The Alpha-Taxonomy of *Ekembo*

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submitted: 13 January 2025; revised 25 March 2025; accepted: 26 March 2025

Handling Editor in Chief: Katerina Harvati

ABSTRACT

Two species of the early ape *Ekembo* are typically recognized in the abundant fossil collections from Rusinga and Mfangano Islands: *Ekembo heseloni* and *Ekembo nyanzae*. Widespread perception that these samples represent an anatomically similar, large and small species pair has led to the unrealistic situation where morphologically female canines were assigned almost exclusively to the 'smaller' species and morphologically male canines to the 'larger' species. This unlikely distribution, combined with discoveries of new specimens over the last 18 years, necessitates a reassessment of the alpha-taxonomy in *Ekembo*. We present revised species diagnoses and specimen allocations of the *Ekembo* sample based on observed and measured craniodental differences that are size-independent. Results of our specimen sorting demonstrate that *Ekembo heseloni* and *Ekembo nyanzae* are craniodentally distinct but overlap substantially in size; *Ekembo nyanzae* is, on average, only modestly larger than *Ekembo heseloni*. Contrary to most previous studies, we place KNM-RU 7290 in *Ekembo nyanzae* and KNM-RU 16000 in *Ekembo heseloni*. The new distribution of specimens also confirms that both species were present at all major collecting areas on Rusinga, rejecting the hypothesis that one species replaced the other over time, and suggests that *Ekembo heseloni* and *Ekembo nyanzae* were similarly abundant and had comparable degrees of sexual dimorphism.

INTRODUCTION

Early Miocene deposits associated with the Kisingiri volcano in western Kenya preserve some of the most important fossil assemblages for understanding floral and faunal transformations in eastern Africa during the early Neogene. Of particular interest to paleoanthropologists is the well-known, medium- to large-sized (cf. Rafferty et al. 1995; Ruff 1989, 2003) early ape *Ekembo* McNulty et al., 2015, previously considered to be part of *Proconsul* Hopwood, 1933. Viewed at the generic level, the combined species sample provides a wealth of information on cranial, mandibular, dental, axial, and appendicular skeletal traits, and constitutes an extensive resource for extracting data on dietary ecology, functional anatomy, and life history. Likewise, its association with large faunal community assemblages (e.g., Michel et al. 2014; 2020; Pickford 1984), proximity to extensive floral remains (e.g., Baumgartner and Peppe 2021; Maxbauer et al. 2013), and age range from ~20–17 Ma (Peppe et al. 2017) make *Ekembo* a prominent figure in evolutionary hypotheses concerning the origin and early diversification of Hominoidea. However, fewer studies have focused on comparisons between the two recognized species, *Ekembo nyanzae* (Le Gros Clark and Leakey, 1950) and *Ekembo heseloni* (Walker et al., 1993).

The most significant obstacle to such comparisons is the lack of a robust alpha-taxonomy that clearly defines each species and allocates specimens according to those definitions. Andrews (1978), in his review of Early Miocene primates of western Kenya, produced the most recent comprehensive alpha-taxonomy that included both diagnoses and hypodigms for *Proconsul nyanzae* (now *E. nyanzae*), exclusively from Rusinga and Mfangano, and for a broadly

conceived *Proconsul africanus* Hopwood, 1933 that encompassed specimens from Koru and Songhor as well as Rusinga and Mfangano. However, when *P. africanus* samples from Rusinga/Mfangano were later transferred to a new species, *Proconsul heseloni* (now *E. heseloni*), those two species were formally contrasted but the distinction between *E. heseloni* and *E. nyanzae*—thought to be a morphologically-similar, size-differentiated species pair—was left unchanged except with regard to three specimens with intermediate anatomy (Walker et al. 1993). Harrison's (2002, 2010) thorough reviews of eastern African fossil catarrhines provided detailed and updated descriptions of *E. heseloni* and *E. nyanzae* but did not allocate individual specimens to species hypodigms; he too specified size as the primary distinction between the species but also identified several craniodental differences. Conversely, the taxonomic revision of *Proconsul* and '*Ugandapithecus*' by Pickford et al. (2009) included allocations for the Rusinga/Mfangano fossils that, in some cases, differed from previous assignments, but the publication did not formally specify anatomical criteria for making those assignments. Finally, McNulty et al. (2015) removed Rusinga/Mfangano specimens from *Proconsul* into *Ekembo* but did not further elaborate on species assignments in the latter genus.

Thus, there is no single recent assessment of species of *Ekembo* that both identifies differences between them and explicitly allocates specimens according to those differences. This lack, combined with the recent transfer of both species to *Ekembo* by McNulty et al. (2015) and the discovery of new specimens in the last 17 years of fieldwork, makes necessary a revision of the alpha-taxonomy of *Ekembo* and reconsideration of the evidence for assigning specimens to either *E. heseloni* or *E. nyanzae*.

ONE OR TWO SPECIES?

Historically, the number of *Ekembo* species recognized on Rusinga and Mfangano has been contentious. Whereas the first-discovered Kisingiri specimens were referred by MacInnes (1943) to the Tinderet species *P. africanus*, considerable variation in size within the growing sample led Le Gros Clark and Leakey (1950) to name a second, larger species: *P. nyanzae*. Setting aside a few outlier specimens (cf. Andrews 1978; Bosler 1981; McNulty 2019; McNulty et al. 2015; Pickford et al. 2010), the consensus view has been that the medium- to large-bodied hominoid fossils from Rusinga/Mfangano comprise two congeneric species.

Kelley (1986; Kelley and Pilbeam 1986), however, argued strongly against this position based on the skewed distribution of male and female canines in the two-species model. Both Greenfield (1972, 1973) and Bosler (1981) had noted biased sex distributions for species of *Proconsul*, but especially problematic was that all canines referred to *P. africanus* were morphologically female whereas those referred to *P. nyanzae* appeared to be exclusively male (Kelley 1986). This distribution seemed improbable given the large samples from Rusinga (see also Pickford et al. 2009), and hence Kelley (1986) proposed that the entire Kisingiri *Proconsul* sample comprised a single, highly size-dimorphic and metrically variable species, *P. nyanzae*, relegating *P. africanus* to the Tinderet sites. Pickford (1986) made similar arguments based on distributions of anatomical measurements, skewed canine sex ratios, and the distinct morphology of '*P. africanus*' from Rusinga compared to specimens from Tinderet sites. This single-species scheme created a more realistic distribution of male and female specimens but also resulted in *P. nyanzae* harboring more variation than is found in modern ape species (Kelley 1986).

New discoveries in the 1980s, particularly of additional postcranial material, added support for the presence of two species (Rafferty et al. 1995; Ruff et al. 1989; Teaford et al. 1988; 1993; Walker et al. 1993; Ward et al. 1993), but did not result in consensus as to how to differentiate them or to allocate specimens. Some advocated for the traditional scheme of one large and one small species, with the size difference between them perhaps exceeding 3:1 based on estimates from limb long bones (Rafferty et al. 1995; Ruff et al. 1989). Others suggested, again based on postcranial remains, that the two species did overlap in size, with *P. heseloni* being smaller on average (e.g., Begun et al. 1994). A fairly complete facial skeleton, KNM-RU 16000, proved difficult to reconcile with either two-species scenario, however; its large canine alveoli suggest crowns within the range of a large *P. nyanzae* whereas its molars are more consistent with a smaller *P. heseloni* (Teaford et al. 1988; Walker et al. 1993). The decision to refer KNM-RU 16000 to *P. nyanzae* was appropriately cautious (Walker et al. 1993), and discussion around this point highlighted the complexities in distinguishing the two species. Ultimately, the many discoveries in the 1980s helped underscore the conclusion arrived at previously by Kelley (1986) and Pickford (1986), that '*Proconsul*' from Rusinga and Mfangano differs from *Proconsul* species found elsewhere (cf. McNulty et al. 2015).

Despite consensus having been achieved concerning the number of species on Rusinga and Mfangano, the problem of improbable canine distributions persists (but see Pickford et al. 2009 for alternative specimen allocations). Likewise, lack of a meaningful diagnosis of *E. heseloni* with respect to *E. nyanzae,* including revised specimen allocations, hinders paleobiological comparisons between these species. Here, we present emended diagnoses of both species based on descriptive and quantitative assessments of their cranial and dentognathic anatomy, and we use these to generate new species hypodigms. Nevertheless, many specimens have been left unassigned to species because we could not identify reliable species-specific anatomy in every element. Importantly, this applies to all postcranial specimens apart from those associated with assignable craniodental remains (e.g., the KNM-RU 2036 skeleton). Our new diagnoses and hypodigms result in characterizations of the two species of *Ekembo* that improve knowledge of the nature of similarities and differences between them.

MATERIALS AND METHODS

The study sample comprised all cranial, mandibular, and permanent dental specimens from the Kisingiri complex of localities (Rusinga Island, Mfangano Island, Karungu, and

Uyoma Peninsula) previously referred to *Proconsul* and later transferred to *Ekembo* (McNulty et al. 2015). Qualitative comparisons from all authors, and measurements taken by one of us (KPM) using digital sliding calipers, were based on original specimens housed at the National Museums of Kenya and the Natural History Museum (London). Measurements included standard mesiodistal lengths and labiolingual or buccolingual breadths for all non-canine crowns. Following Kelley (1986), canine lengths were measured as the longest basal axis of the crown, and breadths as the basal axis perpendicular to the longest axis. Root lengths were measured from the tip of the root to the base of the cementoenamel junction on the buccal surface. Mandibular corpus depth was measured at different tooth positions under the mesiodistal midpoint of the crown when viewed from the external surface; mandibular corpus thickness was measured at the broadest point of the corpus directly beneath that same mesiodistal crown midpoint. Some additional measurements were taken on specific teeth, as described in the appropriate sections below. Broken specimens were not measured, and we did not adjust measurements for interproximal wear. A few characteristics (e.g., incisor root lengths, extra- and retro-molar spaces) that could be reliably observed but, due to breakage, not precisely measured in most specimens, were assessed only qualitatively.

