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2004
BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH
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A new species of *Plesiogulo* (Mustelidae: Carnivora) from the Late Miocene of Africa

Yohannes Haile-Selassie[1], Leslea J. Hlusko[2*] & F. Clark Howell[3]

[1]*Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, OH 44106, U.S.A.*

[2]*Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.*

[3] *Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, U.S.A.*

Receiced 21 October 2003. Accepted 9 November 2004

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 larger than all known Old World *Plesiogulo* species and extends the temporal and spatial range of the genus in Africa. *Plesiogulo botori* sp. nov. documents the earliest occurrence of the genus in Africa in general and the first evidence of its occurrence in late Miocene deposits of eastern Africa. Associated mammalian fauna at both localities where the species has been found indicate a closed/wooded habitat for the genus. This and other occurrences of the genus across Europe, Asia, and the New World indicate that the genus *Plesiogulo* was geographically widely dispersed during the upper Tertiary.

Keywords: Late Miocene, Carnivora, Mustelidae, Kenya, Ethiopia.

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. praecocidens*, and *P. marshalli*) and two are large (*P. lindsayi* and *P. monspessulanus*). The exact relationship between *Plesiogulo* and the living wolverine *Gulo* is uncertain (Kurten 1970; Harrison 1981).

From the Chinese fossil record, Schlosser (1903) described '*Lutra*' *brachygnathus* from an unknown locality. Zdansky (1924) assigned a number of cranial and mandibular specimens to *Plesiogulo brachygnathus.* This is a very small form of *Plesiogulo.* The type specimen is a mandible with p3–m1 (Schlosser 1903). The other specimens come from a total of seven localities in Shansi, China.

Teilhard de Chardin (1945) reassigned most of Zdansky's (1924) *P. brachygnathus* to *P. b. crassa.* He used Licent Collection 10.261 (snout and mandible with teeth) from Yushe, Shansi, as the type specimen and referred Lagrelius Coll. Nos. 1–4, and 6–12, AMNH-26376 (ex-Lagrelius No. 9), AMNH-26377 (ex-Lagelius No. 3), and Yale YPM 13816 (mandible fragment with teeth, Kurtén 1970) from the Dhok Pathan of India (per G.E. Lewis 1934) to this subspecies. Teilhard de Chardin (1945) also assigned a cranium and associated mandible (Licent Coll. No. 553) from K'ingyang, Kansu, to *P. b. minor.* Kurtén (1970) then elevated Teilhard de Chardin's (1945) subspecies to species rank, although he noted there were no tangible morphological differences to distinguish *P. crassa* from *P. minor.* He differentiated *P. crassa* and *P. minor* by size, as he found specimens of *P. minor* to be 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 Cherevichnoe, 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 Cherevichnoe to *P.* cf. *crassa.* These specimens are housed at the Ukrainian Academy of Sciences, Kiev. *P. crassa* is also known from cranial and jaw remains from Paveodar (Irtysh 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).

Another small Chinese species, *Plesiogulo praecocidens,* was named by Kurtén (1970) for specimens from Locality 49 of Baote, Shansi, previously assigned by Zdansky (1924) to *P. brachygnathus.* The type specimen is a left mandible with p3 and m1 (Loc. 49 No. 13; no UPI number) and the hypodigm includes a maxillary fragment with P4-M1 from the same locality (Loc. 49 No. 5; UPI No. M 19). *Plesiogulo praecocidens* has a more expanded M1 than other species of *Plesiogulo* and it also lacks M1 mid-constriction (Kurtén 1970).

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

*Author for correspondence. E-mail: hlusko@socrates.berkeley.edu

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).

Institutional abbreviations: KNM-NK, Kenyan National Museum, Narok specimens; ADD-VP, Adu Dora vertebrate paleontology specimen, National Museum of Ethiopia.

