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A new fossil cercopithecid tibia from Laetoli and its implications for positional behavior and paleoecology

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ABSTRACT

Detailed analyses and comparisons of postcranial specimens of Plio-Pleistocene cercopithecids provide an opportunity to examine the recent evolutionary history and locomotor diversity in Old World monkeys. Studies examining the positional behavior and substrate preferences of fossil cercopithecids are also important for reconstructing the paleoenvironments of Plio-Pleistocene hominin sites. Here we describe a new fossil cercopithecid tibia (EP 1100/12) from the *Australopithecus afarensis*-bearing Upper Laetolil Beds (~3.7 Ma) of Laetoli in northern Tanzania. The fossil tibia is attributed to cf. *Rhinocolobus* sp., which is the most common colobine at Laetoli. In addition to qualitative comparisons, the tibial shape of EP 1100/12 was compared to that of 190 extant cercopithecids using three-dimensional landmarks. Discriminant function analyses of the shape data were used to assess taxonomic affinity and shape variation relating to positional behavior. EP 1100/12 clustered with extant colobines, particularly the large-bodied genera *Nasalis* and *Rhinopithecus*. Comparisons reveal that EP 1100/12 belongs to a large-bodied monkey that engaged in arboreal pronograde quadrupedalism. These findings add further support to previous inferences that woodland and forest environments dominated the paleoenvironment of the Upper Laetolil Beds, which supported the diverse community of cercopithecids at Laetoli. The inferred paleoecology and the presence of large-bodied arboreally-adapted monkeys at Laetoli show that *A. afarensis* had access to a range of diverse habitats, including woodlands and forests. This supports the possibility that *A. afarensis*, with its potential range of positional capabilities, was able to utilize arboreal settings for food acquisition and refuge from predators.

1. Introduction

The postcranial morphology of fossil cercopithecids from Plio-Pleistocene sites in Africa offers crucial evidence to document the past diversity and evolutionary history of positional behavior in Old World monkeys (Jolly, 1967, 1972; Birchette, 1982; Harris et al., 1988; Krentz, 1993; Elton, 2001, 2002; Frost and Delson, 2002; Hlusko, 2006; Frost and Alemseged, 2007; Jablonski et al., 2008a, b; Frost et al., 2009, 2015; Gilbert et al., 2011, 2016; Harrison, 2011a; Frost, 2014). Based on the comparative morphology of extant taxa and evidence from the fossil record, stem cercopithecids are inferred to have been semiterrestrial (Benefit, 1987, 1999; Pickford and Senut, 1988; Strasser, 1988; Harrison, 1989; Ciochon, 1993; McCrossin et al., 1998), with this locomotor mode being primitively retained by early cercopithecines. However, others have argued that stem cercopithecids were primitively arboreal (Jolly, 1966, 1967, 1970; Napier, 1967, 1970; Delson and Andrews, 1975; Rollinson and Martin, 1981), as seen in the majority of modern-day colobines, and that stem cercopithecines acquired postcranial specializations to facilitate greater utilization of terrestrial substrates. The current fossil evidence is insufficient to settle this debate. Postcranial remains of a broader diversity of stem cercopithecids from the Miocene of Africa is needed to establish which of these two evolutionary scenarios is likely to be the most parsimonious. However, fossil finds from the late Miocene and early Pliocene shed light on the diversity of postcranial adaptations and positional behavior of early crown cercopithecids (Birchette, 1982; Harris et al., 1988, 2003; Krentz, 1993; Jablonski et al., 2002, 2008a,

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b; Leakey et al., 2003; Hlusko, 2006, 2007; Frost et al., 2009, 2015; Jablonski and Frost, 2010; Nakatsukasa et al., 2010; Gilbert et al., 2011, 2016; Harrison, 2011a; Frost, 2014; Harrison and Rein, 2016). While early papionins were apparently occupying semiterrestrial and terrestrial niches, contemporary colobines appear to have been predominantly arboreal (Birchette, 1982; Hlusko, 2006, 2007; Jablonski and Frost, 2010; Nakatsukasa et al., 2010), with the exception of a relatively few lineages that were specialized for terrestriality (Leakey, 1982; Jablonski, 2002; Jablonski and Frost, 2010; Table 1).