Species assignments were undertaken by sorting specimens into groups, element-by-element, beginning with the holotypes: NHMUK-P-M 16647 (*E. nyanzae*) and KNM-RU 2036 (*E. heseloni*). Lack of a mandible associated with NHMUK-P-M 16647 complicated the assignment of mandibles and lower dentition but associated cranial elements and mandibles in KNM-RU 2036 and especially KNM-RU 7290 provided a means by which lower teeth and jaws could also be assigned. Elements that could be differentiated into two morphological groups were assigned to species by linking at least one constituent of one group back to a holotype.

Sorting based on qualitative anatomical features upon which all three authors agreed resulted in lists of distinguishing characteristics by which primary assignments were made. Characteristics that were viewed by at least one author as variable within a group to the point of overlapping with the other group were not used to make species assignments. Thus, qualitative traits distinguishing *E. heseloni* from *E. nyanzae* in this study are consistent within our hypodigms. We recognize that closely related species might differ in proportions of trait presence/absence rather than exhibiting only a single character state, but such differences are not reliable for assigning unknown specimens to species and therefore were not evaluated in this study. Incomplete specimens were assigned to species as long as they preserve at least one of the anatomical features identified by us as diagnostic.

Once specimens were sorted into groups based on qualitative anatomy, concordant quantitative features were identified and used to support and augment species assignments. These measurements allowed us to assign a small number of additional specimens, but we did so only in cases where the specimen fell within the range of variation in one species and beyond the 95% prediction interval for the other species. This conservative statistical criterion constitutes a population-based approach and reflects appropriate uncertainty in the true ranges of variation of two closely related species; it resulted in fewer allocations of isolated teeth but also greater confidence in the assignments that were made. In no case did assigning additional specimens in this manner result in a different statistical conclusion from the larger samples. Specimens that could not be assigned to *E. nyanzae* or *E. heseloni* were referred to genus (e.g., *Ekembo* sp.) or to higher-order taxa, pending future discoveries and analyses.

Sex was assigned to specimens based initially on canine qualitative characteristics described by Kelley (1986, 1995). Specifically, female canines are absolutely lower crowned but also lower crowned relative to basal crown dimensions, giving them a more blunt appearance compared to male canines. In female upper canines, the maximum length dimension of the crown at the cervix is typically greater than that of the root measured along the same axis, resulting in apparent bulging of the crown at the cervix. In males, these dimensions are equal or nearly equal, leading to a smooth transition across the cementoenamel junction. Lastly, relative to crown height, female lower canines typically have a relatively shorter mesiolingual ridge than males measured from the crown tip to the intersection of the ridge with the lingual cingulum. Following a final sorting of specimens into species groups, some additional specimens lacking associated canines were assigned to sex based on the distributions of specimens that had been reliably sexed using canines. We left unassigned those specimens near the overlap in size ranges between male and female specimens. Sexual dimorphism was assessed as a composite of dental dimorphism, calculated simply as the average of ratios of mean male tooth crown lengths and breadths to corresponding mean female tooth crown lengths and breadths. However, only specimens that could be reliably assigned to sex based on association with a canine were included in estimates of dimorphism, since size sorting will overestimate differences between means of groups when there is any overlap in ranges.

Body mass estimates (X) were calculated from length-times-breadth approximations of planar occlusal areas (Y) according to the equation $X=aY^b$ and based on regressions in Gingerich et al. (1982) which, unlike other published equations, allow estimates from every tooth position—a useful feature for differentially preserved fossil hypodigms. Calculations were done separately for each sex in upper and lower first and second molars. We recognize the limitations and sources of error in this approach (cf. Yapuncich 2018), and we caution readers to consider these estimates indicators of relative differences. Postcranial joint surfaces are better predictors of body mass (see, e.g., Ruff et al. 1989 and references therein), but the scarcity of *Ekembo* postcranial remains that can be confidently assigned to species makes joint surfaces of little utility to assess interspecific

differences. Estimates computed here, therefore, provide a characterization of the magnitude of body size differences between the species and sexes, and a useful comparison with estimates computed from postcrania, which better characterize size estimates for the genus as a whole, if not currently for the two included species (e.g., Rafferty et al. 1995; Ruff et al. 1989).

Most statistical results were obtained using SAS/STAT software v. 9.4 of the SAS System for Windows (SAS Institute Inc., Cary) with an alpha-value of 0.05 to arbitrate significance. Summary statistics were computed for both species using PROC MEANS and include mean, median, standard deviation, minimum, maximum, and range; summary statistics for canines were computed separately for male and female specimens. Differences between *E. heseloni* and *E. nyanzae* in many variables (see below) were tested using Welch's (1938) unequal variances t-test, implemented using PROC TTEST, because samples were too small to reliably determine whether variances in dimensions were equivalent. Prediction intervals were computed using PROC REG. Bivariate plots were generated using PROC GPLOT, output as pdf files, and opened in Adobe Photoshop to modify axis labels and to create figure legends. Specimen photos were also modified in Photoshop to remove backgrounds. Mandibular depth and thickness plots were generated using PROC GPLOT but modified more extensively in Photoshop to create specimen profiles, semi-transparent hulls, labels and other formatting edits. Estimates of body mass and sexual dimorphism were computed in Microsoft Excel (Excel for Office 365).

SYSTEMATIC PALEONTOLOGY

ORDER Primates Linnaeus, 1758
INFRAORDER Catarrhini É. Geoffroy Saint-Hilaire, 1812
SUPERFAMILY Hominoidea Gray, 1825
FAMILY incertae sedis
GENUS *Ekembo* McNulty et al., 2015
SPECIES *Ekembo nyanzae* (Le Gros Clark and Leakey, 1950)

Synonymy

1933: *Proconsul africanus* Hopwood: Plate 6, Figures 5, 6 (partim).

1950: *Proconsul nyanzae* Le Gros Clark and Leakey (original description).

1965: *Dryopithecus* (*Proconsul*) *nyanzae* (Le Gros Clark and Leakey, 1950); Simons and Pilbeam (new combination).

1978: *Proconsul* (*Proconsul*) *nyanzae* (Le Gros Clark and Leakey, 1950); Andrews (new combination).

2015: *Ekembo nyanzae* (Le Gros Clark and Leakey, 1950); McNulty et al. (new combination).

Type Specimen

NHMUK-P-M 16647, palate and rostrum with right P^3–M^3 and left C^1–M^3 of a large male individual.

Type Locality

R1, Waregi Hill, Rusinga Island, Kenya.

Age

Ca. 20–17 Ma (Peppe et al. 2009; 2017).

Distribution

Rusinga and Mfangano Islands, Kenya.

Referred Material

Table 1.

Diagnosis

A medium- to large-bodied species of *Ekembo*, likely in the range of modern *Symphalangus* to female *Pan*, with moderate sexual dimorphism. It differs from *Ekembo heseloni* in exhibiting the following combination of features (Table 2): narrow inferior nasal aperture with margins that slope steeply toward the base and with smooth, rounded inferolateral borders; ventrally rotated subnasal clivus contributing to shortened rostrum and more vertical facial profile; anteroposteriorly compressed zygomaticoalveolar crest that is directly beneath the inferior orbital margin relative to an alveolar horizontal; deep palate lacking midline ridge along intermaxillary suture and lacking deep grooves anterior to the incisive foramina; little to no extra-molar space or retro-molar space separating mandibular ramus from the M_3; anterior edge of the ramus crosses the alveolar plane at or anterior to M_3; mandibular corpus shallower and narrower relative to M_1 length; continuously curved lingual and buccal margins of basal cross-section in female upper canine contribute to an ovoid crown cross-section; male upper canine buccolingually compressed resulting in ovoid crowns and roots; female lower canine with lingual cingulum angled obliquely to crown cervix and curving gradually into mesial ridge, and with an ovoid basal cross-section; male lower canine with long roots relative to basal crown dimensions; reduced basal flare on upper and lower molars; relatively broader occlusal surface in lower molars but greater differential between M_1 and M_2 breadths; upper central incisors with mesiodistally longer crowns and shorter roots relative to labiolingual breadth (emended from Andrews 1978: 99).

Other Included Species

Ekembo heseloni (Walker et al., 1993).

Synonymy

1933: *Proconsul africanus* Hopwood: Plate 6, Figures 5, 6 (partim).

1965: *Dryopithecus* (*Proconsul*) *africanus* (Hopwood, 1933); Simons and Pilbeam (new combination).

1978: *Proconsul* (*Proconsul*) *africanus* (Hopwood, 1933); Andrews (new combination).

