogulo*.

*Plesiogulo botori* is dated to between 5.54 ± 0.17 myr (Adu Dora, Ethiopia, WoldeGabriel et al. 2001) and 6.04 ± 0.019 myr (Lemudong’o, Kenya, Ambrose et al. 2003). This

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**Table 1. Comparison of upper dental dimensions.**

<table>
<thead>
<tr>
<th></th>
<th><em>P. botori</em></th>
<th><em>P. monspessulanus</em> (= major)</th>
<th><em>P. brachygnathus</em> (ex-Lutra brachygnatha)</th>
<th><em>P. crassa</em> (= minor)</th>
<th><em>P. praecocidens</em></th>
<th><em>P. marshalli</em></th>
<th><em>P. lindsayi</em></th>
<th>G. gulo</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P3</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
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<td>13.9</td>
<td>No data</td>
<td>11</td>
<td>No data</td>
<td>11.6</td>
<td>13.0</td>
<td>10.4</td>
</tr>
<tr>
<td>Width</td>
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<td>9</td>
<td>No data</td>
<td>6.9</td>
<td>No data</td>
<td>8</td>
<td>9.3</td>
<td>6.3</td>
</tr>
<tr>
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<td>1.54</td>
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<td>1.59</td>
<td>No data</td>
<td>1.45</td>
<td>1.39</td>
<td>1.65</td>
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<td><strong>P4</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>24.5</td>
<td>23.2</td>
<td>17.1–20.5</td>
<td>18.3–20.8</td>
<td>17.2</td>
<td>20.1</td>
<td>23.5</td>
<td>19.75</td>
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<td>Width</td>
<td>16.7</td>
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<td>11.1–14.0</td>
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<td>10.9</td>
<td>13.9</td>
<td>17.3</td>
<td>11.9</td>
</tr>
<tr>
<td>Length/width</td>
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<td>1.51</td>
<td>No data</td>
<td>1.45</td>
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<td><strong>M1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Width</td>
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<td>18.6</td>
<td>13.8–19.4</td>
<td>15.8–17.8</td>
<td>13.8</td>
<td>18.2</td>
<td>20.0–21.5</td>
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</tr>
<tr>
<td>Lingual lobe length</td>
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<td>15.4</td>
<td>12.0–16.3</td>
<td>13.2</td>
<td>12.4</td>
<td>15.1</td>
<td>13.3–15.5</td>
<td>8.3</td>
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<td>8.4</td>
<td>7.8</td>
<td>9.1</td>
<td>9.7</td>
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<td>Max length/min length</td>
<td>1.57</td>
<td>1.54e</td>
<td>1.57</td>
<td>1.59</td>
<td>1.67</td>
<td>1.51</td>
<td>1.34e</td>
<td></td>
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<td>Width/lingual lobe length</td>
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<td>1.28</td>
<td>1.11</td>
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<td>No data</td>
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<td>0.55</td>
<td>0.53</td>
</tr>
<tr>
<td>P3/P4 width</td>
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<td>0.58</td>
<td>No data</td>
<td>0.54</td>
<td>No data</td>
<td>0.57</td>
<td>0.53</td>
<td>0.53</td>
</tr>
</tbody>
</table>

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1. Data for *P. monspessulanus*, *P. brachygnathus* and *P. crassa* are from Hendy (1978) and Alcalá et al. (1994), Zdansky (1924) and Kurten (1970), respectively. Dimensions of *P. marshalli* and *P. lindsayi* are from Harrison (1981). Measurements of *Gulo gulo* are from Kurtén & Rausch (1959); e = estimated from published images, all reported measurements are in mm.
species is associated with mammalian taxa with more closed/wooded habitat preferences. The mammalian fauna from the late Miocene of the Middle Awash, Ethiopia, is largely dominated by tragelaphines, cercopithecines, colobines, and reduncines (WoldeGabriel et al. 2001). The Lemdong’o faunal assemblage consists of large birds of prey, colobines, and other indicators of a possibly closed habitat (Ambrose et al. 2003). This indicates a wider habitat preference for Plesiogulo contrary to what has been documented from China, where the genus is associated with open habitat.

A number of mustelid species have been reported from the Lothagam Formation in Kenya. However, no specimens of Plesiogulo have been documented from either the Upper or Lower Nawata Members of the Formation (Werdelin 2003). The paleoenvironment of the 6 million year old Upper Nawata Member has been reconstructed to have been a fairly dry and open environment (Leakey & Harris 2003). The absence of Plesiogulo from these deposits may indicate that the genus was limited to a closed habitat at least in late Miocene East Africa.

Plesiogulo praecocidens has been reported for the 6.1–5.7 myr Tugen Hills site of Lukeino in Kenya (Morales et al. 2004). These specimens have not yet been fully published, but the preliminary report indicates that there may have been two species of Plesiogulo in eastern Africa during the late Miocene.

The Plesiogulo from South Africa and associated fauna are biochronologically attributed to a wide temporal range between 3.5–7 myr (Hendey 1978), but probably closer to 5 myr (Haile-Selassie 2001). Most species of Plesiogulo are known from China. However, the genus has also been documented from some European Turolian (and perhaps older) localities, as well as many North American late Hemphillian ones, indicating a wide temporal range between 3.5–7 myr (Hendey 1978), but probably are biochronologically attributed to a wide temporal range. The absence of Plesiogulo from these deposits may indicate that the genus was limited to a closed habitat at least in late Miocene East Africa.

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