

A systematic revision of *Proconsul* with the description of a new genus of early Miocene hominoid

Kieran P. McNulty*: Evolutionary Anthropology Laboratory, University of Minnesota, 395 Hubert H. Humphrey Center, 301 19th Avenue S., Minneapolis MN 55455, USA

David R. Begun: Department of Anthropology, University of Toronto, Toronto, ON M5S 2S2, Canada

Jay Kelley: Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA
Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA

Fredrick K. Manthi: Department of Earth Sciences, National Museums of Kenya, Nairobi 00100, Kenya

Emma N. Mbua: Department of Earth Sciences, National Museums of Kenya, Nairobi 00100, Kenya

* corresponding author: Tel +1 612 625-0058

Email addresses: kmcnulty@umn.edu (K.P. McNulty); begun@chass.utoronto.ca (D.R. Begun); jkelley.iho@asu.edu (J. Kelley); fredrickmanthi@yahoo.com (F.K. Manthi); enmbua@gmail.com (E.N. Mbua)

Keywords: *Ekembo*, *Ugandapithecus*, fossil hominoid, taxonomy, Tinderet, Rusinga

Abstract

For more than 80 years, *Proconsul* has held a pivotal position in interpretations of catarrhine evolution in East Africa. From early hypotheses of phyletic relationships with modern apes to more recent debates over their position within Hominoidea, the well-preserved fossils of this genus have been a foundation for most evolutionary scenarios regarding the early diversification of hominoids. The majority of what we "know" about *Proconsul*, however, derives from abundant younger fossils found at the Kisingiri localities on Rusinga and Mfangano Islands rather than from the smaller samples found at Koru – the locality of the type species, *Proconsul africanus* – and other Tinderet deposits. One outcome of this is seen in recent attempts to expand the genus "*Ugandapithecus*" (considered here a junior subjective synonym of *Proconsul*), wherein much of the Tinderet sample was referred to that genus based primarily on differentiating it from the Kisingiri specimens rather than from the type species, *P. africanus*. This and other recent taxonomic revisions to *Proconsul* prompted us to undertake a systematic review of dentognathic specimens attributed to this taxon. Results of our study underscore and extend the substantive distinction of Tinderet and Ugandan *Proconsul* (i.e., *Proconsul sensu stricto*) from the Kisingiri fossils, the latter recognized here as a new genus. Specimens of the new genus are readily distinguished from *Proconsul sensu stricto* by morphology preserved in the *P. africanus* holotype, M 14084, but also in I¹s, lower incisors, upper and lower canines, and especially mandibular characteristics. A number of these differences are more advanced among Kisingiri specimens in the direction of crown hominoids. *Proconsul sensu stricto* is characterized by a suite of unique features that strongly unite the included species as a clade. There have been decades of contentious debate over the phylogenetic placement of *Proconsul* (*sensu lato*), due in part to there being a mixture of primitive and more advanced morphology within the single genus. By recognizing two distinct clades that, in large part, segregate these character states, we believe that better phylogenetic resolution can be achieved.

Introduction

The genus *Proconsul* Hopwood, 1933 has been a mainstay in studies of hominoid evolution and diversification since its discovery in the early 20th century. Initially reported from fragmentary remains found in western Kenya, seven decades of subsequent field work, particularly discoveries from the Kisingiri localities on Rusinga and Mfangano Islands, have made *Proconsul* the best documented of all fossil catarrhines. Nearly every element of the *Proconsul* skeleton is now known, often with variation recorded in multiple specimens.

This wealth of information has not ended debates over the taxonomy, phylogeny, functional-adaptive morphology, or ecological preferences of this taxon; rather, one might argue that the expansive evidence has provided grist for milling out new ideas and arguments. One persistent debate regards whether *Proconsul* can be considered a true hominoid or is best placed among stem catarrhines. Following an early period when *Proconsul* species were linked more closely to modern great ape lineages (Hopwood, 1933; Le Gros Clark and Leakey, 1951; Simons and Pilbeam, 1965; but see Leakey, 1943), the consensus view emerged of this genus as a basal hominoid (e.g., Andrews, 1985). Around this time, Harrison (1982, 1987) raised the possibility that *Proconsul* and other East African non-cercopithecoid catarrhines might be better placed among stem catarrhines, phylogenetically preceding the divergence of the hominoid and cercopithecoid lineages. Walker's (Walker and Pickford, 1983; Walker and Teaford, 1989; Walker, 1997; see also Rae, 1993, 1999) resurrection of the hominid (= great ape + human) status for *Proconsul* was ultimately short lived, with most researchers maintaining *Proconsul* as a basal member of the Hominoidea.

Taxonomic history of Proconsul

Germane to the phylogenetic debate is the taxonomic framework within which these fossils are analyzed. *Proconsul* (type species, *Proconsul africanus*) was erected for fossil primate specimens

discovered from 1926-1931 at Koru, a Western Kenya locality situated on the periphery of the extinct Tinderet volcano (Hopwood, 1933; Le Gros Clark and Leakey, 1951). In that first publication, Hopwood (1933: 460) made oblique but favorable comparison to recently discovered but unpublished specimens from Rusinga Island. Yet, L.S.B. Leakey's initial presentation of the Rusinga material characterized it as being quite different from Hopwood's *Proconsul*, leading Sir Arthur Keith to liken it to the younger hominoid *Dryopithecus* (see Myres, 1932; Pickford, 1986). Leakey's formal publication, however, included both Koru and Rusinga specimens into a single genus, which was thought to represent the base of the human-ape clade (Leakey, 1943).

At this time, early Miocene primate localities in Western Kenya were all geographically clustered around either the Kisingiri volcano (Rusinga Island, Mfangano Island, Karungu, Uyoma) or the Tinderet volcano (Koru, Songhor, Legetet Hill, and others; Figure 1). Continued collecting in both regions by the East African Archaeological Expedition and British-Kenya Miocene Expedition gradually revealed substantial size variation in the type species, *Proconsul africanus*, and both the Kisingiri and Tinderet localities were re-interpreted as having a smaller and a larger *Proconsul* species. This prompted Le Gros Clark and Leakey (1950) to erect two new species: *Proconsul major* for the large specimens from Tinderet, and *Proconsul nyanzae* for the large Kisingiri specimens. The smaller species, *P. africanus*, continued to be recognized in both areas by most workers. Large-bodied catarrhines discovered in Uganda expanded the geographic range of *P. major* (Bishop, 1964), although some of this sample was later reassigned to a new taxon, *Morotopithecus bishopi*, by Gebo et al. (1997).

<Figure 1 about here>

This basic taxonomic arrangement remained relatively stable for three decades, although individual specimen identifications did not always adhere to these simple geographic distinctions (e.g.,

Andrews, 1978). Subsequent studies by Bosler (1981), Harrison (1982, 1987), Kelley (1986), and others (Pickford, 1986; Teaford et al., 1988; Walker and Teaford, 1988) further standardized the taxonomic attributions of specimens and thereby reduced the number of *Proconsul* species recognized at each site: *P. nyanzae* and (for some) *P. africanus* associated with Kisingiri localities; *P. major* and *P. africanus* associated with Tinderet localities; Ugandan *Proconsul* restricted to *P. major*.

Fieldwork on Rusinga in the 1980s generated sufficient new evidence to confirm that the smaller Kisingiri *Proconsul* specimens differ morphologically from *P. africanus* (Kelley, 1986), leading Walker et al. (1993) to assign this material to a new species, *Proconsul heseloni*. The presence of two species of *Proconsul* on Rusinga and Mfangano was not universally accepted, however. Kelley, for example, referred all Kisingiri specimens to *P. nyanzae*, voicing concerns over the unlikely distribution of sexes (cf. Kelley, 1986) and the disregard of likely body size variation within the two species (Kelley, 1993). Likewise, Pickford (1986) recognized only *P. nyanzae* from Rusinga and Mfangano, notably highlighting the distinct morphology of Kisingiri *Proconsul* when compared to Tinderet and Ugandan specimens. Despite these and other objections, the presence of *P. nyanzae* and *P. heseloni* at the Kisingiri localities has come to be universally accepted (Begun et al., 1994; Leakey et al., 1995; Rafferty et al., 1995; Ward et al., 1995; MacLatchy and Bossert, 1996; Harrison, 2002, 2010; Smith et al., 2003; Ishida et al., 2004; Nakatsukasa et al., 2007; Deane, 2009; Harrison and Andrews, 2009; Peppe et al., 2009; Pickford et al., 2009; Michel et al., 2014).

The naming of *P. heseloni* after 30 years of relative taxonomic stability heralded a new period of systematic revision. First, Senut et al. (2000) transferred *P. major* into a new genus "*Ugandapithecus*," a genus whose validity is debated within the paleoanthropological community (see Begun, 2007; Harrison and Andrews, 2009; Harrison, 2010), and which we consider to be a junior synonym of *Proconsul* (see below). Pickford and Kunimatsu (2005) subsequently allocated a few isolated teeth from Kipsaraman to this genus under the species name "*Ugandapithecus*" *gitongai*. In addition, the proconsulid material

from Meswa Bridge – long recognized as a distinct species (Andrews et al., 1981) – was given the name *Proconsul meswae* by Harrison and Andrews (2009). In that same year, however, Pickford et al. (2009) published a comprehensive taxonomic revision of *Proconsul* (including "*Ugandapithecus*") based on cranial, mandibular and dental material. In doing so, they identified a number of similarities between "*Ugandapithecus*" *major* and the smaller Tinderet *Proconsul* specimens, particularly with regard to mandibular morphology. In that manner, specimens that have been typically referred to *P. africanus*, plus the smallest specimens referred to *P. major* (cf. Pilbeam, 1969; Bosler, 1981), were transferred to a new species, "*Ugandapithecus*" *legetetensis* (Pickford et al., 2009). Likewise, the mandible KNM-SO 1112 – regarded as *P. africanus* by other workers – was referred to *P. meswae*, and the latter species transferred to "*Ugandapithecus*" (Pickford et al., 2009). As a result of this systematic revision, *P. africanus* was left almost entirely without mandibular representation, whereas "*U.*" *legetetensis* was represented mostly by mandibles and lower teeth (Pickford et al., 2009).

Table 1 summarizes the relevant taxonomic allocations used by different authors according to the geographic distribution of localities. In its broadest conception (e.g., Harrison and Andrews, 2009), the genus *Proconsul* is quite speciose relative to other Miocene hominoid genera, including as many as six distinct species. This number is substantially reduced under the taxonomic scheme proposed by Pickford et al. (2009), wherein half of these species are referred to "*Ugandapithecus*." Those preferring to maintain all of this material in *Proconsul*, however, have noted that the greatest distinction within that sample is between the Kisingiri assemblages on the one hand and those from Tinderet and Uganda on the other (Walker et al., 1993; Begun, 2001, 2007; MacLatchy and Rossie, 2005; Harrison and Andrews, 2009; Harrison, 2010) – an interpretation presaged in some ways by the taxonomy proposed by Kelley (1986) and Pickford (1986), and ultimately echoing the original presentation by L.S.B. Leakey (Myers, 1932).

<Table 1 about here>

In accordance with other researchers (e.g., Harrison, 2002, 2010; MacLatchy, 2004; MacLatchy and Rossie 2005; Suwa et al., 2007; Harrison and Andrews, 2009; McNulty, 2010; Hill et al. 2013), we do not recognize the generic distinction of "*Ugandapithecus*" from *Proconsul*. This is due in part to our findings, detailed below, of a distinct clade uniting *P. africanus* with species assigned to "*Ugandapithecus*." In addition, the most recent characterization of "*Ugandapithecus*," which removed most Tinderet specimens from *Proconsul* and distributed them among new and existing species of "*Ugandapithecus*," was based largely on contrasts with Rusinga specimens rather than with the type species of *Proconsul* (Pickford et al., 2009). This is particularly true for mandibles and the lower dentition – specimens less securely tied to *P. africanus* because the type specimen, M 14084, is a partial maxilla (e.g., Bosler, 1981). We argue here that, if specimens are sorted *without preconceived taxonomic assumptions*, the purported diagnostic features of "*Ugandapithecus*" (sensu Pickford et al., 2009) serve instead to differentiate *all* specimens in the Tinderet and Uganda samples of *Proconsul* (*Proconsul* sensu stricto) from those found at Kisingiri localities (cf. Kelley, 1986; Walker et al., 1993; Begun, 2001, 2007; MacLatchy and Rossie, 2005; Harrison, 2010; Harrison and Andrews, 2009).

Geochronology of Proconsul localities

The chronological framework of *Proconsul* localities provides an important context for understanding historical and current interpretations of species' distributions and relationships. Early researchers, while acknowledging the limitations of their stratigraphic and faunal correlations, were nevertheless able to correctly position the Western Kenyan localities within the lower Miocene, associating some of the deposits with the Burdigalian, a stage defined by marine sediments in Europe and dated between about 16 and 20.5 Ma (Kent, 1942; MacInnes, 1943). The application of radiometric

dating techniques helped refine these estimates, with some of the earliest K-Ar studies conducted on East African localities associated with *Proconsul* (Evernden et al., 1964; Bishop et al., 1969; Van Couvering and Miller, 1969). These dates confirmed an early Miocene age for most localities, with estimates ranging between 23-16 Ma. However, the Kisingiri deposits yielded discrepant results due to post-depositional alteration of the datable biotites (Drake et al., 1988). Re-sampling and further analyses yielded more satisfactory and repeatable age estimates of 17.9-17.8 Ma, but, notably, these were based on only five samples confined to a small segment of the Rusinga geological section (Drake et al., 1988).

Radiometric dates, in conjunction with studies of the associated faunal communities (e.g., Pickford, 1981), created a geochronological framework for *Proconsul* wherein the Tinderet localities are oldest, dating to perhaps 22.5 Ma at Meswa Bridge (see review in Harrison and Andrews, 2009), with Napak in Uganda being approximately contemporaneous with Songhor and Koru (Bishop et al., 1969; Pickford and Andrews, 1981) and the Kisingiri localities preserving the youngest sediments (Pickford, 1981; Drake et al., 1988). However, the most recent re-dating of Kisingiri sites presents a more complex scenario. Rather than being younger than all of the Tinderet sites, the Kisingiri stratigraphic sequence is substantially longer than previously thought, with the oldest fossil strata contemporaneous with those from Koru and Legetet Hill at approximately 20-19 Ma (McCollum et al., 2013). The youngest Miocene fauna from Rusinga is not associated with radiometric dates, but magnetostratigraphic analysis suggests an age near 17 Ma or younger (Peppe et al., 2009). Hence, differences between species of *Proconsul*, and in particular between assemblages from Tinderet and Kisingiri, cannot be simply explained by chronology. Indeed, the great length of the Kisingiri sequence suggests that taxonomic uniformity throughout this time period might require re-evaluation.

Aims of this study

Motivated by new specimens, analyses, and interpretations of *Proconsul* that have appeared in the last several years, we undertook a thorough review of the craniodental and mandibular specimens attributed to this genus and here provide an alternate taxonomic interpretation to those in current use. Our primary objective was to evaluate the morphological homogeneity of the genus *Proconsul* as traditionally constituted (*Proconsul sensu lato*) and explore the possibility that the Kisingiri specimens form a distinct group (Walker et al., 1993; Begun, 2001, 2007; MacLatchy and Rossie, 2005; Harrison and Andrews, 2009). Whereas we agree with Pickford et al. (2009) that the material traditionally referred to *Proconsul* exceeds what can be comfortably accommodated within a single genus, our results conform to the suggestion proposed by Begun (2001, 2007) and later by MacLatchy and Rossie (2005) and Harrison and Andrews (2009) that the Kisingiri specimens from Rusinga and Mfangano Islands constitute a distinct clade with respect to *Proconsul* from the Tinderet and Ugandan localities. Our assessment of the taxonomic and phyletic distinction of the Kisingiri material necessitates generic differentiation of this sample from *Proconsul*.

Systematics

Order Primates Linnaeus, 1758

Infraorder Catarrhini É. Geoffroy Saint-Hilaire, 1812

Superfamily Hominoidea Gray, 1825

Family *incertae sedis*

Ekembo gen. nov.

Synonymy

1950 *Proconsul* Hopwood: Le Gros Clark and Leakey: 260.

1965 *Dryopithecus (Proconsul)* (Hopwood): Simons and Pilbeam: 120.

1978 *Proconsul* Hopwood: Andrews: 90.

1986 *Proconsul* Hopwood: Kelley: 479.

1993 *Proconsul* Hopwood: Walker et al.: 51.

2010 *Proconsul* Hopwood: Harrison: 437.

Type species

Ekembo nyanzae comb. nov. (Le Gros Clark and Leakey, 1950).

Included species

Ekembo nyanzae (Le Gros Clark and Leakey, 1950); *Ekembo heseloni* comb. nov. (Walker et al., 1993).

Etymology

Ekembo means "ape" or "monkey" in the Suba language, which was historically spoken by peoples in western Kenya including those who settled Rusinga and Mfangano Islands (Jack Wanyende, personal communication).

Diagnosis

Medium- to large-bodied and sexually dimorphic hominoid, characterized by the following combination of features. Frontal bone moderately wide at the coronal suture, narrowing anteriorly toward gracile supraorbital rims which are not demarcated by a post-toral sulcus. Large frontal sinuses behind a prominent glabella. Minor postorbital constriction. Temporal lines prominent and situated high on frontal and parietal bones, converging posteriorly without forming a sagittal crest (in female specimens). Nasal bone long and thin. Broad interorbital region flat rather than projecting. Upper face

more vertically oriented relative to the mid- and lower face. Nasolacrimal duct positioned within a broad orbit. Rostrum broad with premaxilla extending up to the nasal bone. Canine jugum prominent in both sexes but canine fossa developed only in males. Nasal aperture broad with widest portion inferior and sometimes near the base. Inferior aperture margin concave or incised in the midline. Nasoalveolar clivus intermediate in height between hylobatids and hominids. Clivus does not overlap palatine process of the maxilla, presenting typical mammalian incisive fenestration anteroposteriorly positioned at or posterior to mid-canine. Maxillary sinus extensive, reaching anteriorly to P³/P⁴ junction. Zygomaticoalveolar crest arises low on the face near M₂. Nearly vertical malar region. Broad anterior palate. A single palatine foramen positioned near the M²/M³ junction. Broad mandibular ramus angled slightly posteriorly from vertical leads to a gradually rounded and gracile gonial region. Mandibular corpora range from short and gracile to taller and moderately robust. Symphysis characterized by moderately developed superior transverse torus and variably developed inferior transverse torus and genioglossal pit. Symphyseal planum and subplanum region vertically or nearly vertically oriented. A single mental foramen positioned near the P₃/P₄ junction, approximately halfway up the corpus or higher.