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo nyanzae	M 16647	M		Holotype. Facial skeleton with right inferomedial orbital margin, right zygomatic root, right P^3–M^3, and left C^1–M^3 (Figures 1A, B)	1,2,3,4,9,13
	RU 1684	M	R	C^1	9
	RU 1685	M[a]	L	I^1	17
	RU 1688	F	R	C^1	8
	RU 1706	F	L	Mandible fragment with P_4–M_3	7,14,15,16
	RU 1707	F	L	C^1	8
	RU 1712	M[a]	R	I^1	17,18
	RU 1713		L	I^1 fragment	18
	RU 1714	M[a]	R	I^1	17
	RU 1717	M	R	C_1	12
	RU 1740	M	R	Mandible fragment with roots of C_1–P_4	12
	RU 1780	M	R	Mandible fragment with P_4–M_1, associated cranial fragments	14
	RU 1792[b]	F	L/R	Left maxilla fragment with roots of I^1–P^3, right maxilla fragment with root fragments of C–P^3, and partial crowns of P^4–M^1	1
	RU 1813	M	L	C^1	9
	RU 1815	M	L/R	Associated C^1s	9
	RU 1824	F[a]	L	Mandible fragment with P_4–M_2	16
	RU 1837		L	I^1	18
	RU 1842	F	L	C_1	10,11
	RU 1846		L	I^1	18
	RU 1891	F	R	C^1	9
	RU 1897		R	Maxilla fragment with broken C^1	8/9
	RU 1904	F[a]	L	Maxilla fragment with M^1–M^2	13
	RU 1914	F	R	C_1	10,11
	RU 1947	M		Distorted but complete mandible with entire dentition	5,6,7,14,15,16
	RU 1955	F	L	Mandible fragment with P_3–M_2	7
	RU 1960	M	L/R	C^1s	9
	RU 1965		L	Maxilla fragment with roots of I^1–C^1	1
	RU 1982	M	L/R	Left mandible fragments with I_2–P_3, M_1–M_3, plus associated right I^2, C_1, P_3, P_4, M_1, M_2, M_3, and left P_4	16

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Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo nyanzae	RU 2034	M	L	C_1	12
	RU 2040	F[a]	L	I^1	17,18
	RU 2041	F	L	C^1	8
	RU 2048	M	R	C_1	12
	RU 2049	F	R	C^1	8
	RU 2088	M	L/R	Right maxilla fragment with M^2–M^3, associated left C^1, P^4, M^1, M^2, M^3, root fragments	9
	RU 4405	F	L	C^1	8
	RU 4424	M	L	C^1	9
	RU 5938	F	R	C^1	8
	RU 7290	F		Skull with nearly complete facial skeleton, partial neurocranium, complete mandible and dentition	1,2,3,4,5,6,7,8,10 11,13,14,15,16,17
	RU 9817	M	R	C^1	9
	RU 14188		L	I^1 fragment	17
	RU 14226	F	L	C_1	10,11
	RU 14239	M	L	C^1	9
	RU 14240	M[a]	R	I^1	(based on assoc. with RU 14239)
	RU 15079	F	L	C_1	10,11
	RU 77065	M	L	C_1	12
	MW 17383	M	L	C_1	12
Ekembo heseloni	M 32632	F	R	C^1	8
	RU 1671	F[a]	L	Upper molar	13
	RU 1672	F[a]	L	M^2	13
	RU 1674	M		Complete mandibular corpus with anterior borders of right and left rami not extending as far as coronoid processes, right M_1–M_3, left C^1–M_3; right maxillary fragment with P^3–M^3, right and left I^2s	5,6,7,13,14,15,16
	RU 1678	M	L	Mandible fragment with P_3 roots and P_4–M_2 crowns	5,14,15,16
	RU 1687	M	L	C^1	9

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.) (continued)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo heseloni	RU 1695	M[a]	R	M_2	14
	RU 1696	M[a]	L	M^2	13
	RU 1705	F	L	Maxilla fragment with C^1–M^1	8
	RU 1711	M	L	Mandible fragment with broken C_1–P_3 plus P_4–M_1	14,15
	RU 1721	M[a]	R	M^2	13
	RU 1728	F	L	Mandible fragment with P_4–M_3	5,6,7,16
	RU 1741		L	M^1	13
	RU 1742		R	M^1	13
	RU 1763	M	L	C^1	9
	RU 1769	F	L/R	Associated right I^1–C^1, I_1–C_1, left I^1, C^1, I_1, C_1 and cranial fragments	8,10,11,17,18
	RU 1789	M[a]	R	M_1	14
	RU 1803	M[a]	L	Maxilla fragment with dP^3–dP^4, M^1; M^2 in crypt	13
	RU 1818	M[a]	L	M_1	14
	RU 1831	F[a]	L	I^1	17,18
	RU 1835		L	M^2	13
	RU 1871	F	L	C^1	8
	RU 1889	M	R	C_1	12
	RU 1900	F	L	C^1	8
	RU 1912	F	R	C^1	8
	RU 1913	F	L	C^1	8
	RU 1933	F[a]	L	I^1	17
	RU 1936	F[a]	L	M^1	13
	RU 1942	F	L	C^1	8
	RU 1951	M[a]	R	I^1	17
	RU 1959	F[a]	L	M_2	14
	RU 1971	M	L	C^1	9
	RU 1973	F[a]	R	Maxilla fragment with M^1–M^2	13
	RU 1974	F	R	C^1	8

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Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo heseloni	RU 1975	M[a]	L	I^1	17
	RU 1977		L	M^1 fragment	13
	RU 1979	F[a]	R	I^1	17
	RU 2000	M[a]	R	M_1	14
	RU 2032	M[a]	R	M_1	14
	RU 2036	F		Holotype. Partial skeleton of subadult, including right P^4-M^2, left P^3-M^1, and all lower dentition back to M_2 plus left M_3 erupting	1,3,4,5,10,11,13, 14,15,16
	RU 2087	M		Mandibular corpus with root of right ramus, right C_1–M_3, left C_1–P_3, M_1–M_2	5,6,7,14,15,16
	RU 3680	F	R	C_1	10,11
	RU 4404	F	R	C^1 fragment	8
	RU 5871		R	Juvenile mandible fragment with P_4–M_3	5,14,15,16
	RU 11078	F	R	C^1	8
	RU 14184	M	L	C_1	12
	RU 14238	F[a]	L/R	I^1s	17
	RU 14243[c]		L	M^2	13
	RU 14244	M	R	C_1	12
	RU 14245		L	C^1 and associated lower incisors	18
	RU 14246	F	L/R	Associated right C_1; left C_1 root, P_4, M_3 germ	10,11
	RU 14247[d]	M[a]	L/R	Left P_3, M_1, dP_4, right M_2, two lower incisor roots	14,15,16
	RU 15077		R	M_2 germ	14,15
	RU 15081	M	L	C_1	12
	RU 16000	M[a]		Facial skeleton including left inferolateral orbital margin and zygomatic, right zygomatic root, right and left P^3–M^3	1,2,3,4,13
	RU 17377	M[a]	L	Mandible fragment with M_2	14
	RU 17381	F[a]	L	M^2	13
	RU 18379		L	Mandible with M_3, roots of M_2	5,6
	RU 39000	M		Palate with right and left C^1–M^3	1,2,4,9,13

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Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo heseloni	RU 47805	M	L/R	Mandible fragment with P_4–M_3 and roots of left I_2–right C_1, plus right canine tip	5,7
	RU 71073[e]	M	L/R	Right P_4, M_2, M_3, left P_4, M_2, M_3, associated lower tooth roots	14,15,16
	RU 77062	F	L	C^1	8
	RU 77063	F	L	C^1	8
	RU 77077[e]	M		Palate with complete dentition (I^1–I^2 loose), temporal fragment, mandibular condyle	1,2,4,9,13
	MW 44	M	L	C_1	12
	MW 46	F	L	Maxilla fragment with C^1, root of I^2	8
	MW 562	F[a]	R	I^1	17
	MW 17389	F	L	C^1	8
	KPS I	M		Partial skeleton	13,14,15,18
	KPS II	M[a]		Partial skeleton	14,15,16
	KPS III	F[a]		Partial skeleton	13,14,15
	KPS IV	F[a]		Partial skeleton	13
	KPS VI	F[a]		Partial skeleton	13
Ekembo sp.	M 32235		R	Worn P_3	
	M 32236	M	R	C_1	
	M 32361			I_1	
	M 47272	F[a]	L	I^1	
	RU 1667		L	Maxilla fragment with inferolateral nasal aperture border, roots of C–P^3	
	RU 1679	M[a]	L	Mandible fragment with P_3 roots, P_4–M_1	
	RU 1683		R	M_2	
	RU 1690		L	I^2	
	RU 1694	M[a]	R	Mandible fragment with M_2	
	RU 1697	M[a]	L	M^3	
	RU 1704		R	I^2 fragment	
	RU 1709		L	Mandible fragment with I_2–P_3 roots	
	RU 1710			Right mandible fragment with P_4, M_2 crowns and M_1 roots, and left mandible fragment with I_1–P_3 roots, P_4–M_2 crowns (pathological)	