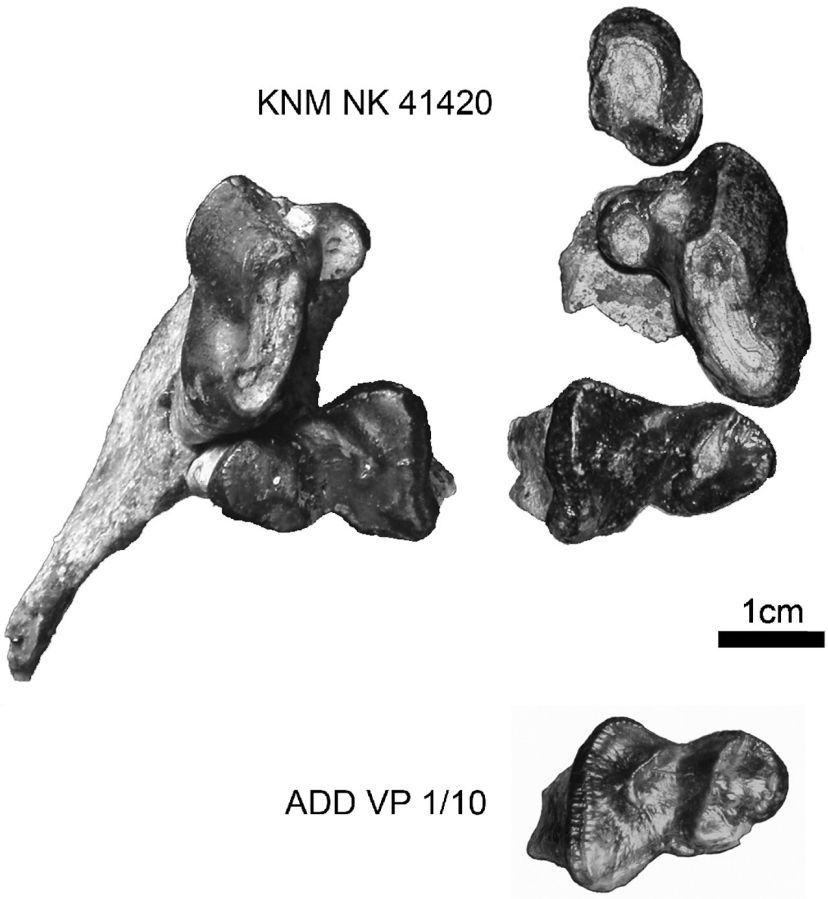


Figure 1. Specimens assigned to *Plesiogulo botori* sp. nov. Anterior is to the top. **A**, Occlusal view of KNM-NK 41420 (the holotype); **B**, occlusal view of ADD-VP-1/10.

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

Table 1. Comparison of upper dental dimensions.[1]

	P. botori sp. nov.	*P. monspessulanus* (= *major*)	*P. brachygnathus* (ex-*Lutra brachygnatha*)	*P. crassa* (= *minor*)	*P. praecocidens*	*P. marshalli*	*P. lindsayi*	*G. gulo*
P3								
Length	14.6	13.9	No data	11	No data	11.6	13.0	10.4
Width	10.2	9	No data	6.9	No data	8	9.3	6.3
Length/width	1.43	1.54	No data	1.59	No data	1.45	1.39	1.65
P4								
Length	24.5	23.2	17.1–20.5	18.3–20.8	17.2	20.1	23.5	19.75
Width	16.7	15.6	11.1–14.0	12.9	10.9	13.9	17.3	11.9
Length/width	1.47	1.49		1.51	No data	1.45	1.36	1.66
M1								
Width	21.2	18.6	13.8–19.4	15.8–17.8	13.8	18.2	20.0–21.5	13.9
Lingual lobe length	15.9	15.4	12.0–16.3	13.2	12.4	15.1	13.3–15.5	8.3
Minimum length	10.1	No data	8.4–11.7	8.4	7.8	9.1	9.7	No data
Max length/min length	1.57	1.54e		1.57	1.59	1.67	1.51	1.34e
Width/lingual lobe length	1.33	1.21		1.28	1.11	1.21	1.41	1.68
P3/P4 length	0.59	0.59	No data	0.57	No data	0.58	0.55	0.53
P3/P4 width	0.61	0.58	No data	0.54	No data	0.57	0.53	0.53

[1]Data for *P. monpessulanus, P. brachygnathus* and *P. crassa* are from Hendy (1978) and Alcalá *et al.* (1994), Zdansky (1924) and Kurtén (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.

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 (Hendey 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/width 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 is 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/width 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

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 Lemudong'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 geographic distribution for this genus. Its African record was thus far limited to Langebaanweg, South Africa. The discovery of *P. botori* from deposits as old as 6 Ma extends the temporal and spatial range of the genus in Africa. This and further (still unpublished) occurrences of the genus indicate an even greater diversity within the upper Tertiary.

We would like to express our appreciation to the Office of the President, Kenya, for authorization to conduct field research in Kenya and to the Ethiopian Ministry of Youth, Sports, and Culture for authorization to conduct field research in Ethiopia. We also thank the Palaeontology Division of the National Museums of Kenya and the National Museum of Ethiopia, for staff assistance and facilities; the Maasai people of Kenya and Afar people of Ethiopia for permission, access and assistance. Financial support was provided by the National Science Foundation grant BCS-0327208 and National Science Foundation HOMINID grant BCS-0321893 (RHOI), the Leakey Foundation, the University of Illinois Center for African Studies, and the University of Illinois Research Board.

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