Upper central and lateral incisors heteromorphic. Central incisor characterized by a narrow lingual tubercle, often consisting of two or three narrow ridges, and distinct but thin marginal ridges that are continuous with the lingual cingulum, with the mesial marginal ridge joining the cingulum at a sharp angle in contrast to a more continuously curving transition from cingulum to distal marginal ridge, resulting in an asymmetric ridge and cingulum morphology. Lateral incisors have well-developed incisal edges and are asymmetric with a moderately developed lingual cingulum. Narrow lower incisors with central and lateral incisors having similar morphology. Upper and lower canines strongly sexually dimorphic with only slight bilateral compression and moderately low-crowned in relation to basal crown dimensions, with apices terminating at a simple point. Canine roots smooth and conical. Cheek tooth cusps low and broad and connected by inflated intercuspal crests. Upper premolars morphologically

similar, with well-developed mesial foveae, only moderate cusp heteromorphy, and cusps positioned at the approximate mesiodistal midpoint of the crown resulting in nearly symmetric buccal profiles.

Molars with moderate buccolingual flare and reduced cingulum development. Upper first and second molars approximately square with nearly straight distal margins and buccally oriented posthypocone cristae. Lower first and second molars rectangular with M_1 substantially narrower than M_2 . Upper and lower third molars vary in degree of distal cusp development.

Forelimbs and hind limbs of similar length. Long vertebral column with six lumbar vertebrae characterized by transverse processes that arise from the dorsal margin of the vertebral centrum and prominent accessory processes for *erector spinae* muscles. Lacking a tail. Thorax long, narrow and dorsoventrally deep. Broad, flat sternbrae. Pelvis long and narrow with sagittally oriented ilia, an elongate ischium lacking evidence of callosities, and a narrow sacrum with a small sacro-iliac joint. Scapula positioned laterally on thorax with a narrow, ovoid and ventrally oriented glenoid fossa. Humerus with a posteriorly directed head, retroflexed shaft with reduced torsion, and a distal articular surface lacking a well-differentiated trochlea and capitulum, and having a narrow zona conoidea and shallow trochlear notch, but lacking an entepicondylar foramen. Radius with a small, ovoid head and flat distal articular surface that mainly contacts the scaphoid. Ulna displays a large olecranon process, narrow semilunar notch with only a slight keel, anteriorly positioned radial notch, and a long distal styloid process that retains articulation with triquetrum and pisiform. Carpals relatively narrow and include an unfused os centrale, a hamate with a small hamulus and a flat, medially oriented triquetral surface. Hand characterized by straight metacarpals with narrow bases and heads. Pollex well developed. Manual and pedal phalanges generally similar to each other but less so than in Old World monkeys. Femur slender with a small head, long neck with a high neck-shaft angle, centrally placed fovea capitis, reduced greater trochanter, and a broad distal end with the medial condyle slightly larger

than the lateral. Broad, flat patella. Tibia long and slender, but fibula robust. Tarsals and metatarsals elongate, with a robust hallux.

<Table 2 about here>

Differential diagnosis

Ekembo can be readily distinguished from all other medium- and large-bodied catarrhine genera from the early Miocene. Cranial, mandibular, and dental differences between *Ekembo* and *Proconsul* are described in detail below and summarized in Table 2; *Ekembo* also differs from *Proconsul* in having a rounder radial head and a femur with a shorter greater trochanter, posteriorly projecting lesser trochanter, less extensive inter-trochanteric crest, more robust phalanges with more strongly developed fibrous flexor sheath ridges, and broader proximal and intermediate phalangeal distal joint surfaces (condyles) with wider trochlear grooves and less sharply defined trochlear ridges (Harrison, 1982; Andrews et al., 1997; Senut et al., 2000; Pickford et al., 2009).

Ekembo differs from *Afropithecus* in having a more inflated glabellar region, no frontal trigon, less strongly developed anterior temporal ridges, less postorbital constriction, a stronger mandibular superior transverse torus, less posterior shallowing of the mandibular corpus, higher-crowned lower canines in relation to mesiodistal length, buccolingually narrower upper premolars relative to molars, upper premolars with cusps positioned closer to the mesiodistal midline, reduced P³ cusp heteromorphy, a more symmetric I₂, and substantially less buccolingual flare in the cheek teeth (Leakey et al., 1988; Rossie and MacLatchy, 2013).

Ekembo differs from *Heliopithecus* in having buccolingually narrower premolars relative to molars, premolar cusps positioned closer to the mesiodistal midline, and reduced P³ cusp heteromorphy (Harrison, 2010).

Ekembo differs from *Equatorius* in having a more gracile mandible, a larger superior but smaller inferior mandibular transverse torus, labiolingually narrower lower incisors with straighter mesial and distal margins, higher-crowned lower canines in relation to mesiodistal length, greater molar cingulum development, a less posteriorly directed humeral medial epicondyle, a more anteriorly directed radioulnar joint, and narrower metacarpal heads (Ward et al., 1999).

Ekembo differs from *Nacholapithecus* in having a shorter subnasal clivus, a more expansive incisive foramen, a broader nasal aperture at the base, a minimally developed mandibular inferior transverse torus, a narrower lingual tubercle on I¹, higher-crowned lower canines in relation to mesiodistal length, a larger humeral radial fossa, a shallower coronoid fossa, a less well developed zona conoidea, a narrower and distally slanted ulnar coronoid process, a longer and lower femoral neck, more posteriorly positioned lesser trochanter, and a smaller posteromedial tubercle on the talus (Ishida et al., 2004).

Ekembo differs from *Nyanzapithecus* in having more anteriorly extended maxillary sinuses, a relatively taller mandibular corpus, less buccolingually compressed upper and lower canines with less curved crowns, lower and more rounded cusps with more inflated occlusal crests on the cheek teeth, P³ and P⁴ that more closely resemble each other and have much less cingular development, a broader P₄ relative to M₁, M¹⁻² occlusal outline more closely approximating a square, lower molars that are broader relative to mesiodistal length with a more mesially placed entoconid relative to the hypoconid (Harrison, 1986, 2010).

Ekembo differs from *Rangwapithecus* in having a broad and expansive palatal fenestration, a wider palate relative to length, a more robust mandible with well-defined superior transverse torus, broader upper and lower incisors relative to height, less buccolingually compressed canines without scimitar-shaped crowns, upper premolars with reduced cingulum and cusps positioned near the mesiodistal midpoint resulting in expanded mesial foveae and symmetric buccal profiles, a broader P₄

relative to M_1 , upper and lower molars that are buccolingually broader relative to length and have more rounded cusps and inflated occlusal crests, more squared upper molars with substantially less cingulum development, and lower molars with a more mesially placed entoconid (Andrews, 1974; Harrison, 2002, 2010; Cote et al., 2013; Hill et al., 2013).

Ekembo differs from *Turkanapithecus* in having an expanded glabellar region, less postorbital constriction, a narrower temporal fossa with less flaring zygomatic arches, the lacrimal fossa within the orbital margin, a relatively broader palate with non-converging tooth rows, narrower nasal bones and interorbital region, a distinct mandibular superior transverse torus, a more robust mandibular corpus, taller mandibular ramus, upper canines more rounded in cross-section, a reduced cingulum on cheek teeth, a well-developed hypocone on M^{1-2} , a more squared M^2 with a protocone subequal to paracone, and broader lower molars relative to length (Leakey and Leakey, 1986; Harrison, 2002, 2010).

Ekembo differs from *Mabokopithecus* in having a relatively broader M_3 crown without distal recurvature of the crown and lacking a buccal concavity, a hypoconulid that is in-line with the buccal cusps, more bunodont cusps, a well-defined protocristid, and a broad open talonid without an accessory cuspid (Harrison, 2002, 2010).

Ekembo differs from *Xenopithecus* in having reduced upper molar flare, a substantially reduced cingulum, no prehypocone crista, molar occlusal profiles more closely approximating a square, and less constricted trigons (Hopwood, 1933; Le Gros Clark and Leakey, 1951; Harrison, 2002, 2010).

Ekembo differs from *Morotopithecus* in having a broader interorbital region, a better developed canine fossa in males, premolars smaller relative to molars, greatly reduced or absent buccal cingula on upper molars, lumbar vertebrae with transverse processes positioned more ventrally on the centrum, a narrower distal femur with a deeper patellar groove and similarly-sized medial and lateral femoral condyles (Gebo et al., 1997; MacLatchy, 2004).

Recently, Stevens et al. (2013) likened the new genus *Rukwapithecus*, represented by a mandible fragment with well-preserved P₄-M₁, to nyanzapithecine species. *Ekembo* can be distinguished from this genus in having a more gradually rounded gonial angle, a less obliquely oriented P₄ with subequal protoconid and metaconid and a broader mesial fovea, less mesially positioned metaconid, reduced buccal cingula and smaller mesial foveae on the molars, smaller hypoconulids, broader M₁₋₂ relative to length, a singular rather than twinned metaconid, no accessory cuspules in the lingual notch, and a well-defined crest between entoconid and hypoconulid.

Family Proconsulidae (Leakey, 1963)

Genus *Proconsul* Hopwood, 1933

Type species

Proconsul africanus Hopwood, 1933.

Included species

Proconsul africanus Hopwood, 1933; *Proconsul major* Le Gros Clark and Leakey, 1950; *Proconsul gitongai* comb. nov. (Pickford and Kunitatsu, 2005); *Proconsul meswae* Harrison and Andrews, 2009.

Diagnosis (replaces the emended diagnosis of Harrison, 2010)

Proconsul species are medium- to large-bodied sexually dimorphic catarrhines that can be distinguished from other proconsulid genera by the following combination of features. Robust mandibular corpus and symphysis, characterized by a long, shallowly sloping planum alveolare terminating at a large superior transverse torus and a subplanum surface oriented posteroinferiorly. Upper incisors heteromorphic, with I¹ exhibiting an inflated lingual tubercle and a near symmetrical

configuration of lingual marginal ridges and cingulum, with a curving transition from cingulum to the mesial marginal ridge. Lower incisors broad relative to crown height. Upper and lower canines with distinct blade-like or burin-like tips in both deciduous and adult teeth. Upper canine roots with broad longitudinal grooves or fluting defining two or three distinct columns, plus numerous small longitudinal striations extending cervically from the root apex. Upper P³s morphologically dissimilar from P⁴s. P³ has substantial cusp heteromorphy (paracone much taller than protocone), with mesially positioned cusps and a notched mesial border that together limit or eliminate a mesial fovea. A long, steeply angled preparacrista contributes to a highly asymmetric buccal profile before being interrupted near the tooth cervix by a mesially projecting flange. The distal margin is strongly curved. P⁴ has a tall paracone relative to crown length. Molars characterized by extensive cingular development, individuated conical cusps connected by sharp occlusal crests, and substantial buccolingual flare. Upper molars rhomboid in shape resulting from a broad trigon and a distally expanded hypocone. M² has a distinct buccal shelf between paracone and metacone, a distolingual cingulum that wraps fully around the hypocone rather than merging into the hypocone on its lingual surface, and a distally oriented posthypocone crista. Lower first and second molars nearly equal in buccolingual breadth.

Comparative morphology of *Ekembo* and *Proconsul*

Samples and comparative methods

The above diagnoses are based on extensive survey and analysis of the original fossil material. Specimens housed in the National Museums of Kenya (NMK) and the Natural History Museum (London) were analyzed by the authors during several separate and two joint (NMK) research visits. Fossils in the Uganda National Museum were assessed by one of us (KPM) during two visits. All measurements were collected by KPM. Dental terminology follows Szalay and Delson (1979).

The following results are organized with respect to the morphology of the Kisingiri sample (attributed to *E. nyanzae* and *E. heseloni*) versus that of *Proconsul* from Tinderet and Napak (traditionally referred to *P. africanus*, *P. major*, and more recently *P. meswae*). Specimens from additional localities that have at one time been attributed to *Proconsul* (e.g., Andrews, 1978; Pickford and Kunimatsu, 2005 [cf. Harrison, 2010]) are, for the most part, not considered here; most are middle Miocene in age and have been transferred to other genera (Harrison, 2002, 2010). Of those that are from early Miocene sites, there is growing evidence that *P. major* can also be found at Moroto and differentiated from *Morotopithecus* (Pickford et al., 2009), an issue of some interest but ultimately not critical to the taxonomic questions being considered here. Where appropriate, however, we do provide observations on a few early Miocene specimens attributed to “*U.*” *gitongai* (Pickford and Kunimatsu, 2005; Pickford et al., 2009; see Harrison, 2010). Yet, while we consider the middle Miocene holotype likely to represent a distinct species, here referred to *Proconsul*, we concur with Harrison (2010) that many specimens placed in this species by Pickford et al. (2009) cannot be distinguished from *P. major*.

Sample sizes, particularly from Tinderet and Ugandan localities, tend to be small, but where possible standard univariate (e.g., t-tests) and bivariate (regression; ANCOVA) statistical analyses were performed. A single eigendecomposition of the covariance matrix of symphyseal measurements was done to characterize the multivariate shape of the mandibular symphysis after accounting for size differences (sensu Jolicouer, 1963). Quantitative results are illustrated as box-and-whisker plots of shape indices or bivariate plots of the measurements. For samples of fewer than five specimens, shape index values are plotted in lieu of box-and-whisker summaries.

Morphological comparisons

Upper incisors Two features of the *Ekembo* upper central incisors distinguish them from those of *Proconsul*, including specimens widely attributed to the type species *P. africanus*. The lingual tubercle in

Ekembo is quite narrow, generally with low relief and often scored by two or more irregular ridges in contrast to the much more inflated or bulbous tubercle in *Proconsul* I¹s (Figure 2). *Ekembo* specimens also have a characteristic morphology in the transition from the lingual cingulum to the mesial marginal ridge (Figure 2): from the mesiodistal mid-point of the crown, the cingulum extends either directly mesially, or even angles slightly cervically, to intersect the mesial marginal ridge at a fairly sharp angle. In contrast, in I¹s of *Proconsul* the cingulum angles incisally from the mid-point and transitions into the mesial marginal ridge in a gradual curve. The expression of these traits varies somewhat in the smaller Tinderet specimens attributed to *P. africanus* compared with those of *P. major* (cf. Pickford et al., 2009). However, these variations are relatively minor with respect to the differences between the two genera. Of 25 I¹s known from Kisingiri localities, only one specimen, KNM-MW 562, somewhat resembles the Tinderet sample in both of these features – having a somewhat less angled transition from the mesial marginal ridge to the cingulum, and a more bulbous lingual tubercle. This is particularly interesting as the specimen was discovered in the Makira Beds, now dated to older than 19.0 Ma and contemporary with the Tinderet localities (McCollum et al., 2013). Nevertheless, its overall morphology is more similar to other *Ekembo* specimens than to *Proconsul* incisors. Two other *Ekembo* specimens, KNM-RU 1677 and RU 1933, have somewhat more inflated lingual tubercles but otherwise resemble other *Ekembo* I¹s.

No consistent differences were found in upper lateral incisors.

<Figure 2 about here>

Upper canines Upper canine crowns of *Ekembo* are typical of those of most catarrhines in terminating in an evenly tapering point. This differs from the *Proconsul* specimens, which have a blade-like (Kelley, 1986; Senut et al., 2000; Harrison, 2010) or “burin-like” (Pickford et al., 2009) canine tip (Figure 3). While blade-like apical morphology has long been recognized as a distinctive characteristic of *P. major*, we

confirm the report by Pickford et al. (2009) that this feature is also present in the *P. africanus* type specimen (Figure 3a), although somewhat understated as expected in the more slender and higher-crowned *P. africanus* canines. Unfortunately, other canines attributed to *P. africanus* (e.g., M 44837, KNM SO 419, LG 921, CA 1910, SO 5353; [Kelley, 1986]) have broken apices and therefore cannot be evaluated for this feature. A blade-like tip is also present in the deciduous upper canines of *P. major* (e.g., KNM-SO 371, MV 10, NAP IV, UMP 62-20) and *P. meswae* (KNM ME 11). Hence, the blade-like upper canine tip unites all Tinderet and Napak *Proconsul* species but is never expressed in *Ekembo* specimens from Rusinga and Mfangano.

Two features of the canine roots also differentiate these genera: longitudinal grooving or fluting along the length of the root (cf. Kelley, 1986), and the development of numerous finer longitudinal striations near the root apex that extend to varying degrees toward the cervix of the tooth. Longitudinal "fluting" consists of broad grooves that segment the root into distinct sections (cf. Pickford et al., 2009; Figure 3e). Most often the root in cross-section has the appearance of a cylinder that has been sectioned longitudinally with the two halves offset from each other, but in some cases there are three segments and the root cross-section is more triangular in appearance (Kelley, 1986). This characteristic was noted by Kelley (1986) in the *P. africanus* canines, but not in those of *P. major*. Here, we affirm that fluting is present on all of the visible upper canine roots attributed to both *P. africanus* and *P. major*; root morphology could not be evaluated in the deciduous upper canine from Meswa Bridge since it is implanted in the maxillary alveolus. None of the *Ekembo* specimens displays this morphology, having a simpler round to ovoid cross-section along the length of the root.

The fine longitudinal striations on *Proconsul* upper canine roots vary in the degree to which they extend toward the cervix (Figure 3e), but they are visible in all specimens attributed to *P. africanus* (KNM-SO 419, 521, 921, 5353; KNM-X 502) and five of six upper canines of *P. major* (excepting KNM-SO 1614). This morphology is also present in UMP 62-12, which was included as part of the *Morotopithecus*

bishopi hypodigm (Gebo et al., 1997). Fine striations along the upper canine root are almost entirely absent in *Ekembo*. Twenty of twenty-three specimens lack this feature; three specimens (KNM-RU 1763, 1845, 1891) exhibit incipient to slight striations, but never developed to the extent seen in *Proconsul* canines.

<Figure 3 about here>

Upper premolars Upper third premolars display some of the greatest differences between *Ekembo* and *Proconsul*; P⁴s tend to differ in similar ways, but the differences are not nearly as marked. *Ekembo* P³s have cusps positioned near the mesiodistal midpoint of the crown, well-developed mesial foveae, pre- and postparacristae of similar length and slope resulting in symmetric or near symmetric buccal profiles, a straight or slightly curved mesial margin, and only moderately curved distal margin (Figure 4).