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.) (continued)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo sp.	RU 1715		L	Maxilla fragment with P^4	
	RU 1716	M[a]	L	Mandible fragment with C–P_4, erupting I_2	
	RU 1718		R	Maxilla fragment with P^{3-4}	
	RU 1719		L	Maxilla fragment with P^4	
	RU 1730		R	I_2	
	RU 1731		R	P_4	
	RU 1733		L	P^4	
	RU 1734	M[a]	R	M_2	
	RU 1735	M[a]	R	M_3	
	RU 1736	M[a]	L	M_2	
	RU 1747		R	M^2	
	RU 1764	M[a]	R	M_3	
	RU 1765		L	P_3	
	RU 1782	M[a]	L	Mandible fragment with M_3, associated P_3	
	RU 1785	F	R	C_1	
	RU 1791	M	R	C_1	
	RU 1795		R	M^1	
	RU 1814	M	L	C^1	
	RU 1820	F[a]	L	M_3	
	RU 1821	F[a]	L	M^3	
	RU 1822	M[a]	R	M_1	
	RU 1823		L	M_2	
	RU 1832		R	Maxilla fragment with M^2, roots of M^3	
	RU 1833		R	I^1	
	RU 1836		R	M^3	
	RU 1840	M[a]		Mandible symphysis with left P_3–right P_3	
	RU 1845	M	L	C^1	
	RU 1861	F[a]	R	M^2	
	RU 1864	F[a]		Mandible fragment with roots of left I_1–right P_4	

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.) (continued)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo sp.	RU 1872		L	Maxilla fragment with M^2	
	RU 1873	F[a]	L	M^2	
	RU 1874	M[a]	L	P^3	
	RU 1878	M[a]	R	M_1	
	RU 1910		L	M^3	
	RU 1920	F[a]	L	M^3	
	RU 1922	F[a]	L	M^3	
	RU 1923	M[a]	L	M_3	
	RU 1924	M[a]	L	P_3	
	RU 1926	M	L	C_1	
	RU 1927	F[a]	R	M_3	
	RU 1928		R	C^1 tip	
	RU 1929	M[a]	R	M^1	
	RU 1931		L	M_3	
	RU 1934		L	M^1	
	RU 1945	F[a]	R	M_2	
	RU 1954	F[a]	L	Upper molar	
	RU 1958		L	P_3	
	RU 1964		R	I^2	
	RU 1968		R	I^1	
	RU 1969		L	I^2	
	RU 1986		R	Lower molar fragment	
	RU 1998		L	I^2	
	RU 2002	F		Symphysis with incisor roots, broken C_1 crown	
	RU 2005		R	P^4	
	RU 2008		L	P_3	
	RU 2010	M	L	C_1	
	RU 2011		R	M^3 fragment	
	RU 2016		L	M^2	

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.) (continued)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo sp.	RU 2019		R	I^2	
	RU 2026	F[a]	R	M^2	
	RU 2031		L	Maxilla fragment with erupting I^2, d^C root, and dP^{3-4} crowns	
	RU 2035		R	I^2	
	RU 2037		L	P^4	
	RU 2038	F[a]	L	M_3	
	RU 2044	F[a]	L	P_4	
	RU 2045	F[a]	L	M_2	
	RU 2059		L	I^2	
	RU 2061	M[a]	L	M^3	
	RU 2071	F	L	C_1	
	RU 2090		R	I_1	
	RU 4420	M	L	C^1 tip	
	RU 5845		R	I^1 fragment	
	RU 9814		R	M_3 fragment	
	RU 14183	M[a]	L	P_3	
	RU 14186		L	Mandible fragment with roots of dP_{3-4}, I_2 germ in crypt	
	RU 14234		L	P^4	
	RU 14237	F[a]	R	P_3, M_1	
	RU 14247[d]	F	L	C_1	
	RU 14248		L/R	Associated lower incisors	
	RU 15075		L	M^3	
	RU 15078		R	P_4	
	RU 17386	F[a]	R	Mandible fragment with P_{3-4}	
	RU 17387		L	Lower molar fragment	
	RU 18373		L	Maxilla fragment with P^4 roots and worn M^1 crown	
	RU 18374	F[a]	L	P^3, M^1	
	RU 18378	M[a]	R	P_4	
	RU 18382	M[a]	R	M_3	

TABLE 1. *EKEMBO* SPECIMEN ASSIGNMENTS. ("M" numbers are NHMUK-P-M [Natural History Museum, London]. All others are KNM [National Museums of Kenya]. Diagnostic characters preserved in each specimen are enumerated in Table 2.) (continued)

Taxon	Accession number	Sex	Side	Element	Diagnostic characters
Ekembo sp.	RU 18386			Mandible symphysis	
	RU 25937		R	Maxilla fragment with I^2, P^3–P^4 roots	
	RU 71069		L	M_3 germ fragment	
	RU 77048		R	M^1 plus associated dI^1, dC, dP^4	
	RU 77058		R	M^1	
	RU 77061		R	C^1 root and crown base	
	MW 43		L	P^4	
	MW 47		R	I^2	
	MW 55		L	P_4	
	MW 56		R	P_4	
	MW 57		R	I^2	
	MW 161		R	M^1	
	MW 194		L	P^4	
	MW 13147	M[a]	L	I^1	
	KPS V	F[a]		Partial skeleton	
	KPS VII			Partial skeleton	
	KPS VIII			Partial skeleton	
	KPS IX			Partial skeleton	
	KPS X			Partial skeleton	
aff. *Ekembo*	M 32309	F	L	C^1	
	RU 1676/77	M	R/L	Associated left C_1–M_3 (RU 1676); right maxilla fragment with P^3–M^3, I^1, C^1, and left I^1, C^1, P^4–M^3 (RU 1677)	

[a]Sex estimated based on size distributions of reliably sexed specimens.
[b]L.S.B. Leakey's field notes documenting this discovery comment that the elements are likely not associated. We could not find any further documentation indicating why they were nevertheless given a single accession number (e.g., whether that opinion changed) nor did we find evidence that elements sorted into different species.
[c]Putatively associated M^3 germ belongs to a suid.
[d]Canine is morphologically female but putatively associated molars are presumed to be male based on size.
[e]These belong to a single individual, as demonstrated by the only break in the dentition, which runs across upper and lower M2s.

TABLE 2. SUMMARY OF TRAITS DISTINGUISHING *E. HESELONI* FROM *E. NYANZAE* (numbers in parentheses after trait descriptions indicate how many specimens in each hypodigm preserve the anatomy).

	Character	*E. heseloni*	*E. nyanzae*
Cranium	1	Broad inferior nasal aperture with margins sloping shallowly toward the base and with sharply defined inferolateral borders (4)	Narrow inferior nasal aperture with margins sloping steeply toward the base and with smoothly rounded inferolateral borders (4)
	2	Subnasal clivus dorsally rotated resulting in more horizontal profile and elongated rostrum (3)	Subnasal clivus more ventrally rotated presenting a steeper profile and shortened rostrum (2)
	3	Broad, rounded zygomaticoalveolar crest positioned anterior to inferior orbital margin relative to an alveolar horizontal (2)	Zygomaticoalveolar crest compressed anteroposteriorly and aligned in this axis with inferior orbital margin relative to an alveolar horizontal (2)
	4	Shallow palate, especially posteriorly, with strong intermaxillary ridge plus deep grooves anterior to incisive foramina (4)	Deeper palate lacking intermaxillary ridge and premaxillary grooves (2)
Mandible	5	Broad extramolar space and extensive retromolar space (8)	Little to no extramolar or retromolar spaces (2)
	6	Anterior edge of ramus crosses alveolar plane posterior to tooth row (4)	Anterior edge of ramus crosses alveolar plane at or anterior to third molar (2)
	7	Taller, thicker corpus relative to M_1 length (4)	Shorter, narrower corpus relative to M_1 length (4)
Upper canine	8	Female canine with sharply angled lingual and buccal margins at base resulting in parallelogram-shaped crown cross-section (16)	Female canine base with lingual and buccal margins continuously curved, resulting in ovoid crown cross-section (8)
	9	Male canine sub-circular in basal crown cross-section (5)	Male canine buccolingually compressed, resulting in ovoid basal crown base extending to ovoid roots (10)

TABLE 2. SUMMARY OF TRAITS DISTINGUISHING *E. HESELONI* FROM *E. NYANZAE* (numbers in parentheses after trait descriptions indicate how many specimens in each hypodigm preserve the anatomy) (continued).

	Character	*E. heseloni*	*E. nyanzae*
Lower canine	10	Female canine mesial portion of lingual cingulum mostly parallel to crown cervix intersecting mesial ridge at approximately a right angle (5)	Female canine mesial portion of lingual cingulum mostly oblique relative to crown cervix describing a continuous curve as it merges into mesial ridge (5)
	11	Female canine triangular in basal crown cross-section with broader crown base relative to length (5)	Female canine ovoid in basal crown cross-section with a narrower crown base relative to length (5)
	12	Male canine roots short relative to basal crown length and breadth (4)	Male canine roots long relative to basal crown length and breadth (6)
M^1–M^2	13	Greater degree of basal flare (20)	Reduced basal flare (3)
M_1–M_2	14	Greater degree of basal flare (19)	Reduced basal flare (4)
	15	Narrower occlusal surface (12)	Broader occlusal surface (3)
	16	M_1 crown breadth more similar to M_2 crown breadth (9)	M_1 crown much less broad than M_2 crown (5)
I^1	17	Mesiodistally shorter crowns relative to labiolingual breadth (8)	Mesiodistally longer crowns relative to labiolingual breadth (5)
	18	Longer roots relative to labiolingual breadth (4)	Shorter roots relative to labiolingual breadth (5)

1993: *Proconsul heseloni* Walker et al. (original description, partim).

2015: *Ekembo heseloni* (Walker et al., 1993); McNulty et al.: Figures 4, 6 (new combination).

Type Specimen
KNM-RU 2036, partial cranium, mandible, and postcranial skeleton of a sub-adult female individual.