In addition to documenting the evolutionary history and diversity of positional behaviors in Old World monkeys, inferences about the locomotor behavior and substrate preferences of fossil cercopithecids offer important evidence for reconstructing the paleoenvironments of Plio-Pleistocene sites (Elton, 2002, 2007; Leakey et al., 2008; Harrison, 2011a). The taxonomic diversity and substrate preferences of modern-day cercopithecids reflect the extent of tree cover, with closed woodland and forest habitats having a greater absolute number of species and a predominance of arboreal taxa than is found in open woodlands and grasslands (Struhsaker, 1981; Bourlière, 1985; Chapman et al., 1999).

In this study, we present a detailed description and morphometric analysis of a complete and well-preserved cercopithecid tibia (EP 1100/12) recently recovered from the *Australopithecus afarensis*-bearing Upper Laetolil Beds (ULB; ~3.7 Ma) of Laetoli in northern Tanzania (Figs. 1 and 2; see Harrison, 2011b). This is the first tibial specimen of a cercopithecid to be recovered from Laetoli. Four species of cercopithecids are known from the ULB (Harrison, 2011a). These include two relatively common species, a medium-size papionin, *Parapapio ado*, and a large colobine, cf. *Rhinocolobus* sp., which comprise 68.4% and 26.6% of craniodental specimens, respectively. The colobine species referred to as cf. *Rhinocolobus* is currently distinguishable from all current African fossil colobines, but more complete craniodental specimens are necessary before formally describing a new taxon (Harrison, 2011a). A smaller colobine, *Cercopithecoides* sp., and a large baboon-sized indeterminate papionin are rare, and constitute only 3.8% and 1.3% of the craniodental specimens, respectively (Harrison, 2011a). Postcranial remains attributed to each species (based on size and morphology, and their direct association with craniodental specimens), allow inferences about their substrate preferences and positional behavior (Table 2). *Parapapio ado* was a relatively slender and agile semiterrestrial monkey, similar in its positional behavior to *Cercocebus* and some species of *Macaca* (Harrison, 2011a). It would have been adept in trees, with a preference for above-branch walking and running on large diameter supports. In addition, it was well adapted for foraging and traveling on the ground (Harrison, 2011a;

Figure 1. EP 1100/12, a left tibia attributed to cf. *Rhinocolobus* sp. from the Upper Laetolil Beds at Laetoli Loc. 9, Tanzania, in posterior view (A), anterior view (B), lateral view (C), and medial view (D).

Table 1
Inferred substrate preference of fossil cercopithecids from the late Miocene and Pliocene of eastern Africa.

Age	Cercopithecid taxa[a]	Substrate preference	References for substrate preference/locomotor behavior
Late Miocene 11.6–5.3 Ma	Colobinae		
	Microcolobus tugenensis	Arboreal	Nakatsukasa et al. (2010)
	Paracolobus enkorikae	Arboreal	Hlusko (2007)
	Papionini		
	Parapapio lothagamensis	Terrestrial	Leakey et al. (2003)
Pliocene 5.3–2.6 Ma	Colobinae		
	Cercopithecoides kerioensis	Unknown	
	Cercopithecoides kimeui	Terrestrial	Jablonski et al. (2008a)
	Cercopithecoides meaveae	Terrestrial	Frost and Delson (2002)
	Kuseracolobus aramisi	Arboreal	Hlusko (2006); Frost et al. (2009)
	Kuseracolobus hafu	Arboreal	Hlusko (2006)
	Paracolobus chemeroni	Arboreal	Birchette (1982)
	Paracolobus mutiwa	Terrestrial	Harris et al. (1988); Jablonski and Frost (2010)
	Rhinocolobus turkanaensis	Arboreal	Jablonski (2002); Jablonski et al. (2008a)
	Papionini		
	Parapapio ado	Semiterrestrial	Harrison (2011a, b, c); Harrison and Rein (2016)
	Parapapio cf. *jonesi*	Semiterrestrial	Frost and Delson (2002); Harrison (2011a, b, c)
	Pliopapio alemui	Semiterrestrial?	Frost et al. (2009)
	Theropithecus darti	Terrestrial	Krentz (1993)
	Theropithecus brumpti	Terrestrial[b]	Jablonski et al. (2002, 2008b); Gilbert et al. (2011); Guthrie (2011)
	Theropithecus baringensis	Unknown	
	Theropithecus quadratirostris	Unknown	

[a] Taxonomy follows Jablonski and Frost (2010).
[b] According to Krentz (1993), *T. brumpti* was more arboreal than *T. darti* (but see Jablonski et al., 2002, 2008b; Gilbert et al., 2011; Guthrie, 2011).