Proconsul P³s are more similar in appearance to those of small-bodied catarrhines from the early Miocene, with cusps positioned mesially on the crown, greatly reducing or eliminating the mesial fovea. They also have a steep preparacrista and more shallowly sloped postparacrista, resulting in a highly asymmetric buccal profile, and an inwardly angled or notched mesial margin but a strongly curved distal margin. This morphology is best characterized in the *P. africanus* holotype (M 14084) but can also be seen in other specimens attributed to this species, as well as those referred to *P. major* (Figure 4d,e). Also noteworthy is a distinctive mesiobuccal flange that mesially extends the buccal portion of the crown but only near the cervical line of the tooth. Pickford et al. (2009) describe this feature in some detail for "*Ugandapithecus*," but in fact this morphology is clearly expressed in the *P. africanus* holotype as well (Figure 4a,d). A single adult P³ germ and two dP³s attributed to *P. meswae* look remarkably similar to those of other *Proconsul* species, including the presence of this flange. In contrast, the *Ekembo* P³ has a well-developed mesial fovea that terminates at a mesiobuccal shoulder positioned

approximately halfway between the paracone tip and the cervix. From this shoulder, the mesial margin angles slightly distally down to the cervix. (Figure 4f).

<Figure 4 about here>

The degree of cusp height heteromorphy in P³ also differentiates *Ekembo* from *Proconsul* (contra Pickford et al. 2009). Only four non-Kisingiri specimens were sufficiently unworn to take measurements, but more worn specimens also appear to express this differential in cusp height. Figure 5a shows the ratio of protocone : paracone height measured from the tooth cervix, and, with only one exception, *Ekembo* P³s have substantially less cusp heteromorphy. This exception, KNM-RU 1677, does not in fact have greater heteromorphy, but instead has an abnormal extension of the enamel onto the buccal (paracone) root, which skews the measurement. Hence, cusp relief relative to the occlusal surface in RU 1677 is not nearly as heteromorphous as in *Proconsul*, and when this is taken into account the difference between genera is significant (t-test: $df = 11$, $t = 2.83$, $p = 0.0165$). The adult P³ germ from Meswa Bridge is incompletely formed and therefore could not be measured. However, the difference between paracone and protocone heights with respect to the occlusal surface appears to be as great as that in the *P. africanus* holotype. It does not appear that sex is an important determinant of this feature, since well-established male (e.g., M16647, KNM-RU 16000) and female (KNM-RU 2036, 7290) specimens do not segregate across the Kisingiri range of variation.

Upper fourth premolars of *Ekembo* are broadly similar in morphology to *Ekembo* P³s; in fact, the similarity between P³ and P⁴ is substantially greater in *Ekembo* than in *Proconsul* (Figure 4a,c). Likewise, most of the morphological differences that discriminate the P³s of these genera also tend to differentiate the P⁴s, but less clearly. Cusp heteromorphy does not distinguish P⁴s of these genera, but

the overall height of the P⁴ paracone in *Ekembo* is significantly greater relative to crown length than in *Proconsul* P⁴s (t-test: $df = 14$, $t = 3.16$, $p = 0.0069$; Figure 5b).

<Figure 5 about here>

Upper molars Cusps of *Ekembo* upper molars are uniformly more bunodont than those of *Proconsul*, occupying more of the occlusal surface. Intercuspal crests are more fully incorporated into the cusps in *Ekembo* molars giving them a more inflated appearance. This is particularly evident in the crista obliqua, which is very broad in *Ekembo* but thin and knife-like in *Proconsul* (Figure 6). Cusps of *Proconsul* molars stand more as individual cones. Pickford et al. (2009) have further differentiated the cusp morphology of smaller and larger Tinderet specimens, arguing that the latter have more bulbous cusps. While accurate, this difference is minor compared with the morphological difference between *Ekembo* and *Proconsul*, and we regard the within-*Proconsul* cuspal variation as size-related. In fact, the intermediately sized *P. meswae* has cusp morphology that is appropriately intermediate between that of *P. africanus* and the larger *P. major*.

Other differences between *Ekembo* and *Proconsul* upper molars are most evident in M². We concur with previous assessments that the Kisingiri upper molars have less developed cingula than non-Kisingiri molars (e.g., Senut et al., 2000; Harrison, 2002, 2010; Harrison and Andrews, 2009). More specifically, *Ekembo* M²s lack or have only rudimentary buccal cingula between the paracone and metacone. Likewise, the lingual cingulum is discontinuous, merging into the hypocone lingually and then re-emerging as a distal marginal ridge (Figure 6). *Proconsul* M²s display substantially more cingular development overall, and in particular exhibit a prominent buccal shelf between the paracone and metacone and a distinct distolingual cingulum that is continuous around the hypocone to where it merges with the distal marginal ridge.

The occlusal profiles of *Ekembo* M²s are squarish in shape with relatively straight and equal sides, with a posthypocone crista that is distobuccally to buccally directed. In contrast, the occlusal profiles of *Proconsul* M²s have a more rhomboid shape, with substantial basal flare around the mesial cusps and a distally expanded hypocone with a distally directed posthypocone crista resulting in a strongly curved distal margin (Figure 6). Even in specimens with less curved distal margins, the posthypocone crista is still more distally directed compared to the condition in *Ekembo*. These features are characteristic not only of *P. africanus*, *P. meswae*, and *P. major*, but are also expressed in the isolated M² from Moroto, Uganda (MOR IIb 2'98) attributed by Pickford et al. (2009) to "*U.*" *gitongai*, but regarded here as belonging to *P. major*.

As noted by others (e.g., Harrison and Andrews, 2009), the degree of buccolingual molar flare differs among these samples. Quantified as the distance between the tips of the mesial cusps divided by maximum crown breadth, the degree of molar flare in *Ekembo* M²s is significantly less than in *Proconsul* M²s (t-test: $df = 29$, $t = 3.96$, $p = 0.0004$). In a bivariate plot of these two measures, the distributions of *Ekembo* and *Proconsul* teeth barely overlap, with only KNM-RU 1677 encroaching into *Proconsul* territory (Figure 7).

<Figures 6 and 7 about here>

These differences in M² morphology also tend to distinguish *Ekembo* from *Proconsul* M¹s but not always as clearly. Whereas M²s more consistently express distinct morphotypes, the M¹s in both genera show more variation in these features.

The degree of upper third molar development – i.e., whether M³ has four distinct cusps or the distal cusps are reduced or absent – has long been cited as taxonomically informative for these species, or groups of these species (e.g., Hopwood, 1933; Le Gros Clark and Leakey, 1951; Andrews, 1978;

Pickford et al., 2009). However, we found this tooth to be unreliable for taxonomic purposes. Within primates, M³s are typically the most variable molars in both size and shape (Blankenship et al., 2007; Kavanagh et al., 2007), and this is observable even in small samples of *Proconsul* species. The *P. africanus* holotype has a substantially reduced M³ whereas in KNM-CA 2250 - attributed by most authors to this species (Andrews, 1978; Pickford et al., 2009) - it is fully developed. Similarly, the hypodigm of *P. major* includes both fully developed M³s (e.g., KNM-CA 389, LG 1815) and specimens with reduced or missing hypocones (KNM-CA 397, 1299). *Ekembo* displays comparable ranges of variation, from highly reduced to fully developed M³s in both species. Thus, these species and genera cannot be distinguished based on M³ development, and we did not find any other distinguishing characteristics between *Ekembo* and *Proconsul* in the upper third molars.

Mandible Pickford et al. (2009) enumerated several traits that readily distinguish Kisingiri from non-Kisingiri mandibles, and these distinctions are entirely consistent with the distinction of *Ekembo* from *Proconsul*. Our analyses specifically underscore differences in the symphyseal region. The planum alveolare in both male and female specimens of *Ekembo* is short and more vertically oriented; even the most elongate of these (KNM-RU 47805; McNulty et al., 2007) is substantially more vertical compared to specimens of *Proconsul*. In contrast, the planum alveolare in *Proconsul* is conspicuously long and nearly horizontally oriented. Well-preserved mandibles attributed to *P. major* (e.g., KNM-SO 396 and 404) exhibit this morphology in extreme fashion (Figure 8); smaller specimens (KNM-SO 1112; *P. africanus*) show less extreme expression but are still readily distinguishable from *Ekembo* mandibles. For its size, KNM-LG 452 has a surprisingly short planum alveolare, though not to the degree seen in Rusinga mandibles. Correlated to the short planum alveolare in *Ekembo* is a reduced superior transverse torus, which, while well-developed, does not approach the robusticity expressed in *Proconsul* mandibles. This difference is reflected in an index of symphyseal robusticity (thickness perpendicular to the long axis of

the symphysis/length of the long axis), which shows *Ekembo* and *Proconsul* to be significantly different (t-test: $df = 14$, $t = -4.30$, $p = 0.0007$).

<Figures 8 about here>

Development of the inferior transverse torus – often used to differentiate among species of *Proconsul* (e.g., Pickford et al., 2009; Harrison, 2010) – was found to be highly variable and inconsistently expressed within these samples. However, the overall orientation of the subplanum region (as defined by a line connecting the posterior-most midline points of the superior and inferior transverse tori, or the posterior-most midline point of the inferior margin of the symphysis in the absence of the latter) does distinguish *Ekembo* from *Proconsul* mandibles. The orientation of this line in relation to the alveolar margin in the vicinity of the postcanine teeth was assessed qualitatively by placing a small rod (e.g., a dental pick) in the midline internally along the two reference points and recording the point, in lingual perspective, at which the rod intersected the alveolar margin (Figure 9). In *Ekembo*, the subplanum region is more vertically oriented so that the rod intersects the alveolar margin most often in the premolar field. Not surprisingly, there is a difference between sexes with females having a reduced superior transverse torus and therefore a more vertically oriented subplanum region compared to males. In contrast with *Ekembo*, *Proconsul* mandibles have much more inclined subplanum surfaces, with the rod intersecting the lingual alveolar margin in the vicinity of the M_1 (females) or M_2 (males; Figure 9). When sex is taken into account, therefore, the distributions of *Ekembo* and *Proconsul* in this feature are discrete. Note that male and female mandibles attributed to both *P. africanus* and *P. major* are included in this assessment, and are surprisingly similar despite dramatic size differences.

<Figure 9 about here>

We quantified internal symphyseal morphology using three measures: symphyseal height (infradentale–gnathion), planum alveolare length (posterior-most point on the superior transverse torus–infradentale), and subplanum length (posterior-most point on the superior transverse torus–gnathion), a combination that incorporates not only the lengths of these intervals but also the angular relationships among them. To compare symphyseal shape across a range of sizes, we chose a simple principal components approach to partition size onto the first eigenvector (cf. Jolicouer, 1963). While this is not the preferred method for partitioning size in most datasets (Jungers et al., 1995), for this particular set of measurements Mosimann shape variables were still significantly correlated with size (see discussion in Coleman, 2008). Hence, we assessed differences in symphyseal morphology between *Ekembo* and *Proconsul* using the second and third principal components of the three variables. Distributions of the two genera are distinct in this shape space (Figure 10; Supplementary table 1).

<Figure 10 about here>

Robusticity of the mandibular corpus also differs between these samples, though it is more difficult to test due to differential preservation among specimens. Corpus thickness and depth under P_4 can be measured in the greatest number of specimens, and comparison of these measures suggests a difference between groups in the scaling of corpus robusticity (Figure 11). Among large, presumably male specimens, *Ekembo* mandibles are substantially less robust than those of *Proconsul*. However, among smaller mandibles only a single *Proconsul* specimen (KNM-SO 372) could be included, and it is similar in robusticity to *Ekembo* mandibles of this size. Considered together, the impression is that corpus robusticity may scale differently in *Ekembo* than it does in *Proconsul*, and a test for differences in slopes using an ANCOVA design of the logged variables was significant ($df = 2$, $F = 24.81$, $p < 0.0001$).

Nevertheless, additional specimens are needed to properly evaluate the influence of taxonomy, sex, and size on corpus robusticity; a reasonable alternative interpretation of Figure 11 is that it demonstrates a significant difference between *P. major* and all other species of both *Proconsul* and *Ekembo*.

Figure 11 about here

Lower incisors *Ekembo* specimens are uniformly narrower in mesiodistal length than incisors attributed to *P. africanus*, *P. major* and *P. meswae*, both absolutely and in relation to crown height (Figure 12).

This is true for both I_1 and I_2 . A t-test adjusted for non-independent observations (e.g., I_1 and I_2 from the same mandible) confirmed the difference as significant (t-test: $df = 12$, $t = -2.58$, $p = 0.0242$). Moreover, while the measurable *Proconsul* sample was small, this same pattern is observable in other specimens whose tips were slightly to moderately worn and therefore not measured.

<Figure 12 about here>

Lower canines The only lower canine trait that discretely separates these genera is the pointed crown tip in *Ekembo* (Figure 3d) contrasted with a blade-like (or “burin”) tip in *Proconsul* (Figure 3c). This feature is well-established for *P. major*, but is also expressed in KNM-CA 1772, which was referred to *P. africanus* by Kelley (1986) and is too small to be either *P. major* or *P. meswae*. Two other specimens commonly attributed to *P. africanus*, KNM-CA 2149 and KNM-SO 1112, both have broken canine tips. Likewise, a new specimen (Kor 65'04) attributed to *P. africanus* by Pickford et al. (2009) also has a broken tip and cannot be evaluated (see Pickford et al., 2009: Fig. 23). As with the upper canines, the blade-like tip is also present in the deciduous lower canines of *P. major* (e.g., KNM-CA 361, SO 5352) and *P. meswae* (KNM-ME 1).

Lower premolars Like most previous authors (e.g., Andrews, 1978; Harrison, 2002, 2012; Pickford et al., 2009), we found neither qualitative nor quantitative characteristics of the lower premolars with any taxonomic value.

Lower molars Differences in lower molar morphology are few and relatively subtle, but in some cases mirror those seen in the upper molars. Cusps on the lower molars of *Ekembo* are more bunodont than those in *Proconsul* and occupy more of the occlusal surface. Broad inter-cuspal crests are incorporated into the *Ekembo* cusps making them appear more inflated. Molar cusps of *Proconsul* are more distinct from one another and are linked by narrower, sharper inter-cuspal crests. The lower molars of *Ekembo* also have a substantially less developed buccal cingulum than those of *Proconsul* (Harrison, 2002, 2010; Harrison and Andrews, 2009). Lastly, and again as seen in the upper molars, the two genera can be distinguished by the significantly greater amount of lower molar flare in *Proconsul* (Figure 13; t-test: $df = 59$, $t = 7.13$, $p < 0.0001$; see also Harrison and Andrews, 2009).

<Figure 13 about here>

Relative molar size has been used to distinguish species of *Proconsul*, but we observed the primary difference to be in relative buccolingual breadths of M_1 and M_2 . In *Ekembo*, M_1 is substantially narrower than M_2 than is the case in *Proconsul* (Figure 14; Harrison, 2002, 2010). Although none of the smaller *Proconsul* mandibles preserve complete crowns for both M_1 and M_2 , KNM-SO 1112 has an intact M_2 and at least preserves the cervix for M_1 . However, if even the cervical measurement is used for its M_1 breadth – thus underestimating the true crown breadth – KNM-SO 1112 still has a broader first molar in relation to M_2 than would be expected in *Ekembo*. If crown breadth is estimated from the ratio of cervix

breadth to maximum crown breadth in other *Proconsul* fossils, the range of likely breadths for the SO 1112 M₁ clearly distinguishes it from the *Ekembo* sample (Figure 14). Testing this relationship on logged variables using the mean estimate for the SO 1112 M₁ (Figure 14) reveals a significant difference between the two groups (ANCOVA: $df = 1$, $F = 24.24$, $p = 0.0002$).

As with upper third molars, we find a great deal of variation in M₃ morphology and mistrust the taxonomic significance sometimes placed on characteristics of this tooth – at least with regard to these taxa. Harrison (2002, 2010) cited the mesiodistal position of the M₃ entoconid as differentiating Kisingiri third molars from those attributed to *P. africanus*. We concur with his assessment, but found the entoconid position to vary in specimens attributed to *P. major*. Thus, this character does not differentiate *Ekembo* from all *Proconsul* species, but may distinguish it from the type species, *P. africanus*.

<Figure 14 about here>

Discussion

The distinctiveness of the Kisingiri large catarrhine material from that at Tinderet and Ugandan localities has been noted previously by several authors (Pickford, 1986; Walker et al., 1993; Begun, 2001, 2007; MacLatchy and Rossie, 2005; Harrison and Andrews, 2009; Harrison, 2010). What had not been fully documented was the nearly complete lack of overlap between these samples in a number of features, and this despite very large assemblages from Rusinga and Mfangano. On descriptive criteria alone (Table 2), many isolated teeth (I¹, C¹, P³, M², C₁) and all of the mandibles can be assigned to either *Proconsul* or *Ekembo* with very little chance of misattribution. That some of the most diagnostic features occur in the upper dentition – the only anatomy preserved in the *P. africanus* type specimen – adds weight to the taxonomic arrangement proposed here. The morphology of the upper teeth in all

Proconsul species compellingly unites them into a single clade, distinct from *E. heseloni* and *E. nyanzae*. This is reinforced by numerous features of the mandible and mandibular dentition that further distinguish these samples. The number and variety of these features are such that *Proconsul* and *Ekembo* are more different from one another than are many closely-related modern catarrhine genera.

Derived morphology of Ekembo and Proconsul

It is premature to formally assign primitive and derived status to the individual features of *Ekembo* and *Proconsul* before completing a formal phylogenetic analysis. This is especially true given the abundance of evidence available for *Ekembo* and hence the potential impact that our generic revision could have on phylogenetic interpretations. Nevertheless, in comparison with both extant hominoids and the small-bodied catarrhines from the early Miocene, it is informative to differentiate the evolutionary grades of these genera. Many characteristics of *Ekembo* are more advanced in the direction of modern apes compared to those of *Proconsul* (Table 2). General trends such as expanded and more bunodont cusps, broader molar crests, reduced cingulum, and morphological similarity between P³ and P⁴ all represent morphologies that presage those of later fossil and extant hominoids. The more advanced morphologies of P³ and M² are particularly conspicuous compared not only with those of *Proconsul* but to most early Miocene catarrhines. In contrast, the mesially positioned, strongly heteromorphic cusps on the P³ of *Proconsul*, plus the corresponding asymmetric buccal profile, notched mesial margin, and missing mesial fovea are characteristic of other early Miocene catarrhines such as *Dendropithecus*, *Rangwapithecus*, and *Limnopithecus*, and are likely primitive among East African catarrhines. The more symmetric P³ of *Ekembo*, with midline positioned cusps and reduced cusp heteromorphy, is reminiscent of later hominoids, and even hominid taxa such as *Rudapithecus* (e.g., Kordos and Begun, 2001).