Type Locality
R114, Kiakanga Hill, Rusinga Island, Kenya.

Age
Ca. 20–17 Ma (Peppe et al. 2009; 2017).

Distribution
Rusinga and Mfangano Islands, Kenya.

Referred Material
See Table 1 below.

Diagnosis
A medium- to large-bodied species of *Ekembo*, likely in the range of modern *Symphalangus* to female *Pan*, with moderate sexual dimorphism. It differs from *Ekembo nyanzae* in exhibiting the following combination of features (see Table 2 below): broad inferior nasal aperture with margins that slope shallowly toward the base and with sharp inferolateral borders; dorsally rotated subnasal clivus contributing to lengthened rostrum and more horizontal facial profile;

broad, rounded zygomaticoalveolar crest positioned anterior to the inferior orbital margin relative to an alveolar horizontal; palate is shallow, especially posteriorly, with intermaxillary ridge and with deep grooves anterior to incisive foramina; mandibular ramus set apart from M_3 by expansive extra-molar and retro-molar spaces; anterior edge of the ramus crosses the alveolar plane posterior to tooth row; mandibular corpus deeper and thicker relative to M_1 length; sharply angled lingual and buccal margins of female upper canine base resulting in parallelogram-shape basal cross-section; male upper canine with sub-circular basal cross-section; female lower canine with mesial portion of the lingual cingulum mostly parallel to crown cervix meeting mesial ridge at approximately a right angle, and with a triangular basal cross-section; male lower canine with short roots relative to basal crown dimensions; greater basal flare on upper and lower molars; relatively narrow occlusal surface in lower molars with M_1 and M_2 breadths more similar; upper central incisors with mesiodistally shorter crowns and longer roots relative to labiolingual breadth (emended from Walker et al. 1993: 51–52).

RESULTS

Features that distinguish *E. heseloni* from *E. nyanzae* were found in the cranium, mandible, upper and lower canines, upper and lower first and second molars, and upper central incisors (see Table 2). Assignments of individual specimens to species and sex are given in Tables 1 and 3, and summary statistics for basic dental measurements are provided in Table 4. Measurement data for this project are permanently archived in the University of Minnesota's University Digital Conservancy and can be accessed at https://hdl.handle.net/11299/271539; bivariate plots of length by breadth for all teeth are also in the Supplementary Material (Figures S2–S15), except for canine plots, which are in the main text below. Based on the conservative criteria outlined above, we assign 46 specimens to *E. nyanzae* and 73 to *E. heseloni*; a further 119 specimens are identified as *Ekembo* sp. and two specimens (NHMUK-P-M 32309, KNM-RU 1676/1677) are referred to aff. *Ekembo* (see Table 1). Twenty-eight specimens commonly assigned to *Ekembo* are excluded from that genus and instead referred to other genera or identified only at higher taxonomic levels (see Table 3). Although we anticipate that future discoveries will add to and refine our list of diagnostic features, it seems unlikely that every element will be distinguishable between these congeners.

DIFFERENCES BETWEEN *EKEMBO HESELONI* AND *EKEMBO NYANZAE* IN CRANIAL AND MANDIBULAR MORPHOLOGY

Crania

Holotypes of both species preserve substantial cranial anatomy. Additional well-preserved material includes a skull (KNM-RU 7290), partial facial skeleton (KNM-RU 16000), palates (e.g., KNM-RU 39000, 77077) and several maxillary fragments (KNM-RU 1705, 1792, 1803, 1872, 1904, 1973, 1965, 25937, and MW 46). Because only KNM-RU 7290 preserves substantial neurocranial anatomy, cranial differences between species were limited primarily to the maxillary/premaxillary and zygomatic regions.

The nasal aperture and premaxilla clearly distinguish two groups, with *E. heseloni* characterized by a broad inferior nasal aperture with shallowly sloping margins and sharply defined inferolateral borders (Figure 1A). This contrasts with *E. nyanzae*, in which a narrow inferior nasal aperture exhibits steeply sloping margins and inferolateral borders that are smoothly rounded. Further, the subnasal clivus in *E. heseloni* is dorsally rotated compared to that of *E. nyanzae*, presenting a more horizontal profile and contributing to an elongated rostrum (Figure 1B). *Ekembo heseloni* also has a broad and rounded zygomaticoalveolar crest that is positioned anterior to the inferior orbital margin when viewed laterally oriented to an alveolar horizontal; in *E. nyanzae*, the zygomaticoalveolar crest is compressed anteroposteriorly and is positioned directly inferior to the inferior orbital margin in this orientation. Finally, the palate of *E. heseloni* is shallower than that of *E. nyanzae*, especially posteriorly, with a strong ridge along the oral intermaxillary suture and deep grooves anterior to the incisive foramina. The palate of *E. nyanzae* is deeper and lacks the midline ridge and grooves.

Notably, KNM-RU 7290 resembles the *E. nyanzae* holotype in all of these diagnostic criteria and is therefore referred to that species. This allocation runs counter to most previous assignments of this specimen (but see Begun 2004, 2015; Begun and Kordos 2004; Walker 1992). The partial facial skeleton KNM-RU 16000 is referred to *E. heseloni*, which differs from the assignment suggested by Walker et al. (1993) but is consistent with an earlier assignment made by the same authors (Teaford et al. 1988). These and other specimen assignments are listed in Table 1.

Mandibles

Mandibular remains are common in the *Ekembo* sample, ranging from nearly complete mandibles (e.g., KNM-RU 1947, 7290) to complete (e.g., KNM-RU 1674, 2087) or partial (e.g., KNM-RU 1678, 1711) corpora. Only a few are reliably associated with upper dentitions, but KNM-RU 2036 and RU 7290 both provide important links between mandible and cranium; the mandible KNM-RU 1674 is also associated with an upper dentition (Le Gros Clark and Leakey 1951).

The most striking differences in mandibular morphology occur near the junction of the corpus and ramus. In *E. heseloni*, a broad extra-molar space and extensive retro-molar space separate the ramus from the third molar (Figure 2A). *Ekembo nyanzae* mandibles lack both features, with rami positioned proximate to the M_3. Viewed laterally, the anterior margin of the ramus in *E. heseloni* crosses the alveolar plane posterior to the tooth row, whereas in *E. nyanzae* the anterior margin is positioned more anteriorly, partially or even entirely eclipsing the third molar (see Figure 2A). Together, these features clearly distinguish two morphs among the *Ekembo* mandibles. Although the final position of the ramus and the presence of a retro-molar space cannot be properly

TABLE 3. SPECIMENS COMMONLY ASSIGNED TO *EKEMBO* BUT EXCLUDED FROM THAT GENUS IN THIS STUDY.

Accession Number	Attribution	Side	Element
KNM-RU 1680[a]	Catarrhini	R	Mandible fragment with P_4–M_1
KNM-RU 1691	*Nyanzapithecus vancouveringorum*	L	P^3
KNM-RU 1693[b]	Catarrhini	R	M^1
KNM-RU 1698	Catarrhini	R	C_1
KNM-RU 1899	Catarrhini	L	Mandible fragment with C_1
KNM-RU 1722[c]	Catarrhini	R	C^1
KNM-RU 1723[c]	Catarrhini	L	C^1
KNM-RU 1762	Suidae		Premolar
KNM-RU 1797[c]	Catarrhini	R	C^1
KNM-RU 1830[c]	Catarrhini	R	C^1
KNM-RU 1956	Primates?		Mandible fragment with molar
KNM-RU 1958	Catarrhini	L	P_3
KNM-RU 1999[c]	Catarrhini	L	C_1
KNM-RU 2039	Catarrhini	L	Maxilla fragment with broken P^3–P^4
KNM-RU 2093	Catarrhini	R	Mandible fragment with M_1 erupting
KNM-RU 2779	Catarrhini	R	Mandible fragment with molar
KNM-RU 14232	*Dendropithecus macinnesi*	R	M^3
KNM-RU 15084	Primates?	R	I^1
KNM-RU 17391	Catarrhini	L	C^1
KNM-MW 42	Suidae	L	Lower incisor
KNM-MW 45	Catarrhini	L	C_1
KNM-MW 50	*Nyanzapithecus vancouveringorum*	L	Lower M_2
KNM-MW 160	Catarrhini	R	C_1
KNM-KA 5	Suidae	L	I_1
KNM-KA 6	Catarrhini	L	M^2
KNM-KA 163	Catarrhini		Molar fragment
KNM-KA 164	Primates?		Three cusp fragments
KNM-CU 118	Primates?		Incisor

[a]Designated as the holotype of "*Turkanapithecus rusingensis*" Pickford et al., 2010.
[b]Accessioned as a dP^4 but identified here as an M^1.
[c]Identified by Kelley (1986) as nyanzapithecine.

evaluated in juvenile specimens, the extra-molar space is already visible in the subadult *E. heseloni* holotype KNM-RU 2036 (whose third molar crowns are fully formed but not erupted; Walker et al. 1983) as a buccal expansion of the alveolar platform in the vicinity of distal M^1 (Figure 2B).

Sorting mandibles according to these qualitative features reveals additional species differences in corpus dimensions (Figure 3). *Ekembo heseloni* has deeper and broader corpora relative to first molar length than *E. nyanzae*. Sexual dimorphism clearly influences corpus depth variation—males of both species have relatively taller corpora than females. Hence, overlap between species in this index is primarily between one female *E. heseloni* (KNM-RU 1728) and one male *E. nyanzae* (KNM-RU 1947). Sexual dimorphism is also a factor in relative thickness of the symphysis but appears to have little impact on postcanine corpus thickness—from P_4 to M_3, the relative thickness in *E. heseloni* is greater than that of *E. nyanzae*, regardless of sex (see Figure 3).

TABLE 4. SUMMARY STATISTICS FOR TEETH OF *E. HESELONI* AND *E. NYANZAE*.

Species	Tooth	Measure	Sex	*n*	Mean	Median	St. Dev.	Min.	Max.	Range
E. heseloni	I^1	Length[a]	Pooled	9	7.9	7.6	0.8	7.2	9.4	2.2
		Breadth[b]	Pooled	11	5.8	5.5	0.7	4.8	7.1	2.3
	I^2	Length	Pooled	2	5.6	5.6	0.2	5.4	5.7	0.3
		Breadth	Pooled	3	6.5	6.3	0.7	5.9	7.3	1.4
	C^1	Length[c]	Female	14	9.1	9.3	0.6	7.7	10.0	2.3
			Male	5	13.1	12.7	1.3	11.8	15.1	3.3
		Breadth[d]	Female	15	7.9	7.8	0.6	6.6	8.7	2.1
			Male	5	11.3	11.4	0.7	10.6	12.3	1.7
	P^3	Length	Pooled	7	6.2	6.3	0.6	5.0	6.8	1.8
		Breadth	Pooled	8	9.6	10.0	1.2	7.9	11.0	3.1
	P^4	Length	Pooled	6	5.6	6.0	1.0	4.3	6.4	2.1
		Breadth	Pooled	5	9.8	10.1	0.9	8.5	10.8	2.3
	M^1	Length	Pooled	14	8.4	8.4	0.7	7.1	9.5	2.4
		Breadth	Pooled	13	9.8	9.7	0.9	7.9	11.2	3.3
	M^2	Length	Pooled	16	9.7	9.9	1.2	7.8	11.1	3.3
		Breadth	Pooled	16	11.1	11.6	1.2	9.2	13.1	3.9
	M^3	Length	Pooled	6	10.1	10.5	1.6	7.1	11.8	4.7
		Breadth	Pooled	6	12.1	12.6	1.7	9.1	13.6	4.5
	I_1	Length	Pooled	1	3.9	3.9	—	3.9	3.9	0.0
		Breadth	Pooled	2	4.2	4.2	0.5	3.8	4.5	0.7
	I_2	Length	Pooled	2	4.2	4.2	0.0	4.2	4.2	0.0
		Breadth	Pooled	3	6.6	6.5	1.2	5.5	7.8	2.3
	C_1	Length[c]	Female	5	8.1	8.1	0.7	7.3	9.0	1.7
			Male	7	12.1	12.2	0.9	10.8	13.4	2.6
		Breadth[d]	Female	6	6.0	6.0	0.5	5.3	6.6	1.3
			Male	7	9.5	9.5	0.7	8.3	10.2	1.9
	P_3	Length[c]	Pooled	6	10.0	9.9	1.2	8.4	11.4	3.0
		Breadth[d]	Pooled	5	6.7	6.7	0.3	6.3	7.1	0.8
	P_4	Length	Pooled	10	6.7	6.8	0.9	5.1	8.3	3.2
		Breadth	Pooled	8	6.8	7.0	0.7	5.7	7.5	1.8
	M_1	Length	Pooled	15	9.0	9.1	0.8	7.0	10.5	3.5
		Breadth	Pooled	14	8.0	8.1	0.6	6.7	9.0	2.3
	M_2	Length	Pooled	16	10.8	10.5	1.4	9.0	13.3	4.3
		Breadth	Pooled	15	9.2	9.0	1.2	7.5	11.1	3.6
	M_3	Length	Pooled	9	12.0	12.2	1.6	9.7	14.2	4.5
		Breadth	Pooled	8	9.6	9.9	1.3	7.7	11.1	3.4

TABLE 4. SUMMARY STATISTICS FOR TEETH OF *E. HESELONI* AND *E. NYANZAE* (continued).

Species	Tooth	Measure	Sex	*n*	Mean	Median	St. Dev.	Min.	Max.	Range
E. nyanzae	I^1	Length[a]	Pooled	5	7.9	8.3	1.0	6.8	9.0	2.2
		Breadth[b]	Pooled	8	6.5	6.4	0.6	5.4	7.3	1.9
	I^2	Length	Pooled	1	5.1	5.1	—	5.1	5.1	0.0
		Breadth	Pooled	1	6.0	6.0	—	6.0	6.0	0.0
	C^1	Length[c]	Female	8	8.8	8.7	0.6	8.0	9.8	1.8
			Male	9	13.8	14.2	0.8	12.5	14.8	2.3
		Breadth[d]	Female	8	7.1	7.2	0.6	6.2	8.1	1.9
			Male	9	11.1	11.5	1.1	9.0	12.2	3.2
	P^3	Length	Pooled	2	7.4	7.4	1.2	6.5	8.2	1.7
		Breadth	Pooled	2	10.3	10.3	1.3	9.4	11.2	1.8
	P^4	Length	Pooled	3	5.2	5.2	0.3	4.9	5.5	0.6
		Breadth	Pooled	3	10.1	9.5	1.4	9.1	11.7	2.6
	M^1	Length	Pooled	4	8.3	8.2	1.1	7.1	9.8	2.7
		Breadth	Pooled	4	9.8	9.7	1.3	8.3	11.5	3.2
	M^2	Length	Pooled	4	9.9	9.6	1.5	8.5	12.1	3.6
		Breadth	Pooled	4	11.1	11.0	1.7	9.1	13.4	4.3
	M^3	Length	Pooled	3	9.5	9.1	1.5	8.3	11.1	2.8
		Breadth	Pooled	3	12.1	11.7	1.6	10.8	13.9	3.1
	I_1	Length	Pooled	2	4.1	4.1	0.3	3.9	4.3	0.4
		Breadth	Pooled	2	5.5	5.5	1.4	4.5	6.5	2.0
	I_2	Length	Pooled	2	4.7	4.7	0.6	4.3	5.1	0.8
		Breadth	Pooled	3	6.9	6.8	1.0	6.0	7.9	1.9
	C_1	Length[c]	Female	5	8.5	8.3	0.7	7.8	9.3	1.5
			Male	7	12.4	12.2	0.8	11.1	13.3	2.2
		Breadth[d]	Female	5	5.8	5.8	0.3	5.4	6.2	0.8
			Male	7	9.6	9.6	0.8	8.3	10.5	2.2
	P_3	Length[c]	Pooled	4	10.2	10.1	2.2	7.7	12.8	5.1
		Breadth[d]	Pooled	4	6.2	6.5	1.0	4.7	7.0	2.3
	P_4	Length	Pooled	7	6.9	6.7	0.9	5.6	8.4	2.8
		Breadth	Pooled	7	6.7	6.6	0.6	6.0	7.7	1.7
	M_1	Length	Pooled	7	8.8	8.4	0.8	7.9	10.0	2.1
		Breadth	Pooled	7	7.7	7.4	0.8	6.5	8.6	2.1
	M_2	Length	Pooled	6	10.6	9.9	1.3	9.4	12.8	3.4
		Breadth	Pooled	5	9.7	9.0	1.4	8.5	11.7	3.2
	M_3	Length	Pooled	4	12.8	12.8	1.7	11.1	14.4	3.3
		Breadth	Pooled	4	10.1	10.1	1.5	8.4	11.4	3.0

[a]Mesiodistal dimension for all teeth except canines and P_3.
[b]Labiolingual or buccolingual dimension for all teeth except canines and P_3.
[c]Greatest basal dimension.
[d]Basal dimension perpendicular to greatest dimension.