Proconsul is likewise united by a suite of features that are, for the most part, characteristic only of this lineage (Table 2). The morphology of both upper and lower canines is unique to this genus and shared by all three well-known species plus the poorly represented middle Miocene *P. gitongai* (Pickford and Kunimatsu, 2005). The mandibular symphysis is also distinctive in *Proconsul* compared with other catarrhines, with its very long and shallowly sloping planum alveolare and steeply inclined subplanum surface. Indeed, even the small, edentulous anterior mandibular fragment KNM-SO 372 is readily placed within *Proconsul* and excluded from other similarly sized catarrhine taxa, such as *Rangwapithecus* and *Ekembo*, based on this unique symphyseal morphology (Figures 8, 9).

Other differences between *Ekembo* and *Proconsul* are of uncertain evolutionary polarity (e.g., orientation of the posthypocone crista) or may be of taxonomic relevance without broader phylogenetic significance (e.g., degree of molar flare; Table 2). We recognize that there are morphological differences within *Proconsul*, particularly between the better known species *P. africanus* and *P. major*. However, many of these differences are likely related to size and represent variations on a single generic theme that are markedly different from the morphology of *Ekembo*. The recent description (Harrison and Andrews, 2009) of the intermediately sized *P. meswae* underscores the broad morphological unity within *Proconsul* and further substantiates a well-defined *Proconsul* clade comprising Tinderet and Ugandan species.

Based on the abundant morphological and morphometric evidence supporting genus-level distinction between *Proconsul* and *Ekembo*, we are currently conducting a more detailed phylogenetic analysis of all early Miocene catarrhines in order to better understand the distribution and evolutionary significance of these and other morphological features. We anticipate that the debates surrounding the phylogenetic relationships of an historically constituted sample of *Proconsul* can be more satisfactorily resolved now that the Kisingiri material is appropriately recognized as a distinct genus.

The generic disposition of "Ugandapithecus" species

A great many features said to characterize "*Ugandapithecus*" were added to the original diagnosis of the genus by Pickford et al. (2009) in their systematic revision of *Proconsul* (sensu lato). As part of that study, they also erected a new species, "*U.*" *legetetensis*, and transferred *P. meswae* to "*Ugandapithecus*." Evaluating the same set of features across the entire available sample, however, we were unable to find support for this more expansive conception of "*Ugandapithecus*" for several reasons. First, some diagnostic features cited in Pickford et al. (2009) were quite variable within the "*Ugandapithecus*" sample. As an example, marked reduction of the M₃ entoconid to a bead on the lingual cingulum is not shared by several "*U.*" *major* specimens, such as KNM-CA 393, NAP I 49'00, and Kor 253'04 (see Pickford et al., 2009: Fig. 33e), and was likely not a feature of a few of the more worn specimens: e.g., BUMP 600 and BUMP 601, or even the holotype of *P. major*, M 16648. Second, some diagnostic features of "*Ugandapithecus*" were found to be variably present in *Ekembo*, arguing against their utility for distinguishing "*Ugandapithecus*" from Pickford et al.'s (2009) combined *P. africanus*+Kisingiri conception of *Proconsul*. For example, significantly reduced curvature of the I¹ distal margin in "*Ugandapithecus*" is also found in some Kisingiri specimens, including KNM-RU 1685, 1712, 1714, 1831, 1846, and 1951; several more Rusinga specimens have moderately reduced curvature. Third, some features that purportedly distinguish "*Ugandapithecus*" from *P. africanus* are likely related to size. For example, the somewhat more central position of the P³ paracone in "*U.*" *major* is not seen in the smaller "*U.*" *meswae*, whose paracone is positioned similarly to that of the holotype of *P. africanus* (see Harrison and Andrews, 2009: Fig. 6d).

However, the major part of the evidence for recognizing "*Ugandapithecus*" (sensu Pickford et al., 2009) was assembled by re-assigning specimens traditionally attributed to *P. africanus* into new species of "*Ugandapithecus*." The *P. africanus* holotype was left in association with the Rusinga sample, despite having morphology overwhelmingly characteristic of other Tinderet specimens. The resulting

specimen allocations left *P. africanus* morphologically impoverished – stripped of much of its hypodigm – so that *Proconsul* for Pickford et al. (2009) came to be characterized primarily by the Rusinga sample (see similar comments in Harrison and Andrews, 2009). Within that conceptual framework, any specimen that differs from those at Rusinga could not be *Proconsul* but must instead belong to “*Ugandapithecus*.” Thus, specimens such as the KNM-SO 1112 mandible were erroneously assigned to “*Ugandapithecus*” because they were (correctly) perceived as differing from their Rusinga counterparts (Pickford et al., 2009).

Here, we restore the *P. africanus* hypodigm and associate it with the other Tinderet fossils according to their shared morphology. Specimens assigned to “*Ugandapithecus*” revert to *Proconsul*, and many of the features cited to support a speciose “*Ugandapithecus*” (Pickford et al., 2009) instead become diagnostic features of *Proconsul*. This correction serves to highlight the distinctiveness of the Kisingiri remains and the need to recognize this distinctiveness at the generic level.

As demonstrated above, specimens from Kisingiri do not display the morphology of *Proconsul* as represented by the holotype of *P. africanus*, M 14084. Given that this specimen preserves only the upper canine and cheek teeth, similarities with or departures from this morphology represent the most compelling arguments for assessing inclusivity in the genus. However, for the mandible and lower dentition, if one simply sorts the specimens by element without relying on taxonomic preconceptions, the overwhelming distinction within the traditionally constituted *Proconsul* sample is between Kisingiri material on the one hand and that from Tinderet and Uganda on the other (cf. Walker et al., 1993; Begun, 2001, 2007; MacLatchy and Rossie 2005; Harrison and Andrews, 2009; Harrison, 2010). Additionally, with the Kisingiri specimens removed to *Ekembo*, the postcranial differences used to partly justify a distinct “*Ugandapithecus*” lose their relevance (see Harrison and Andrews, 2009).

We have differed among ourselves in our past treatment of *P. major* as generically distinct from the smaller species of *Proconsul* (Begun, 2007; McNulty, 2010). Morphologically, many of the unique

features of *P. major* can be interpreted as size-related variants on the smaller *P. africanus* morphology. Even if so, the question is whether these are sufficiently different and numerous to warrant generic distinction; that is, do they suggest that *P. major* belongs in a separate clade from *P. africanus* and *P. meswae*? As we have demonstrated, differences among these three species are certainly fewer and show less morphological distinction than those between *Ekembo* and any of the three. Nevertheless, while we ultimately agree with Harrison and Andrews (2009; see also Begun, 2007) that the features distinguishing "*U.*" *major* from *P. africanus* are consistent with those that distinguish congeneric species, and are at least partly due to differences in size, we concede the possibility that the largest *Proconsul* species could belong in a separate genus (Senut et al., 2000; Pickford and Kunimatsu, 2005). However, whether or not one recognizes a separate genus for *P. major*, the *P. africanus* material does not sort morphologically with the Kisingiri material. Therefore, the taxonomic alternatives are either two genera, *Proconsul* and *Ekembo*, or three, *Proconsul*, *Ugandapithecus* and *Ekembo*, with *Proconsul* and *Ugandapithecus* united in a clade exclusive of *Ekembo*. Thus, while we strongly favor the first alternative, recognizing *Ugandapithecus* does not change the fundamental argument concerning the need to refer the Kisingiri species to a generically and cladistically distinct taxon from the species represented at Tinderet and the Ugandan sites.

Specimens of interest

Despite the substantial dental and gnathic differences between *Proconsul* and *Ekembo*, there are a few specimens whose taxonomic affinities require additional scrutiny.

KNM-RU 1676-77 This set of associated upper and lower teeth is a consistent outlier among *E. heseloni* and *E. nyanzae* specimens. In some ways, this specimen more closely resembles Tinderet *Proconsul* in the features that distinguish it from *Ekembo*. Molar cusp morphology and cingulum development, I¹

lingual tubercle development, and M² shape and posthypocone crista orientation are more consistent with specimens from the Tinderet sites. On the other hand, it otherwise resembles *Ekembo* and lacks the strongest diagnostic features that unite species of *Proconsul*, such as the distinctive canine and P³ morphology. Overall, this specimen does not fit unambiguously into either genus; in fact, the degree of buccolingual flare, cusp morphology, enamel wrinkling, and especially the long extension of enamel onto the anterior root in P³ are in some ways reminiscent of *Afropithecus* although it clearly differs from that genus as well (cf. Rossie and MacLatchy, 2013).

Were these characteristics individually distributed among the large Kisingiri sample one might attribute this to intra-generic variation, but when found together in a single specimen from a large sample, it suggests a unique individual. One of us (KPM) thinks it likely that the specimen was not actually found at a Kisingiri locality, based on its unique preservation compared to other Rusinga fossils and on other examples of mis-provenienced specimens (Leakey, 1967; Andrews and Molleson, 1979; Pickford, 1986; Kelley, 1986). However, we recognize that relying too frequently on this explanation allows almost any scenario to be justified, and suggest some alternative possibilities. One is that the specimen was found on Rusinga but in the much older Wayando Formation strata instead of the Hiwegi Formation. The differences in morphology in that case might reflect more than a million years of temporal change (McCollum et al., 2013), with KNM-RU 1676-77 preserving certain more primitive, *Proconsul*-like features. As an alternative, it is reasonable to assume that fossil assemblages as vast as those from Rusinga will include not only abundant taxa, but also rare or infrequent inhabitants of the local biome. There are many examples of this from Rusinga's mammalian community, e.g., "*Hemicyon*," *Kulutherium*, *Tadarida*, cf. *Hyainailouros*, cf. *Archaeobeleidon*, *Kelba* (see relevant chapters in Werdelin and Sanders, 2010). As such, KNM-RU 1676-77 may simply represent a rare and well-preserved specimen of some other catarrhine taxon that lived among or visited a primate community dominated by *Ekembo*.

KNM-SO 1112 This specimen was initially referred to *Rangwapithecus*, but soon after was transferred to *P. africanus* (Bosler, 1981; Martin, 1981) – a designation that most subsequent authors have followed (Kelley, 1986, 1995; Pickford, 1986; Nengo and Rae, 1992; Walker et al., 1993; MacLatchy and Rossie, 2005; Hill et al., 2013). Pickford et al. (2009) more recently referred this specimen to "*U.*" *meswae* citing two primary reasons. First, they reiterated Bosler's (1981) concern that its P₃ differs from others attributed to *P. africanus*. However, at that time the majority of what was considered to be *P. africanus* would have been from Rusinga Island. In fact, while noting its contrasting morphology, Bosler suggested that differences between KNM-SO 1112 and other P₃s might reasonably be attributed to sexual dimorphism, noting that this specimen provides "a not implausible match for the *P. (P.) africanus* holotype maxilla, M 14084" (1981: 152). That assessment is borne out in this study. Using the much larger sample of *Ekembo* P₃s as a model, variation can be seen to encompass specimens with well-developed mesial beaks and those with more bilaterally compressed crowns and parallel sides. The latter morphology is predominantly found among male specimens (KNM-RU 1674, 1924, and KPS I and III), thus supporting Bosler's (1981) suggestion that this variation is related to sexual dimorphism and, hence, that KNM-SO 1112 is a male *P. africanus*.

The second feature cited by Pickford et al. (2009) in referring this specimen to "*U.*" *meswae* was posterior shallowing of the mandibular corpus. However, because they redefined "*Ugandapithecus*" to include *all* of the well-preserved Tinderet mandibles (Pickford et al., 2009) – leaving *Proconsul* to be represented only by Rusinga specimens – their only alternative within this scheme for a specimen the size of SO 1112 was to refer it to "*U.*" *meswae*. It seems odd, though, to assign this specimen to a species from a (perhaps much) older site when the *Proconsul africanus* holotype is of appropriate size and similar age, and as there are no other adult mandibles from either species with which to compare it. In any case, mandibular shallowing is variable in both *Ekembo* and *Proconsul*, with some Kisingiri

specimens exhibiting considerable shallowing (e.g., KNM-RU 2087) and some "*Ugandapithecus*" specimens having very little (e.g., M 14086).

We therefore see no morphological grounds to assign SO-1112 to *P. meswae*, but do find some morphological evidence to assign it as a male *P. africanus*, which occurs at Songhor.

KNM-LG 452 This very complete mandible was originally recognized as a female of *P. major* based on the size of the dentition and robusticity of the mandible (Martin, 1981). Bosler (1981), however, left this specimen unassigned, noting similarities to *P. major* in P₃-M₁ size but having distinctly smaller M₂₋₃. In this, she likened KNM-LG 452 to a few other specimens (notably, M 14086) that are smaller in their distal molars in a manner more consistent with taxonomic rather than sex differences (Bosler, 1981; see also Pilbeam, 1969). Kelley (1986, 1995) also assigned this specimen as a female of *P. major* based on canine size and morphology, but noted that the canine lacked the shallowly-sloping mesial ridge typical of most female anthropoid canines. This is also true, however, of two other canines assigned as female *P. major*, KO 9 and SO 373 (Kelley, 1986), and so might simply be an unusual characteristic of *P. major* female lower canines. In the end, Kelley (1995) concluded that, considering all of the criteria for distinguishing male and female canines, the evidence that KNM-LG 452 is female remains questionable.

Pickford et al. (2009) further developed the idea that two species are represented within the *P. major* sample, and made KNM-LG 452 the holotype of a new species "*U.*" *legetetensis*. We concur that this specimen is unique among the well-preserved Tinderet mandibles in some important features. Whereas male and female mandibles of *P. major* have long internal symphyseal planes, expansive extra- and retromolar sulci, and rami that cross the occlusal plane at distal M₃, KNM-LG 452 has a shorter symphyseal plane (though not to the extent seen in *Ekembo*), a moderate extramolar sulcus but no retromolar sulcus, and a ramus that crosses the occlusal plane more mesially. If KNM-SO 396 and SO 404

represent males and females, respectively, of *P. major*, then the morphology of KNM-LG 452 appears distinct.

At present, however, we do not think there is sufficient evidence to differentiate this specimen from either *P. major* or *P. meswae*. Pickford et al. (2009) argue that KNM-LG 452 cannot belong to the latter species because of its larger size. The size differences, however, are well within the range of variation seen in *P. major*, *E. heseloni*, and *E. nyanzae*. Moreover, whereas the Legetet mandible is larger than most of the *P. meswae* hypodigm, an adult P₄ referred to this species (KNM-ME 25) substantially exceeds its counterpart in KNM-LG 452. Should the Legetet mandible ultimately prove to be a male specimen, size alone would not rule out its attribution to *P. meswae*. On the other hand, if it is female then it becomes harder to justify its inclusion in that sample of mostly smaller specimens. If female, therefore, it could represent a separate species, for which the binomial *Proconsul legetetensis* comb. nov. is available. Recently collected fossils from the Songhor/Kapurthay area provide some additional support for the possibility that three species of *Proconsul* existed at these localities (McNulty 2014a,b). However, to convincingly demonstrate this and determine whether a third species can be differentiated from *P. meswae* will require a more detailed analysis of variation among *Proconsul* species, a corresponding study of variation in modern taxa, and – almost certainly – additional fossil specimens. For now, then, we regard “*U.*” *legetetensis* as a subjective junior synonym of *P. major*.

Conclusions

The genus *Proconsul* has been central to studies of ape and human evolution since its first description by Hopwood (1933). As one of the best known fossil catarrhines, represented by nearly every skeletal element, our knowledge of *Proconsul*'s functional anatomy, positional behavior, and overall morphology has made it the foundation for paleoanthropological research in the early Miocene, as well as studies on the origin and early diversification of hominoids. With respect to systematics,

however, *Proconsul* is less well understood; the type species, *P. africanus*, is known from a relatively small number of specimens from sites in the Tinderet area, and no postcranial bones can be unambiguously assigned to it. Rather, it is the copious and well-preserved specimens from the Kisingiri sites of Rusinga and Mfangano Islands that have formed the basis for the common image of *Proconsul*.

We argue here that the Kisingiri species traditionally referred to *Proconsul* – *P. heseloni* and *P. nyanzae* – are generically distinct from *P. africanus*, and hereby transfer them into a new genus, *Ekembo*, based on a substantial number of morphological differences (Table 2). Considering only those traits preserved in the *P. africanus* holotype, the entire sample from Rusinga and Mfangano differs markedly in the morphology of the upper canine, P³, P⁴, and M². Additional differences in the I¹, lower incisors and canines, molar cusp and occlusal crest morphology, degree of flare in all molars, and especially mandibular features, clearly distinguish the Kisingiri from non-Kisingiri samples in a way that is incompatible with congeneric species. With the transfer of *E. heseloni* and *E. nyanzae*, *Proconsul* becomes a well-defined clade comprising at least three species – *P. africanus*, *P. major*, and *P. meswae* – united by several features that are unique for the genus (Table 2).

We found no support in this study for the genus "*Ugandapithecus*" as constructed by Pickford et al. (2009). In that paper, they transferred the vast majority of *Proconsul* fossils from the Tinderet and Napak localities into "*Ugandapithecus*," leaving *P. africanus* represented only by its holotype and a small number of isolated teeth, and aligning it with the material from Rusinga and Mfangano. When the *P. africanus* hypodigm is reconstituted and properly affiliated with the other Tinderet species according to its morphology, much of the evidence marshaled by Pickford et al. (2009) for "*Ugandapithecus*" actually supports the distinction between the Tinderet and Kisingiri samples, i.e., the generic distinction of *Ekembo*. In addition, some of the traits enumerated by Pickford and colleagues in support of "*Ugandapithecus*" were revealed in our analysis to be variable within one or more species and therefore of questionable taxonomic utility. We do not reject out of hand the original conception of

"*Ugandapithecus*" (Senut et al., 2000) as either a monotypic genus distinguishing "*U.*" *major*, or perhaps including a closely allied middle Miocene "*U.*" *gitongai* as well (Pickford and Kunimatsu, 2005), but we have for now retained the early Miocene specimens of both in *Proconsul* pending further study. However, even if *Ugandapithecus* is a taxonomically valid genus comprising just the latter two species, their morphology indicates that they would still be united in a clade with *Proconsul*, and they lack several more advanced features that partly define *Ekembo*. Better understanding of the role that body size plays in mediating differences in *Proconsul* will help to further clarify the relationships among these species.

Despite the existence of one well-represented and several less complete skeletons of what was long assumed to be *Proconsul*, the phylogenetic status of this genus has defied consensus. This is largely due, in our view, to *Proconsul* having been an admixture of two distinct genera, one more advanced in the direction of extant apes than the other. As we demonstrate here, the material from Rusinga and Mfangano traditionally referred to *Proconsul*, and which includes all of the more complete skeletal material, is distinct from the Tinderet and Napak material and belongs in a separate genus, *Ekembo*. By disentangling these distinct clades, we anticipate being able to achieve better phylogenetic resolution for both genera, thereby improving our knowledge of early hominoid evolution and diversification.