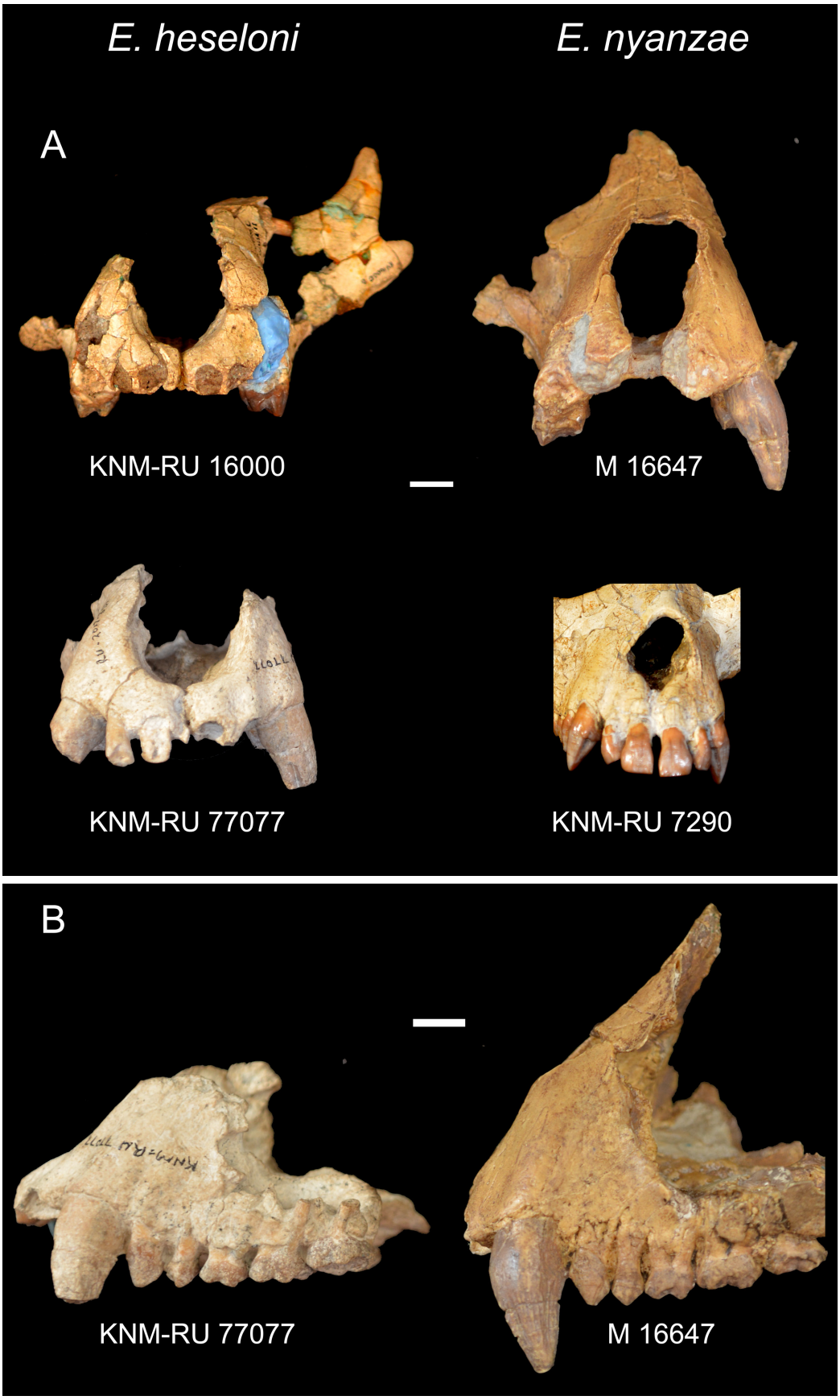

Figure 1. Craniofacial differences between E. heseloni *(KNM-RU 16000, 77077) and* E. nyanzae *(NHMUK-P-M 16647, KNM-RU 7290) depicted in A) frontal and B) lateral views. See text and Table 2 for descriptions (scale bars=1cm). Specimen NHMUK-P-M 16647 represented in this photo by a cast.*

Figure 2. A) Mandibular differences in extramolar and retromolar spaces, and the corresponding position of the ramus relative to the dentition in E. heseloni *(KNM-RU 1674) and* E. nyanzae *(KNM-RU 1947). B)* E. heseloni *holotype (KNM-RU 2036) depicting a burgeoning extramolar space in this subadult, and of KNM-RU 7290 depicting the* E. nyanzae *condition of reduced extramolar and retromolar spaces (scale bars=1cm).*

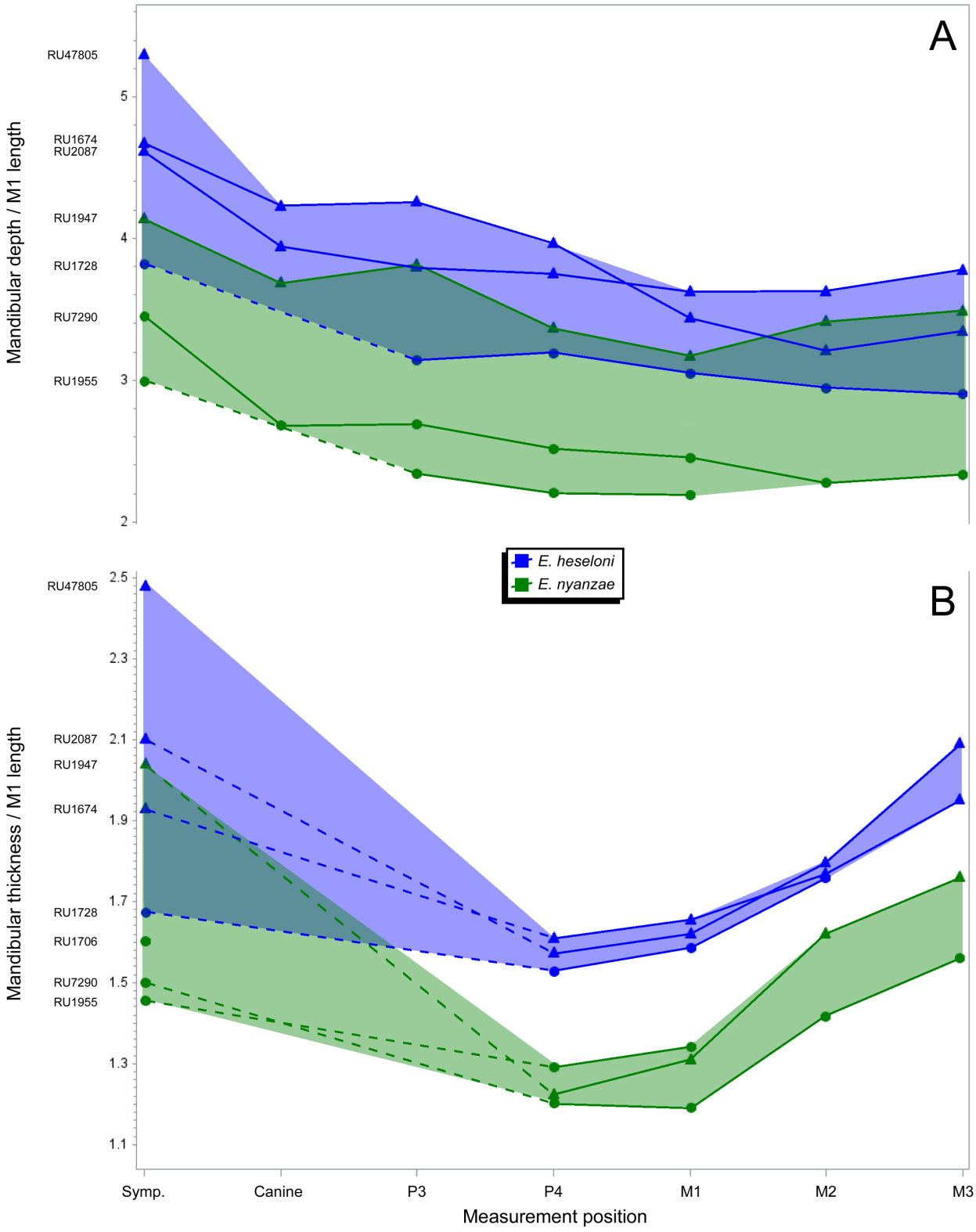

Figure 3. Adult: A) mandibular corpus depth and B) mandibular corpus thickness at different tooth positions, scaled by M_1 mesiodistal length (modeled after Andrews 1978). Males are indicated by triangles, females by circles. Corpus depth measurements were collected on the external surface; symphyseal depth was collected on the internal surface, which was preserved in more specimens. Corpus thickness was not measured below the canine and P_3 due to the difficulty of consistently positioning calipers in this region in smaller specimens. Lines connecting individual specimens' measurements are dashed when bypassing a measurement that could not be taken. Shaded hulls indicate the greatest area occupied by each species.

DIFFERENCES BETWEEN *EKEMBO HESELONI* AND *EKEMBO NYANZAE* IN DENTITION

Upper Canines

After first sorting canines by sex, we identified within each sex two distinct basal cross-sectional shapes by which most specimens could be sorted. Female upper canines were assigned to species when they sorted with either KNM-RU 7290 (female *E. nyanzae*, see above) or RU 2036 (female *E. heseloni*); male upper canines were assigned to species based on belonging (or not) to the group containing NHMUK-P-M 16647 (male *E. nyanzae*). Female upper canines of *E. heseloni*, when viewed occlusally, have sharply angled lingual and buccal margins at the base, resulting in a parallelogram-shaped crown cross-section (Figure 4A). In females of *E. nyanzae*, the lingual and buccal margins of the basal cross-section are continuously curved, resulting in an ovoid crown cross-section. In males, the situation is somewhat different. *Ekembo heseloni* male upper canines are sub-circular in basal crown cross-section, whereas male specimens of *E. nyanzae* are buccolingually compressed, resulting in an ovoid basal crown cross-section that extends to very ovoid roots (Figure 4B).

Basal crown dimensions of the upper canines broadly reflect these cross-sectional differences although there is overlap between the two species (Figure 5). An index of bilateral compression reveals significant differences between species groups (t-test: df=32.443, t=4.46, p<0.0001)—both male and female upper canines of *E. nyanzae* are more compressed than their *E. heseloni* counterparts. Based on this index, we were able to statistically assign KNM-RU 1897 to *E. nyanzae* even though our qualitative assessment of it was indeterminate. As discussed by McNulty et al. (2015) and below, the associated upper and lower dentition KNM-RU 1676/1677 (Figure S1) has qualitatively distinct canines and is therefore not assigned to either species. A very small female specimen, NHMUK-P-M 32309, has a basal cross-section similar to that of *E. heseloni*, but other aspects of the crown do not fit comfortably within that species (see below). For that reason, we refer it to aff. *Ekembo* and excluded it from statistical analyses of either species.