Acknowledgements

We thank many people and agencies that assisted with the development and completion of this project. This research was initiated as a result of funding from the Wenner-Gren Foundation and the Johns Hopkins School of Medicine to D.R. Begun in 1987-9 and was renewed following research and travel generously funded by multiple Leakey Foundation grants to K. McNulty, National Science Foundation grants to K. McNulty (0852609, 1241807), the McKnight Foundation, the University of Minnesota, the Lloyd A. Wilford Endowment, the Leverhulme Foundation, and the Turkana Basin

Institute. J. Kelley gratefully acknowledges support from the Institute of Human Origins, Arizona State University. D.R. Begun also wishes to acknowledge the Alexander Humboldt Stiftung and NSERC for funding support. We are grateful to Rose Mwanja, Ezra Musiime, Tom Mukhuyu, Samuel Muteti, James Yatich, and Mary Muungu for access to and assistance with specimens in their care. Many people provided assistance, comments, criticisms, insights, and suggestions on various aspects of this work, and we especially thank Holly Dunsworth, Will Harcourt-Smith, Tom Lehmann, Dan Peppe, Nicole Garrett, Kirsten Jenkins, Rutger Jansma, Susy Cote, Isaiah Nengo, Andrew Hill, and Brenda Benefit. K. McNulty acknowledges the evolutionary anthropology faculty and students at Durham University for their helpful comments on an early version of this manuscript, and for their gracious hospitality. We are likewise grateful to the anonymous reviewers, associate editor, and editor whose comments strengthened the paper. This manuscript is publication #1 supporting Research on East African Catarrhine and Hominoid Evolution (REACHE).

References

- Andrews, P., 1974. New species of *Dryopithecus* from Kenya. *Nature* 249, 188–190.
- Andrews, P., 1978. A revision of the Miocene Hominoidea of East Africa. *Bull. Brit. Mus. (Nat. Hist.) Geol.* 30, 85–225.
- Andrews, P., 1985. Family group systematics and evolution among catarrhine primates. In: Delson, E. (Ed.), *Ancestors: The Hard Evidence*. Liss, New York, pp. 14–22.
- Andrews, P., Harrison, T., Martin, L., Pickford, M., 1981. Hominoid primates from a new Miocene locality named Meswa Bridge in Kenya. *J. Hum. Evol.* 10, 123–128.
- Andrews, P., Begun, D., Zylstra, M., 1997. Interrelationships between functional morphology and paleoenvironments in Miocene hominoids. In Begun, D., Ward, C., Rose, M. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*. Plenum Press, New York, pp. 29-58.
- Beard, K.C., Teaford, M.F., Walker, A., 1986. New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. *Folia Primatol.* 47, 97–118.
- Begun, D.R., 2001. African and Eurasian Miocene hominoids and the origins of the Hominidae. In: de Bonis, L., Koufos, G.D., Andrews, P. (Eds.), *Hominoid Evolution and climatic Change in Europe: Phylogeny of the Neogene Hominoid Primates of Eurasia*. Cambridge University Press, London, pp. 231-253.
- Begun, D.R., 2007. Fossil record of Miocene hominoids. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Paleoanthropology*. Springer, Berlin, pp. 921-977.
- Begun, D.R., Teaford, M.F., Walker, A.C., 1994. Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *J. Hum. Evol.* 26, 89–165.
- Bishop, W.W., 1964. More fossil primates and other Miocene mammals from North-East Uganda. *Nature* 203, 1327-1331.

- Bishop, W.W., Miller, J.A., Fitch, F.J., 1969. New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Am. J. Sci.* 267, 669–699.
- Blankenship, J.A., Mincer, H.H., Anderson, K.M., Woods, M.A., Burton, E.L., 2007. Third molar development in the estimation of chronologic age in American blacks as compared with whites. *J. Forensic. Sci.* 52, 428–433.
- Bosler, W., 1981. Species groupings of early Miocene dryopithecine teeth from East Africa. *J. Hum. Evol.* 10, 151–158.
- Coleman, M.N., 2008. What does geometric mean, mean geometrically? Assessing the utility of geometric mean and other size variables in studies of skull allometry. *Am. J. Phys. Anthropol.* 135, 404–15.
- Corruccini, R.S., Henderson, A.M., 1978. Palatofacial comparison of *Dryopithecus (Proconsul)* with extant catarrhines. *Primates* 19, 35–44.
- Cote, S., Malit, N., Nengo, I., 2013. Additional mandibles of *Rangwapithecus gordonii*, an early Miocene catarrhine from the Tinderet localities of Western Kenya. *J. Hum. Evol.* 153, 341–352.
- Davis, P.R., Napier, J., 1963. A reconstruction of the skull of *Proconsul africanus* (R.S. 51). *Folia Primatol.* 1, 20–28.
- Deane, A.S., 2009. Early Miocene catarrhine dietary behavior: the influence of the Red Queen Effect on incisor shape and curvature. *J. Hum. Evol.* 56, 275–285.
- Drake, R., Van Couvering, J.A., Pickford, M., Curtis, G., Harris, J.A., 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, western Kenya. *J. Geol. Soc. Lond.* 145, 479–491.
- Evernden, J.F., Savage, D.E., Curtis, G.H., James, G.T., 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. *Am. J. Sci.* 262, 145–198.
- Gebo, D.L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J., Pilbeam, D., 1997. A hominoid genus from the Early Miocene of Uganda. *Science* 276, 401–404.

- Geoffroy Saint-Hilaire, É., 1812. Tableau des Quadrumanes, 1. Ord. Quadrumanes. Ann. Mus. Hist. Nat., Paris. 19, 85–122.
- Gray, J.E., 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. Ann. Philos. 10, 337–344.
- Harrison, T., 1982. Small-bodied apes from the Miocene of East Africa. Ph.D. Dissertation, University of London.
- Harrison, T., 1986. New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Oreopithecidae. Am. J. Phys. Anthropol. 71, 265–284.
- Harrison, T., 1987. The phylogenetic relationships of the early catarrhine primates: A review of the current evidence. J. Hum. Evol. 16, 41–80.
- Harrison, T., 1993. Cladistic concepts and the species problem in hominoid evolution. In: Kimbel, W.H., Martin, L.B. (Eds.), Species, Species Concepts, and Primate Evolution. Plenum Press, New York, pp. 354–371.
- Harrison, T., 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: Hartwig, W.C. (Ed.), The Primate Fossil Record. Cambridge University Press, Cambridge, pp. 311–338.
- Harrison, T., 2010. Dendropithecoidea, Proconsuloidea and Hominoidea (Catarrhini, Primates). In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, pp. 429–269.
- Harrison, T., Andrews, P., 2009. The anatomy and systematic position of a new species of early Miocene proconsulid from Meswa Bridge, Kenya. J. Hum. Evol. 56, 479–496.
- Hopwood, A.T., 1933. Miocene primates from Kenya. J. Linn. Soc. Zool. 38, 437–464.
- Hill, A., Nengo, I.O., Rossie, J.B., 2013. A *Rangwapithecus gordonii* mandible from the early Miocene site of Songhor, Kenya. J. Hum. Evol. 65, 490–500.

- Ishida, H., Kunimatsu, Y., Takano, T., Nakano, Y., Nakatsukasa, M., 2004. *Nacholapithecus* skeleton from the middle Miocene of Kenya. *J. Hum. Evol.* 46, 69–103.
- Jolicouer, P., 1963. The multivariate generalization of the allometry equation. *Biometrics*, 19, 497–499.
- Jungers, W.L., Falsetti, A.B., Wall, C.E., 1995. Shape, relative size, and size-adjustments in morphometrics. *Am. J. Phys. Anthropol.* 38(S2), 137–161.
- Kavanagh, K.D., Evans, A.R., Jernvall, J., 2007. Predicting evolutionary patterns of mammalian teeth from development. *Nature* 449, 427–433.
- Kelley, J., 1986. Species recognition and sexual dimorphism in *Proconsul* and *Rangwapithecus*. *J. Hum. Evol.* 15, 461–495.
- Kelley, J., 1995. Sex determination in Miocene catarrhine primates. *Am. J. Phys. Anthropol.* 96, 390–417.
- Kelley, J., 1993. Taxonomic implications of sexual dimorphism in *Lufengpithecus*. In: Kimbel, W.H., Martin, L.B. (Eds.), *Species, Species Concepts and Primate Evolution*. Springer, New York, pp. 429–458.
- Kent, P.E., 1942. The country round the Kavirondo Gulf of Victoria Nyanza. *The Geographic Journal*, 100, 22–31.
- Kordos, L., Begun, D.R., 2001. A new cranium of *Dryopithecus* from Rudabánya, Hungary. *J. Hum. Evol.* 15, 689–700.
- Le Gros Clark, W.E., Leakey, L.S.B., 1950. Diagnoses of East African Miocene Hominoidea. *Quart. J. Geol. Soc. Lond.* 105, 260–263.
- Le Gros Clark, W.E., Leakey, L.S.B., 1951. The Miocene Hominoidea of East Africa. In: *Fossil Mammals of Africa*, No. 1. British Museum (Natural History), London.
- Leakey, L.S.B., 1943. A Miocene anthropoid mandible from Rusinga, Kenya. *Nature* 152, 319–320.
- Leakey, L.S.B., 1963. East African fossil Hominoidea and the classification within this super-family. In: Washburn, S.L. (Ed.), *Classification and Human Evolution*. Aldine, Chicago, pp. 32–49.

Leakey, L.S.B., 1967; Notes on the mammalian faunas from the Miocene and Pleistocene of East Africa.

In Bishop, W. W., Clark, J. D. (Eds.), *Background to Evolution in Africa*. University of Chicago Press, Chicago, pp. 7–29.

Leakey, R.E., Leakey, M.G., 1986. A new Miocene hominoid from Kenya. *Nature* 324, 143–146.

Leakey, R.E., Leakey, M.G., Walker, A.C., 1988. Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. Phys. Anthropol.* 76, 289–307.

Leakey, M.G., Ungar, P.S., Walker, A., 1995. A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. *J. Hum. Evol.* 28, 519–531.

Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines genera, species cum characteribus, differentris, synonymis, locis*, tenth ed. Laurentii Salvii, Stockholm.

MacInnes, D.G., 1943. Notes on the East African Miocene primates. *J. E. Afr. Uganda Nat. Hist. Soc.* 17, 141–181.

MacLatchy, L., 2004. The oldest ape. *Evol. Anthropol.* 13, 90–103.

MacLatchy, L., Rossie, J.B., 2005. The Napak hominoid: still *Proconsul major*. In: Lieberman, D.E., Smith, R.J., Kelley, J. (Eds.), *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*. Brill Academic Publishers, Boston, pp. 15–28.

MacLatchy, L., Bossert, W. H., 1996. An analysis of the articular surface distribution of the femoral head and acetabulum in anthropoids, with implications for hip function in Miocene hominoids. *J. Hum. Evol.* 31, 425–453.

Manser, J., Harrison, T., 1999. Estimates of cranial capacity and encephalization in *Proconsul* and *Turkanapithecus*. *Am. J. Phys. Anthropol.* 110 (Suppl. 28), 189.

Martin, L., 1981. New specimens of *Proconsul* from Koru, Kenya. *J. Hum. Evol.* 10, 139–150.

- McCollum, M.S., Peppe, D.J., McNulty, K.P., Dunsworth, H.M., Harcourt-Smith, W.E.H., Andrews, A.L., 2013. Magnetostratigraphy of the early Miocene Hiwegi Formation (Rusinga Island, Lake Victoria, Kenya). *Geological Society of America Abstracts with Programs*, 45, 12.
- McHenry, H. M., Andrews, P., Corruccini, R. S., 1980. Miocene hominoid palatofacial morphology. *Folia Primatol.* 33, 241–252.
- McNulty, K.P., 2003. Geometric morphometric analyses of extant and fossil hominoid craniofacial morphology. Unpublished PhD Dissertation, City University of New York.
- McNulty, K.P., 2010. Apes and tricksters: the evolution and diversification of humans' closest relatives. *Evol. Edu. Outreach* 3, 322–332.
- McNulty, K.P., Harcourt-Smith, W.E.H., Dunsworth, H.M., 2007. New primate fossils from Rusinga Island, Kenya. *Am. J. Phys. Anthropol.* 132(S44), 170.
- McNulty, K.P., MacLatchy, L., Peppe, D.J., Nengo, I., Manthi, F.K., Miller, E.R., Stevens, N.J., Cote, S., Lehmann, T., Kingston, J., 2014a. A regional approach to East African early Miocene paleobiology. *J. Vert. Paleontol. SVP Program and Abstracts Book*, 2014, 185.
- McNulty, K.P., MacLatchy, L., Rossie, J.B., Peppe, D.J., Deino, A.L., Mbua, E.N., Manthi, F.K., Nengo, I.O., Stevens, N.J., Cote, S., Lehmann, T., Gutiérrez, M., 2014b. Research on east African catarrhine and hominoid evolution: results from the first year. *Am. J. Phys. Anthropol.* 153(S58), 182.
- Michel, L.A., Peppe, D.J., Lutz, J.A., Driese, S.G., Dunsworth, H.M., Harcourt-Smith, W.E.H., Horner, W., Lehmann, T., Nightengale, S., McNulty, K.P. 2014. Remnants of an ancient forest provide ecological context for Early Miocene fossil apes. *Nature Comm.* 5, 3236.
- Myres, J.L., 1932. *Africa. Man* 32, 208.
- Nakatsukasa, M., Kunimatsu, Y., Nakano, Y., Takano, T., Ishida, H., 2007. Vertebral morphology of *Nacholapithecus kerioi* based on KNM-BG 35250. *J. Hum. Evol.* 52, 347–369.

- Napier, J.R., Davis, P. R., 1959. The fore-limb skeleton and associated remains of *Proconsul africanus*. Fossil Mammals Afr. 16, 1–69.
- Peppe, D.J., McNulty, K.P., Cote, S.M., Harcourt-Smith, W.E.H., Dunsworth, H.M., Van Couvering, J.A., 2009. Stratigraphic interpretation of the Kulu Formation (Early Miocene, Rusinga Island, Kenya) and its implications for primate evolution. J. Hum. Evol. 56, 447–461.
- Pickford, M., 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. J. Hum. Evol. 10, 73–97.
- Pickford, M., 1986. Sexual dimorphism in *Proconsul*. Hum. Evol. 1, 111–148.
- Pickford, M., Andrews, P.J., 1981. The Tinderet Miocene sequence in Kenya. J. Hum. Evol. 10, 11–33.
- Pickford, M., Kunimatsu, Y., 2005. Catarrhines from the Middle Miocene (ca. 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. Anthropol. Sci. 113, 189–224.
- Pickford, M., Senut, B., Gommery, D., Musiime, E., 2009. Distinctiveness of *Ugandapithecus* from *Proconsul*. Estudios Geol. 65, 183–241.
- Pilbeam, D.R., 1969. Tertiary Pongidae of East Africa: Evolutionary relationships and taxonomy. Bulletin of the Peabody Museum of Natural History 31, 1–185.
- Rae, T.C., 1993. Phylogenetic analysis of proconsulid facial morphology. Ph.D. Dissertation, State University of New York at Stony Brook.
- Rae, T.C., 1999. Mosaic evolution in the origin of the Hominoidea. Folia Primatol. 70, 125–135.
- Rafferty, K.L., Walker, A., Ruff, C., Rose, M. D., Andrews, P. J., 1995. Postcranial estimates of body weights in *Proconsul*, with a note on a distal tibia of *P. major* from Napak, Uganda. Am. J. Phys. Anthropol. 97, 391–402.
- Rose, M.D., 1983. Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither, or both? In: Ciochon, R. L., Corruccini, R. S. (Eds.), New Interpretations of Ape and Human Ancestry. Plenum Press, New York, pp. 405–420.

- Rose, M.D., 1993. Locomotor anatomy of Miocene hominoids. In Gebo, D.L. (ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 252–272.
- Rose, M.D. 1994. Quadrupedalism in some Miocene catarrhines. *J. Hum. Evol.* 26, 387–411.
- Rossie, J.B., MacLatchy, L., 2013. Dentognathic remains of an *Afropithecus* individual from Kalodirr, Kenya. *J. Hum. Evol.* 65, 199–208.
- Rossie, J.B., Simons, E.L., Gauld, S.C., Rasmussen, D.T., 2002. Paranasal sinus anatomy of *Aegyptopithecus*: Implications for hominoid origins. *Proc. Nat. Acad. Sci. USA* 99, 8454–8456.
- Sanders, W.J., Bodenbender, B.E., 1994. Morphometric analysis of lumbar vertebra UMP 67–28, Implications for spinal function and phylogeny of the Miocene Moroto hominoid. *J. Hum. Evol.* 26, 203–237.
- Senut, B., Pickford, M., Gommery, D., Kunimatsu, Y., 2000. Un nouveau genre d'hominoïde du Miocène inférieur d'Afrique orientale: *Ugandapithecus major* (Le Gros Clark and Leakey, 1950). *C.R. Acad. Sci. Paris* 331, 227–233.
- Simons, E.L., Pilbeam, D.R., 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthropeidea). *Folia Primatol.* 3, 81–152.
- Smith, T.M., Martin, L.B., Leakey, M.G., 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J. Hum. Evol.* 44, 283–306.
- Stevens, N.J., Seiffert, E.R., O'Connor, P.M., Roberts, E.M., Schmitz, M.D., Krause, C., Gorscak, E., Ngasala, S., Hieronymus, T.L., Temu, J., 2013. Palaeontological evidence for an Oligocene divergence between Old World monkeys and apes. *Nature* 497, 611–614.
- Suwa, G., Kono, R.T., Katoh, S., Asfaw, B., Beyene, Y., 2007. A new species of great ape from the late Miocene epoch in Ethiopia. *Nature* 448, 921–924.
- Szalay, F.S., Delson, E., 1979. *Evolutionary History of the Primates*. Academic Press, New York.

- Teaford, M.F., Beard, K.C., Leakey, R.E., Walker, A., 1988. New hominoid facial skeleton from the Early Miocene of Rusinga Island, Kenya, and its bearing on the relationship between *Proconsul nyanzae* and *Proconsul africanus*. *J. Hum. Evol.* 17, 461–477
- Van Couvering, J.A.H., Miller, J., 1969. Miocene stratigraphy and age determinations, Rusinga Island, Kenya. *Nature* 221, 628–632.
- Walker, A., 1997. *Proconsul* function and phylogeny. In: Begun, D.R., Ward, C.V., Rose, M.D. (Eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptation*. Plenum Press, New York, pp. 209–224
- Walker, A., Pickford, M., 1983. New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In: Ciochon, R.L., Corruccini, R.S. (Eds.), *New Interpretations of Ape and Human Ancestry*. Plenum Press, New York, pp. 325–351
- Walker, A., Teaford, M., 1988. The Kaswanga primate site: An Early Miocene hominoid site on Rusinga Island, Kenya. *J. Hum. Evol.* 17, 539–544.
- Walker, A., Teaford, M., 1989. The hunt for *Proconsul*. *Sci. Amer.* 260, 76–82.
- Walker, A., Teaford, M.F., Martin, L., Andrews, P., 1993. A new species of *Proconsul* from the early Miocene of Rusinga/Mfangano Islands, Kenya. *J. Hum. Evol.* 25, 43–56.
- Ward, C. V., Ruff, C.B., Walker, A., Rose, M.D., Teaford, M.F., Nengo, I.O.. 1995. Functional morphology of *Proconsul* patellas from Rusinga Island, Kenya, with implications for other Miocene-Pliocene catarrhines. *J. Hum. Evol.* 29, 1–19.
- Ward, S., B. Brown, A. Hill, J. Kelley, and W. Downs. 1999. *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science* 285, 1382–1386.
- Werdelin, L., Sanders, W.J., 2010. *Cenozoic Mammals of Africa*. University of California Press, Berkeley.
- Whybrow, P.J., Andrews, P., 1978. Restoration of the holotype of *Proconsul nyanzae*. *Folia. Primatol.* 30, 115–125.

Table 1: Identifications of *Proconsul* (sensu lato) species by different authors, listed by region^a.

Authors	Kisingiri localities	Tinderet Localities	Ugandan Localities
Hopwood, 1933	--	<i>P. africanus</i> ^b	--
MacInnes, 1943	<i>P. africanus</i>	<i>P. africanus</i>	--
Le Gros Clark and Leakey, 1950	<i>P. africanus</i> <i>P. nyanzae</i> ^b	<i>P. africanus</i> <i>P. major</i> ^b	--
Andrews, 1978	<i>P. africanus</i> <i>P. nyanzae</i> <i>P. major?</i>	<i>P. africanus</i> <i>P. major</i>	<i>P. major</i>
Bosler, 1981	<i>P. africanus</i> <i>P. nyanzae</i> <i>P. major</i>	<i>P. africanus</i> <i>P. nyanzae</i> <i>P. major</i>	<i>P. major</i>
Kelley, 1986	<i>P. nyanzae</i>	<i>P. africanus</i> <i>P. major</i>	<i>P. major</i>
Pickford, 1986	<i>P. nyanzae</i>	<i>P. africanus</i> <i>P. major</i>	<i>P. major</i>

Walker et al., 1993	<i>P. heseloni</i> ^b	<i>P. africanus</i>	<i>P. major</i>
	<i>P. nyanzae</i>	<i>P. major</i>	
Senut et al., 2000	<i>P. nyanzae</i>	<i>P. africanus</i>	<i>U. major</i>
		<i>U. major</i> ^c	
Harrison and Andrews, 2009 ^d	<i>P. heseloni</i>	<i>P. africanus</i>	<i>P. major</i>
	<i>P. nyanzae</i>	<i>P. major</i>	
		<i>P. meswae</i> ^b	
Pickford et al., 2009	<i>P. heseloni</i>	<i>P. africanus</i>	<i>U. major</i>
	<i>P. nyanzae</i>	<i>U. major</i>	<i>U. legetetensis</i>
		<i>U. legetetensis</i> ^b	<i>U. gitongai</i>
		<i>U. meswae</i> ^c	
This paper ^d	<i>E. heseloni</i> ^c	<i>P. africanus</i>	<i>P. major</i>
	<i>E. nyanzae</i> ^c	<i>P. major</i>	
		<i>P. meswae</i>	

^a Very small samples from other regions (e.g., Buluk) that have been attributed to *Proconsul* (sensu lato) are not included here as they are not critical to understanding the placement of Kisingiri specimens.

^b New genus and/or species named in this publication.

^c Existing species transferred to a new genus.

^d *Proconsul gitongai* from the middle Miocene Muruyur Formation (Kipsaraman) is also recognized, but not at the early Miocene localities assessed in this paper.

Table 2: Dentognathic features that distinguish *Ekembo* from *Proconsul*^a.

Feature	<i>Ekembo</i>	<i>Proconsul</i>
General		
cusp morphology	more bunodont, occupying more of the occlusal surface area	more distinct, individuated cones
molar crests	inflated, incorporated into cusps	sharper, more distinct from cusps
cingulum	reduced	extensive
Upper central incisor		
lingual pillar	narrow, generally low relief	inflated/bulbous
marginal ridges & cingulum	asymmetric with sharply angled cingulum-mesial ridge transition	more symmetric with curving cingulum-mesial ridge transition
Upper canine		
tip	point	blade-like
root fluting	absent	present
root striations	rare and weakly developed	very common and well developed
Upper third premolar^b		
mesiodistal cusp position	crown midpoint	mesial
mesial fovea	well developed	absent or reduced
buccal profile	symmetric	asymmetric

mesial crown margin	straight or slightly curved	notched
distal crown margin	slight to moderately curved	strongly curved
cuspid heteromorphy	reduced	strong
crown shape	converges on P ⁴ shape	distinct from P ⁴
mesiobuccal flange	no	yes

Upper fourth premolar

paracone height	taller relative to crown length	shorter relative to crown length
-----------------	---------------------------------	----------------------------------

Upper second molar^c

occlusal crown shape	squarish	rhomboid
distal margin	straight to slightly curved	strongly curved
buccal cingulum	absent or rudimentary	distinct cingular shelf
distolingual cingulum	merges into hypocone	distinct from hypocone
posthypocone crista	distobuccally to buccally oriented	distally to distobuccally oriented
buccolingual flare	reduced	pronounced

Mandible

planum alveolare	short, vertically inclined	long, more horizontally oriented
superior transverse torus	moderate to well-developed	strongly developed
orientation of subplanum area	more vertically oriented	more posteriorly inclined

corpus robusticity	more gracile	more robust
Lower incisors		
crown shape	narrow relative to height	broad relative to height
Lower canines		
tip	point	blade-like
Lower molars		
buccolingual flare	reduced	pronounced
M ₁ : M ₂ breadth	M ₁ narrower relative to M ₂	M ₁ more similar to M ₂

^a Although presented here as discrete characteristics for descriptive purposes, some of these features are undoubtedly correlated aspects of single evolutionary changes.

^b Nearly all of these features tend to distinguish P⁴s as well, but in that tooth the differences are not as pronounced.

^c These features tend to distinguish M¹s as well, but in that tooth the differences are not as pronounced.

Supplementary table 1: Results of principal component analysis of symphyseal variables.

	Eigenvalue	Proportion		Eigenvector 1	Eigenvector 2	Eigenvector 3
PC 1	155.956751	0.9802	infradentale–gnathion	0.697812	-0.368673	0.614116
PC 2	2 1.824719	0.0115	infradentale–superior torus	0.640912	-0.061452	-0.765151
PC 3	3 1.328915	0.0084	gnathion–superior torus	0.319829	0.927526	0.193405

Figure Legend

Figure 1: Map depicting the major *Proconsul* localities. Early Miocene localities clustering around the Tinderet volcano include Koru, Legetet Hill, Chamtwara, Meswa Bridge, Songhor, Kapurtay, and Mteitei Valley. The middle Miocene type locality of *P. gitongai* is not shown here.

Figure 2: Upper central incisors of *Proconsul* and *Ekembo*. Lingual views of *Ekembo* (KNM-RU 1685, cast), left and *Proconsul* (KNM-CA 1300), right. Note the differences in the transition between the lingual cingulum and the mesial marginal ridge, which is more rounded in *Proconsul* and more angled in *Ekembo*. The central pillar is also more bulbous or inflated and without ridging in *Proconsul*. Additional specimens illustrating the *Proconsul* morphology are shown in Pickford et al. (2009; figure 17, page 197), but referred in that manuscript to *Ugandapithecus*.

Figure 3: Canines of *Proconsul* and *Ekembo*: a) Upper canine of the *P. africanus* holotype (M 14084), lingual view; b) Upper canine of *P. major* (KNM-CA 2127), lingual view, c) Lower canine of *P. major*, buccal view, d) lower canine of *Ekembo* cf. *nyanzae* (KNM-RU 1676), buccal view; and, e) Upper canine of *P. major* (KNM-SO 584), distal view. Note the blade-like or “burin-like” tip of the unworn *Proconsul* canines, including on the nearly unworn canine tip of the *P. africanus* type specimen (a). *Ekembo* canines have more typical pointed tips. *Proconsul* canines also have longitudinal grooves and fine striations on the root (e); *Ekembo* lacks these features. Scale bars = 1cm.

Figure 4: Upper premolars of *Proconsul* and *Ekembo*, occlusal (a-c) and lingual (d-f) views: a) P³⁻⁴ of the *P. africanus* holotype (M 14084); b) P³ of *P. major* (M 14331); c) P³⁻⁴ of the *E. heseloni* holotype (KNM-RU 2036); d) P³ of the *P. africanus* holotype (M 14084); e) P³ of *P. major* (M 14331); f) P³ of the *E. heseloni*

holotype (KNM-RU 2036). Note the mesially positioned cusps, lack of mesial fovea, and strongly asymmetric crown in *Proconsul* compared to *Ekembo* (see text for further comparisons). Image of M14331 reversed for easier comparison. Photo 4a courtesy of Rutger Jansma. Scale bars = 1cm.

Figure 5: Box-and-whisker plots. a) P^3 cusp heteromorphy index (protocone height / paracone height). Results of a t-test show this difference to be significant ($p = 0.0165$). The *Ekembo* outlier, KNM-RU 1677, only appears to have extreme heteromorphy because of extensive expansion of the buccal enamel onto the anterior root (see text). b) P^4 relative paracone height (paracone height / mesiodistal crown length). Results of a t-test show this difference to be significant ($p = 0.0069$).

Figure 6: Occlusal view of the M^2 s of *Proconsul* and *Ekembo*. Left, *P. africanus* holotype (M 14084). Right, *E. heseloni* holotype (KNM-RU 2036). Note in *Proconsul* the overall difference in crown shape as well as the more conical, individuated cusps and narrower cristae, strongly developed lingual cingulum that continues to the distal aspect of the crown, broad buccal cingular shelf, and more distally directed posthypocone crista. In *Ekembo* the cusps are more bunodont and expanded, the cristae are broader with better developed accessory tubercles, the lingual cingulum merges into the hypocone, there is no buccal shelf, and the posthypocone crista is more buccally directed.

Figure 7: Scatter plot depicting the degree of buccolingual flare in M^2 .

Figure 8: Mandibles of *Proconsul* and *Ekembo*. Occlusal views of *P. major*: a) KNM-SO 396; b) KNM-SO 404; c) KNM-LG 452. Occlusal views of *Ekembo*: d) KNM-RU 2087; e) KNM-RU 1674; f) KNM-RU 7290. Occlusal views of *P. africanus*: g) KNM-SO 372; h) KNM-SO 1112. i) Lingual view of *P. africanus* (KNM-SO

1112. Note the long, more horizontally oriented planum alveolar in *Proconsul*, resulting in a pronounced superior transverse torus. The planum alveolar is shorter and more vertical in *Ekembo* such that one can see the inferior mandibular border from occlusal view.

Figure 9: Line drawing of a hemimandible depicting different orientations of the subplanum area in *Ekembo* and *Proconsul*. Females are denoted using shorter vectors, males with longer vectors. Vector is estimated in M 14086, which is broken at the midline. *Ekembo* specimens have a more vertical subplanum compared to those from Songhor and Legetet, but within both groups females have more vertically oriented regions than males. Hence, even the most ventrally rotated subplanum in the largest *Ekembo* male specimen (KNM-RU 47805) groups with the Tinderet females in this feature.

Figure 10: Scatter plot of principal component scores based on an eigenanalysis of three variables: symphyseal height (infradentale–gnathion), planum alveolare length (most posterior point on the superior transverse torus–infradentale), and subplanum length (most posterior point on the superior transverse torus–gnathion). The first component primarily captures size differences among specimens (Jolicouer, 1963; see text and Supplementary Table 1), and thus PC 2 and PC 3 illustrate the residual shape variance (72% and 28%, respectively) in the symphyseal variables.

Figure 11: Scatterplot showing mandibular corpus robusticity under P_4 . Trendlines were computed using ordinary least squares (OLS) regression. Similar relationships are observable at other parts of the corpus, but differential preservation results in smaller samples at those positions. Slopes are significantly different ($p < 0.0001$, tested on logged variables).

Figure 12: Scatter plot of lower incisor crown proportions. Differences between *Ekembo* and *Proconsul* are significant ($p = 0.0242$).

Figure 13: Box-and-whisker plot of buccolingual flare in lower molars, measured as the average distance between the mesial buccal and lingual cusps divided by overall buccolingual crown breadth. Differences between *Ekembo* and *Proconsul* are highly significant ($p < 0.0001$).

Figure 14: Relative buccolingual dimensions of M_1 and M_2 . KNM-SO 1112 has a preserved M_2 but only the cervix of M_1 . Its M_1 breadth was estimated based on the ratio to cervix breadth to maximum crown breadth in other Tindret fossils. Even the cervical breadth of SO 1112 is broader than would be predicted for the crown breadth of a Kisingiri M_1 . Trend lines computed using OLS regression and using the average estimate of SO 1112 M_1 breadth. Group differences were significant ($p = 0.0002$).

Figure 1
[Click here to download high resolution image](#)



Figure 2
[Click here to download high resolution image](#)



Figure 3
[Click here to download high resolution image](#)

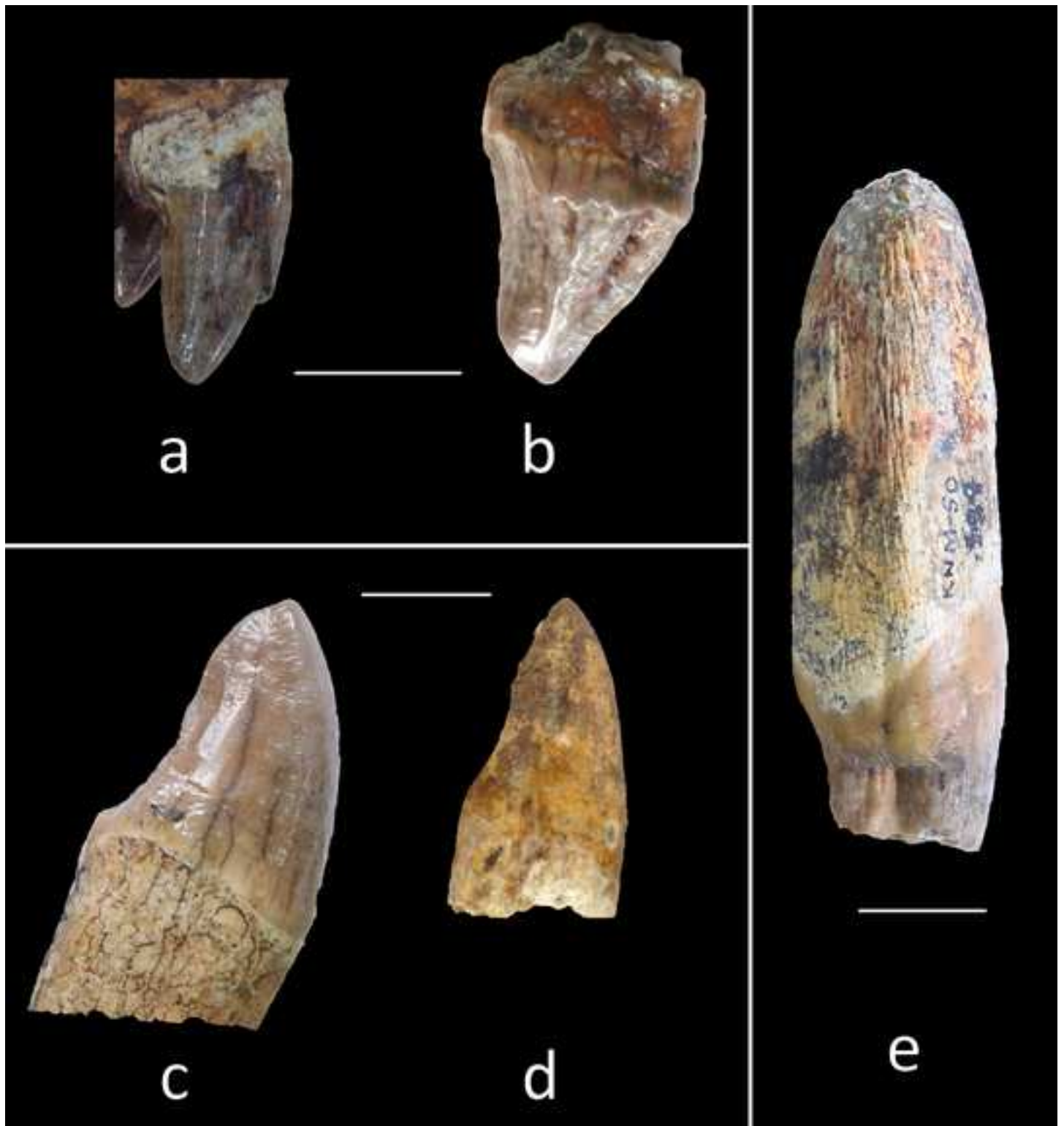


Figure 4
[Click here to download high resolution image](#)

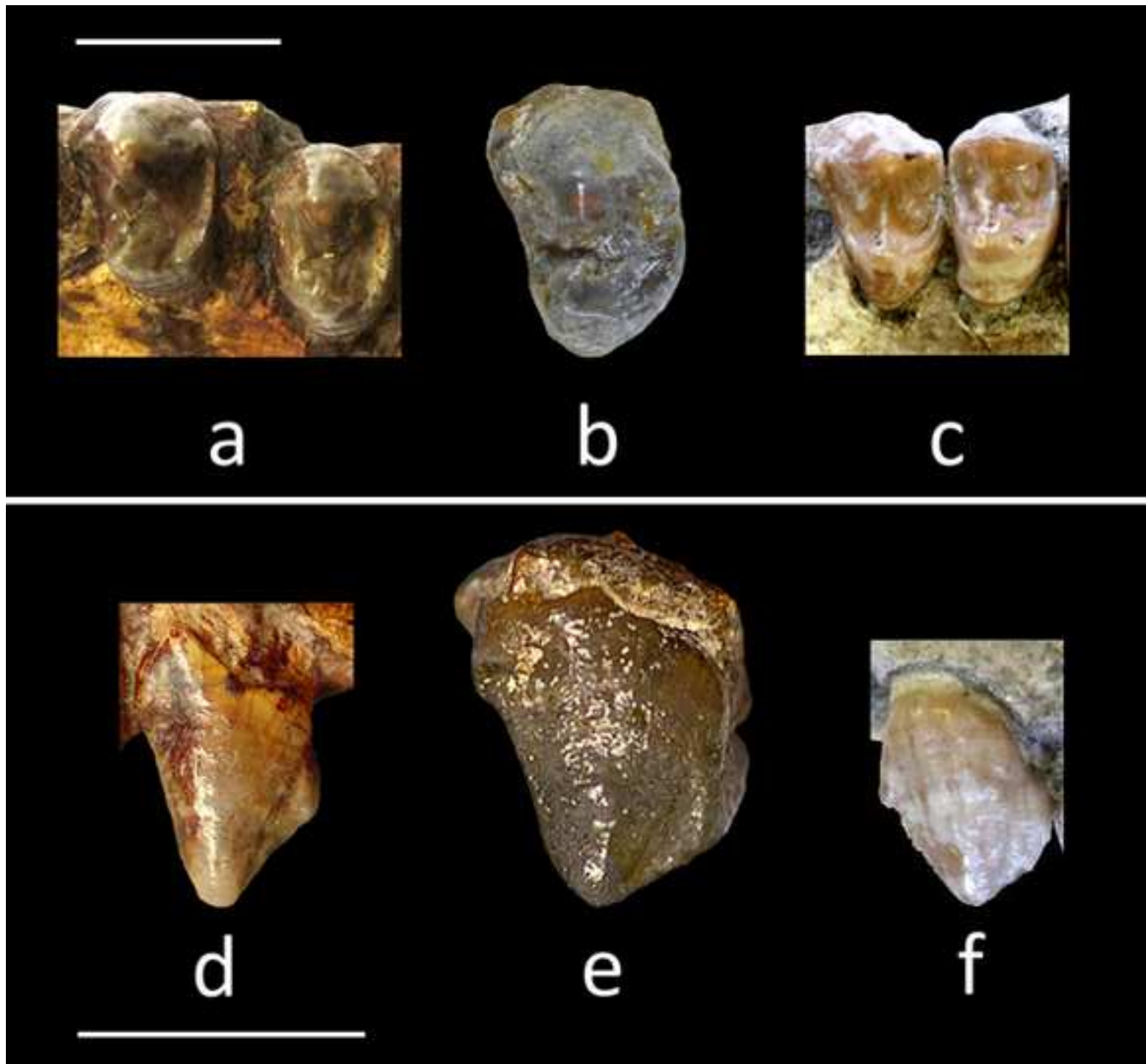


Figure 5
[Click here to download high resolution image](#)

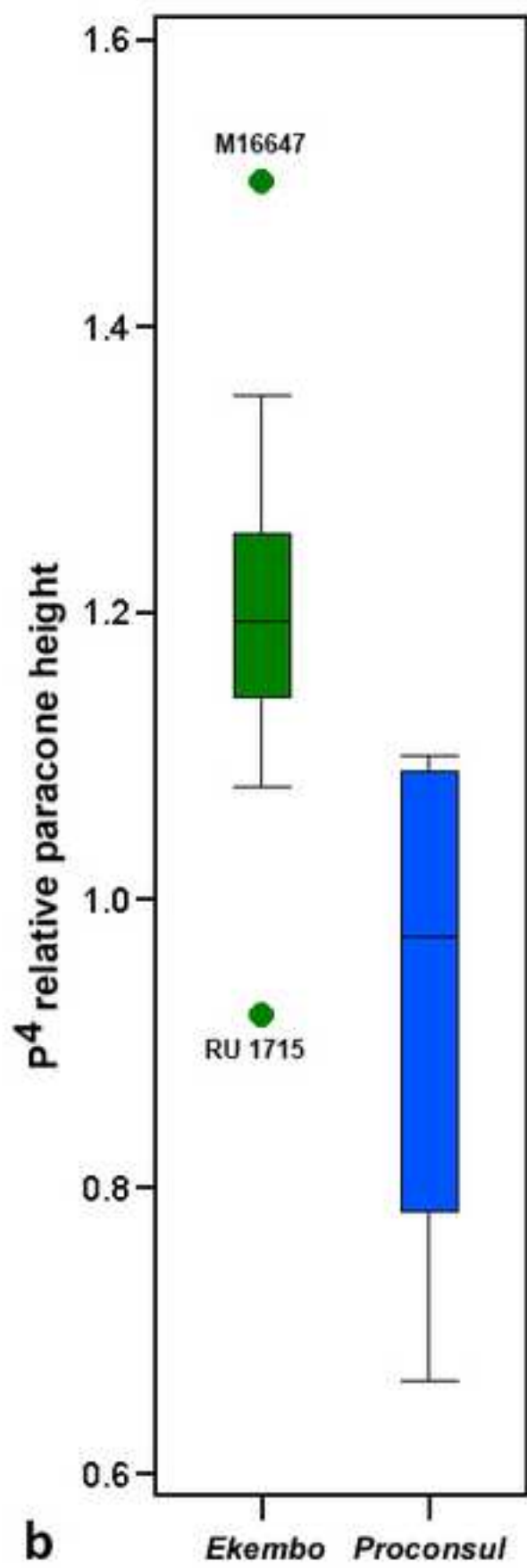
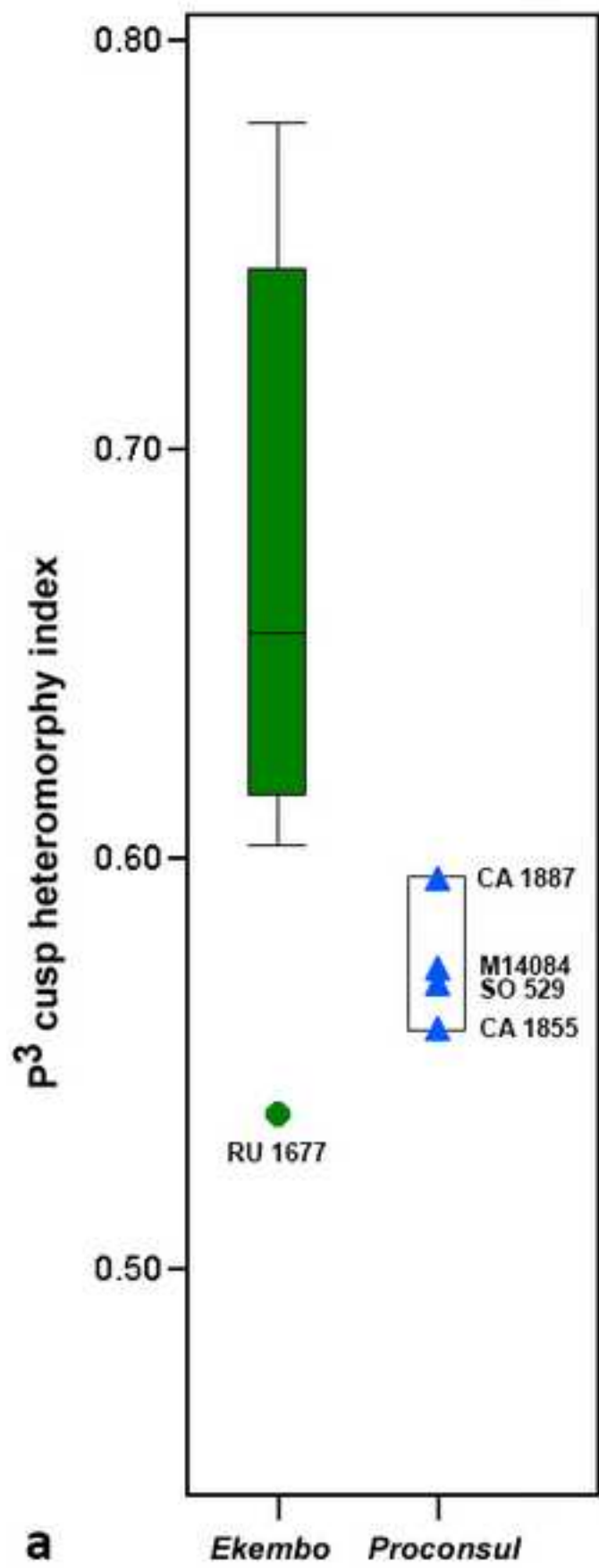


Figure 6
[Click here to download high resolution image](#)

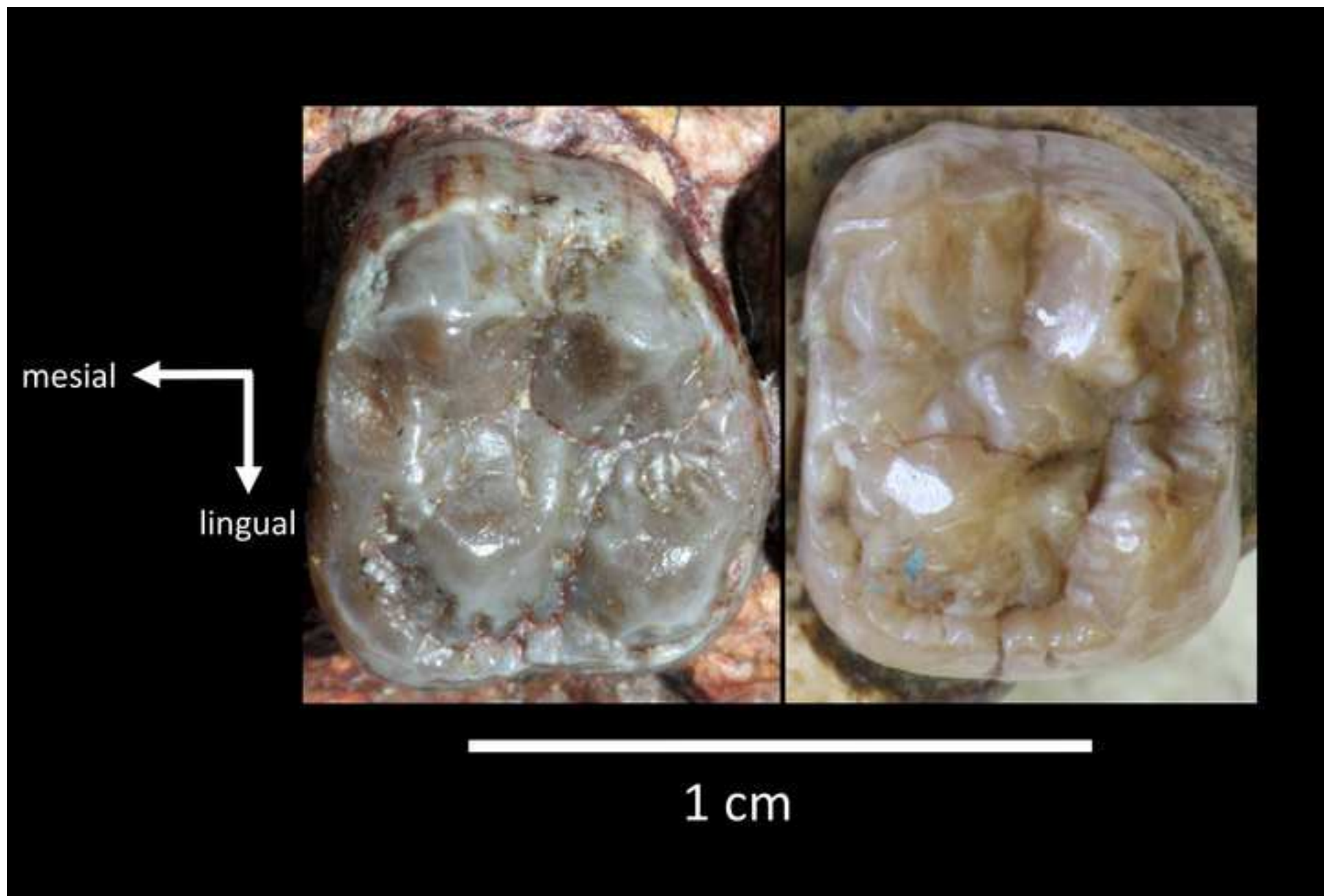


Figure 7
[Click here to download high resolution image](#)

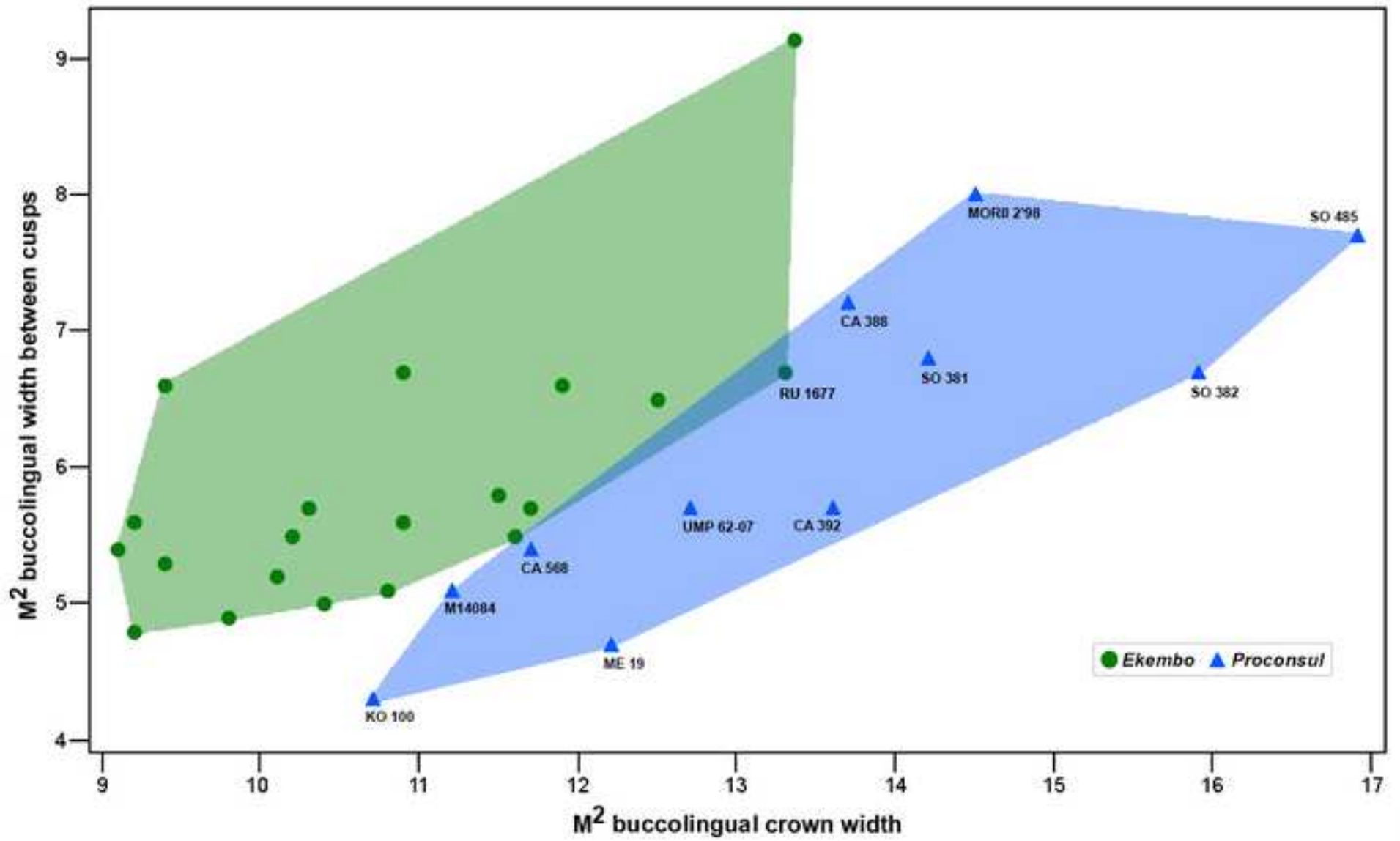


Figure 8
[Click here to download high resolution image](#)

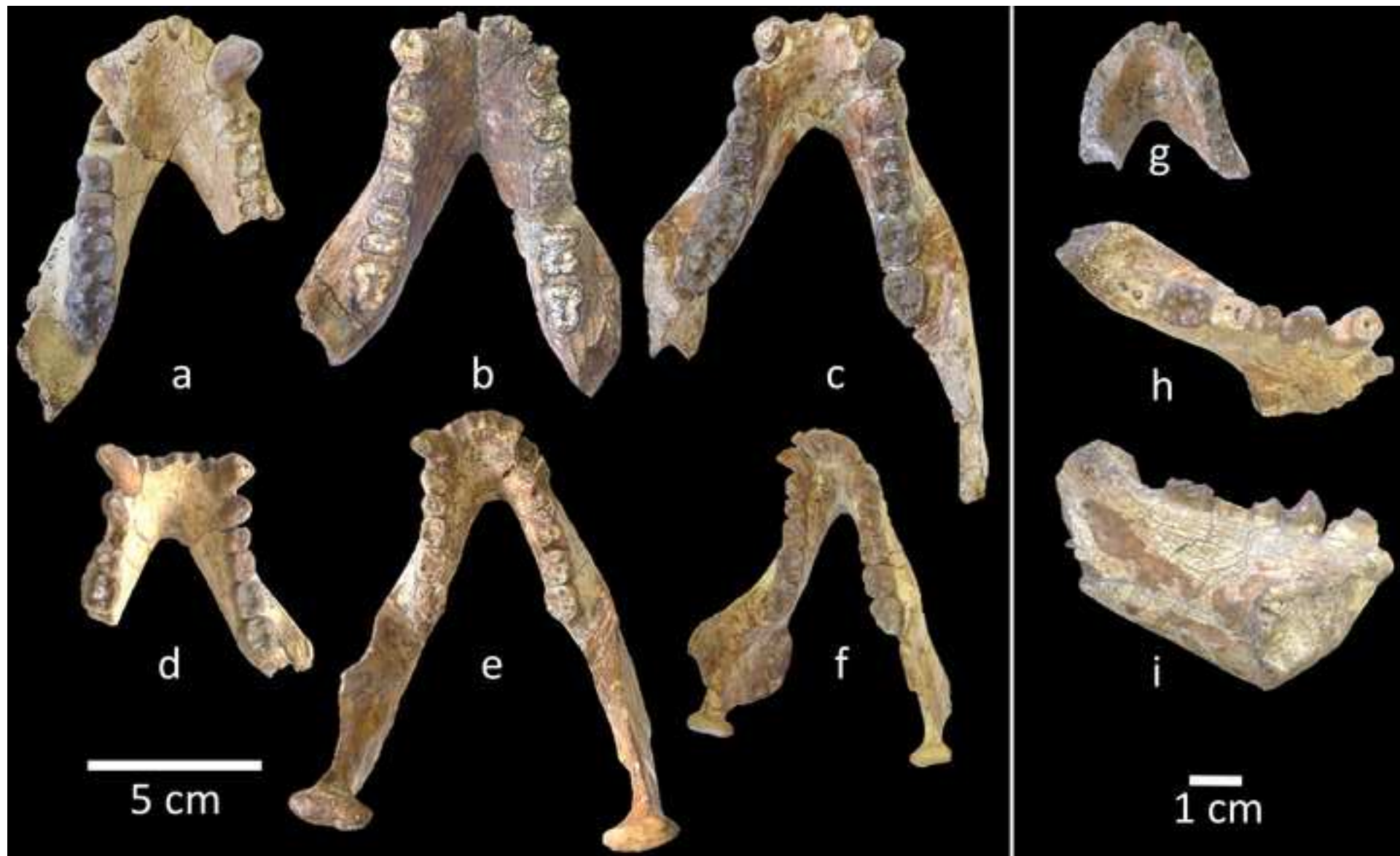


Figure 9
[Click here to download high resolution image](#)

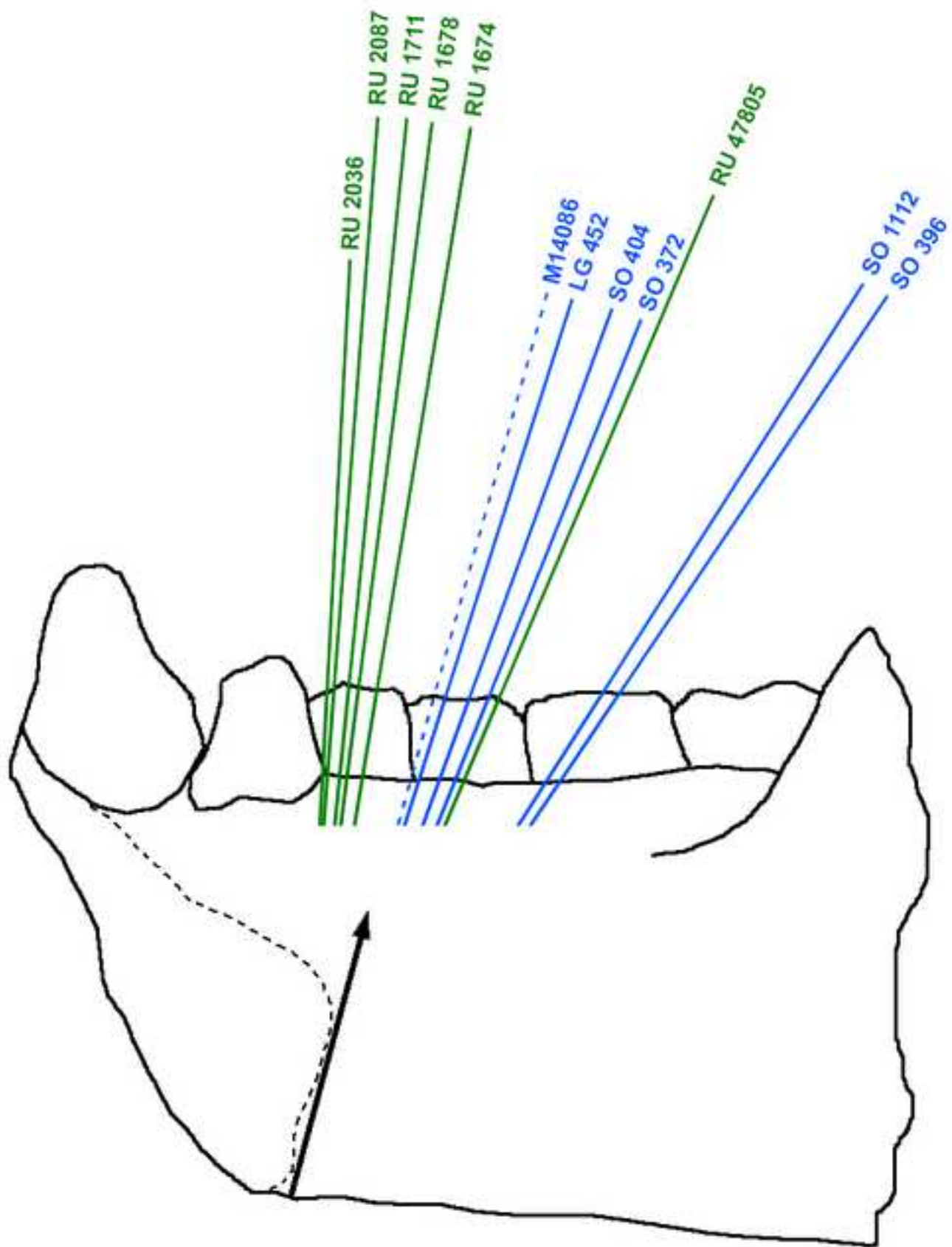


Figure 10
[Click here to download high resolution image](#)

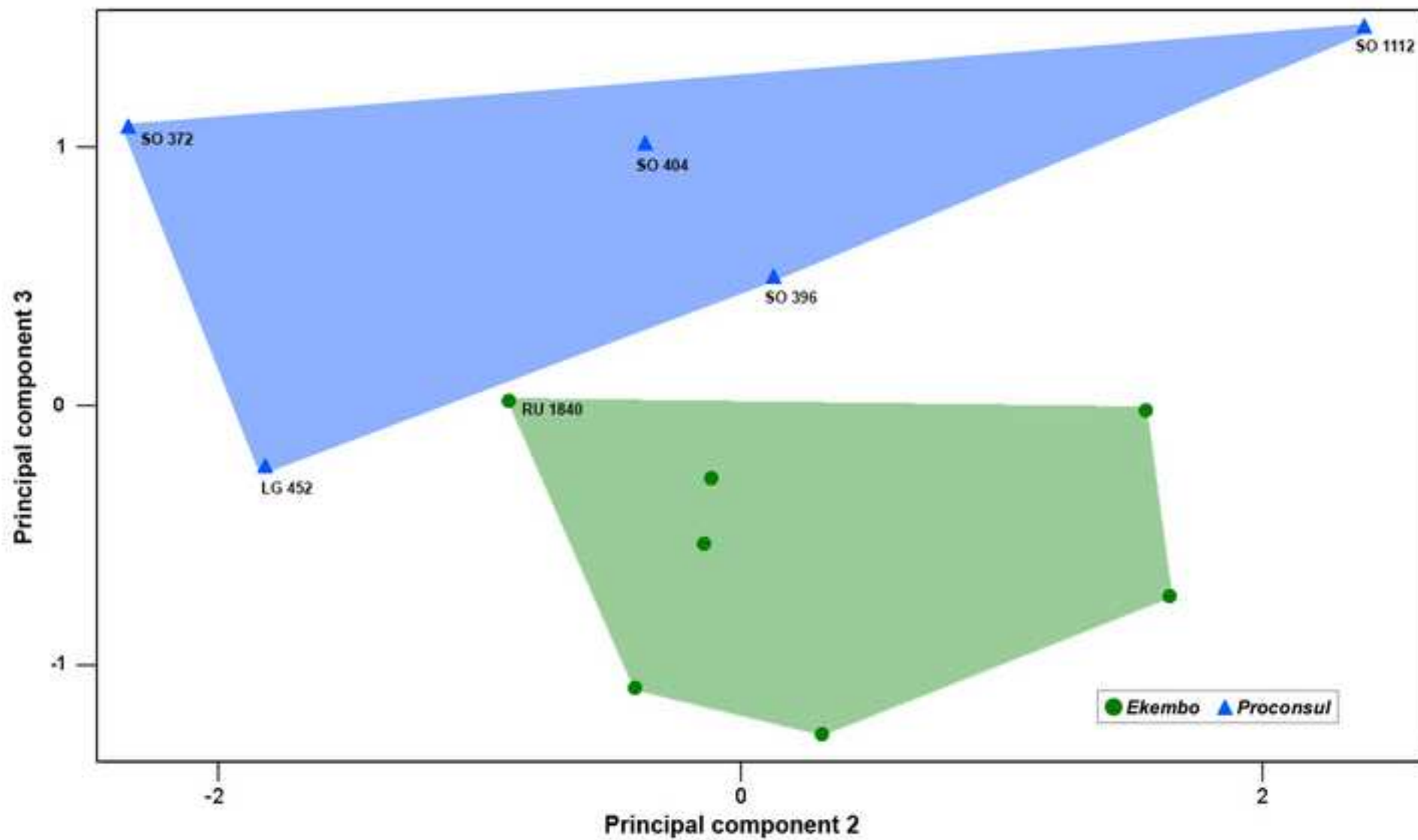


Figure 11
[Click here to download high resolution image](#)

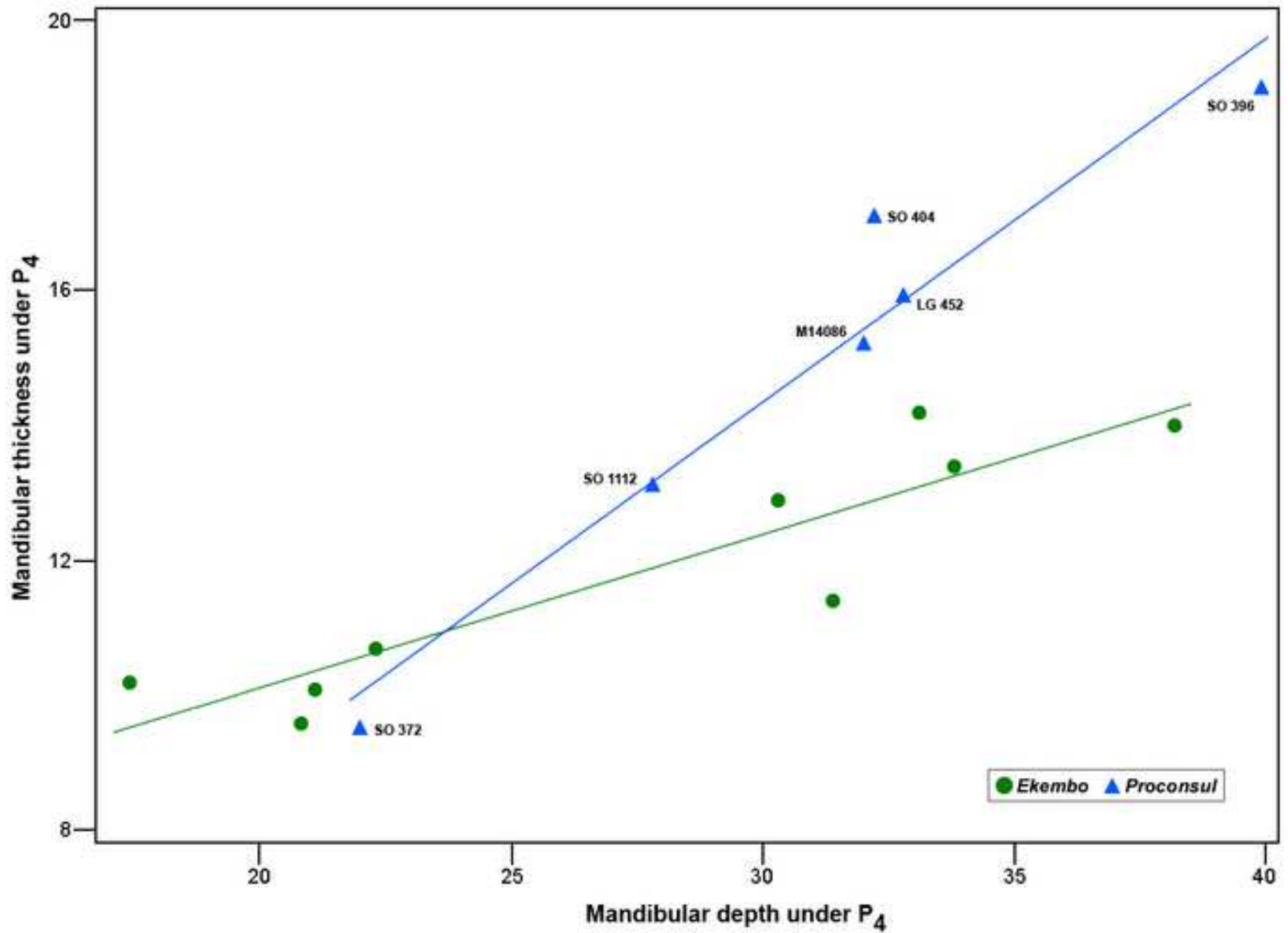


Figure 12
[Click here to download high resolution image](#)

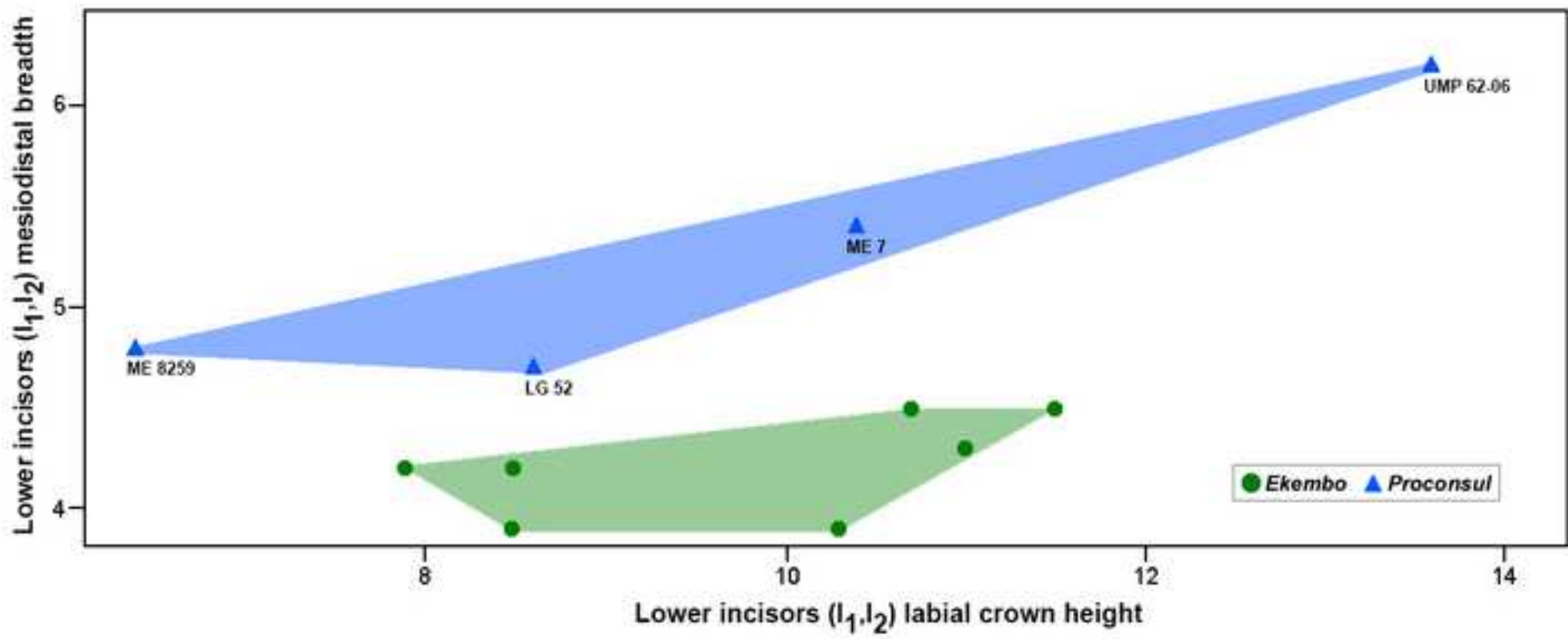


Figure 13

[Click here to download high resolution image](#)

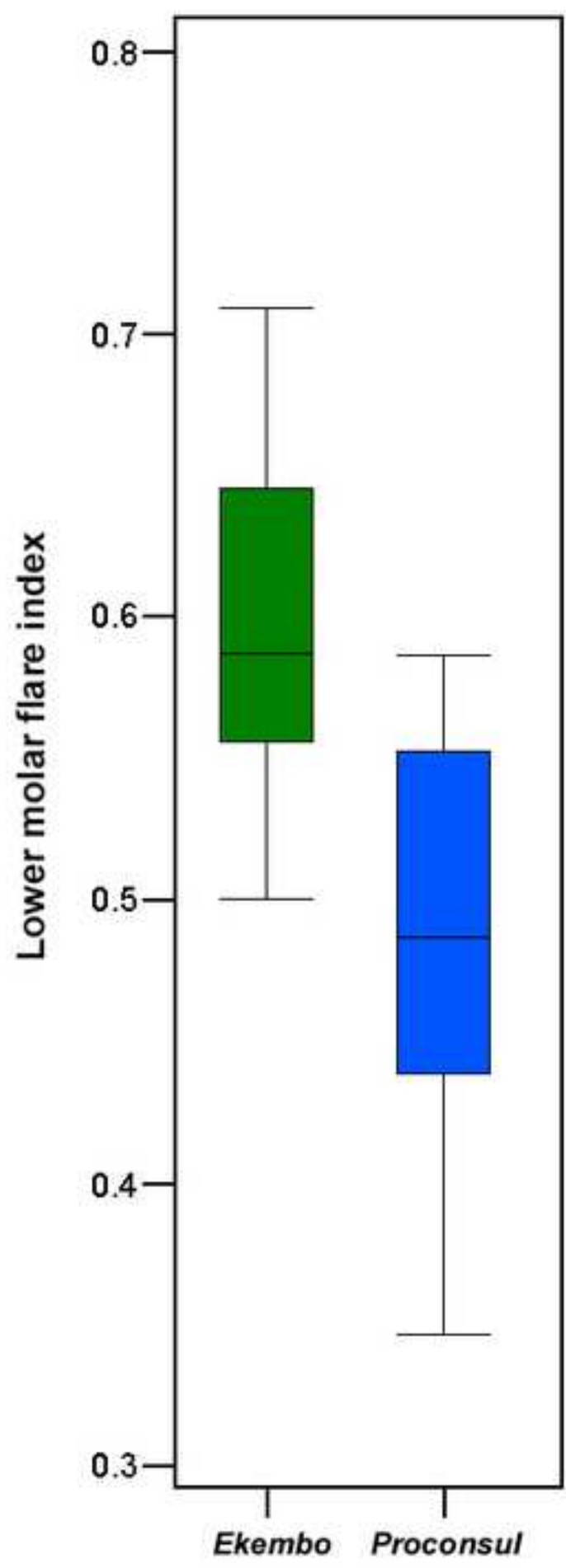


Figure 14
[Click here to download high resolution image](#)