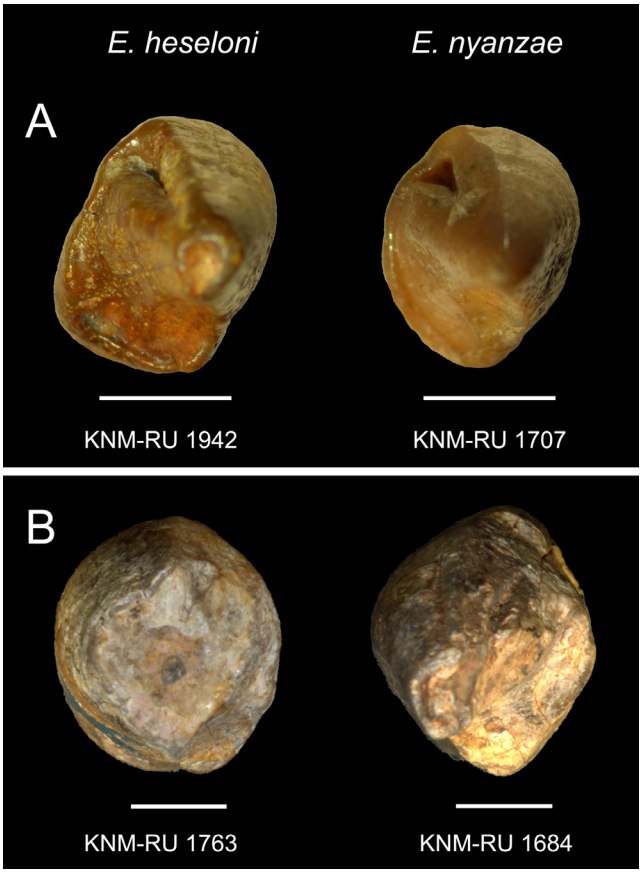

Figure 4. Occlusal views of representative A) female and B) male upper canines of E. heseloni *(left column) and* E. nyanzae *(right column). KNM- RU 1942: left upper female canine; KNM- RU 1707: left upper female canine; KNM-RU 1763: left upper male canine (reversed for comparison); KNM-RU 1684: right upper male canine (scale bars=0.5cm).*

Lower Canines

As with upper canines, lower canines were first sorted by sex (Kelley 1986, 1995a, b), and then further separated into two morphotypes within each sex. Two groups were readily identified among the female sample, one of which includes the *E. heseloni* holotype. Specimens in this group have a lingual cingulum that is more or less parallel to the crown cervix and intersects the mesial ridge separating the lingual surface from the mesiobuccal surface at approximately a right angle (Figure 6A); the crown base in this group appears triangular in cross-section (Figure 6B). In contrast, the lingual cingulum in the other group, including KNM-RU 7290, angles obliquely upward from the distal margin of the crown describing a continuous curve as it merges into the mesial ridge; the crown base in *E. nyanzae* female lower canines is ovoid in cross-section. We note that the canine of KNM-RU 14247, identified as female by anatomy and by size, was accessioned together with two lower molars that are well outside the range of female specimens but near the average of male specimens in all standard crown dimensions. It seems unlikely that these belong to a single individual, and for that reason we treat these specimens separately in Table 1.

Among male lower canines, the only strong difference we found was in root length—a number of specimens have roots that are notably longer, both absolutely and in relation to crown size, than the remainder of the sample. When sorted visually by this criterion, the resulting groups are statistically different whether scaled by basal crown length (t-test: df=6.8268, t=2.72, p=0.0304) or perpendicular basal crown breadth (t-test: df=6.936, t=2.98, p=0.0209). However, despite our identification of two morphotypes among the isolated teeth, it is difficult to associate either group with a species. Most specimens with strong evidence for species affinity—those with associated dentitions—cannot be assessed for canine root length since they are embedded in jaws. One specimen (KNM-RU 1982) has a measurable, long-rooted canine associated with molars assigned to *E.*

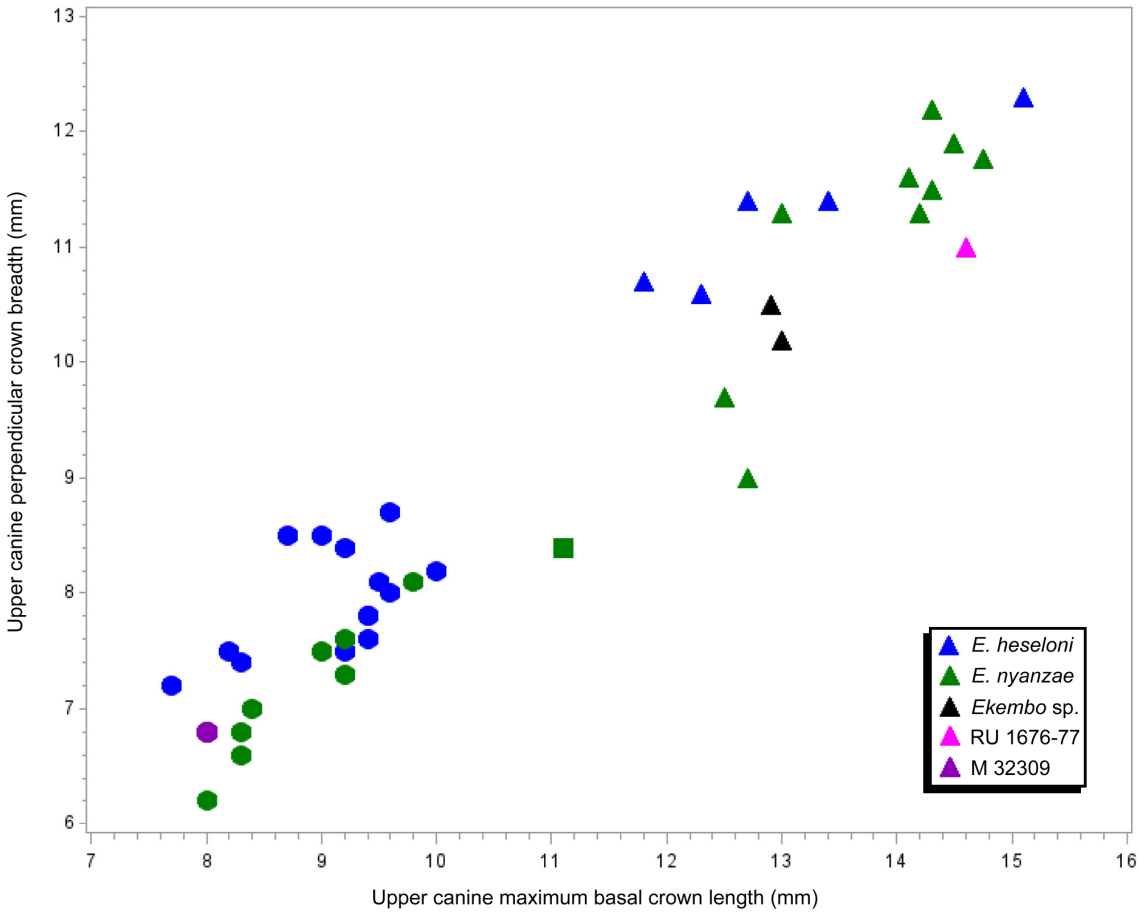

Figure 5. Bivariate plot of upper canine basal crown dimensions. Males are indicated by triangles, females by circles, and one specimen of undetermined sex by square. Species identifications according to qualitative anatomical features (see text, Table 2).

nyanzae (see below), and therefore we assign other long-rooted specimens to this species; short-rooted canines are, as a consequence and by default, assigned to *E. heseloni*. The edentulous mandibular fragment RU 1740 can be tentatively referred to *E. nyanzae* based on its exposed canine root. Radiographic measurements of mandibular specimens could further refine or challenge these assignments. Nevertheless, we derive additional confidence in these associations from the fact that longer roots relative to maximum basal crown length also distinguish *E. nyanzae* from *E. heseloni* in the pooled-sex lower canine sample (t-test: df=11.993, t=3.02, p=0.0107) and is consistent with differences in relative root length observed in upper central incisors (see below). Altogether, canine identifications were possible for all but four female and four male specimens (Figure 7).

Upper First and Second Molars

Upper molars of *E. heseloni* and *E. nyanzae* are distinguished primarily by the degree of basal flare in M^1 and M^2, measured as the ratio of the average buccolingual breadth between mesial and distal cusp pairs to maximum buccolingual crown breadth; intercuspal distances were estimated in lightly worn teeth based on cusp morphology but not collected on moderately to heavily worn teeth. Because we could not clearly distinguish these teeth based on qualitative anatomical features alone, only those molars associated with other elements assigned to species were used to estimate species' ranges for this trait. *Ekembo heseloni* specimens have broader crowns relative to their average intercusp breadth, reflecting a greater degree of basal flare than in *E. nyanzae* upper molars (t-test: df=18.233, t= -6.33, p<0.0001). Based on this difference, we subsequently assigned several isolated molars (KNM-RU 1671, 1672, 1696, 1721, 1741, 1742, 1835, 1936, 1977) to *E. heseloni*, but no additional specimens could be assigned to *E. nyanzae* according to our conservative statistical criterion. Specimen KNM-RU 1677 has one molar exclusively in the prediction interval of *E. heseloni*, whereas the other overlaps both species' intervals.

Lower First and Second Molars

As with upper molars, only quantitative differences were identified in lower molars. However, three such features consistently differentiate *E. heseloni* from *E. nyanzae* (Figure 8), as identified by associated elements. First, differences in basal flare, measured as noted above, showed the same pattern of taxonomic variation (t-test: df=18.25, t= -6.47,

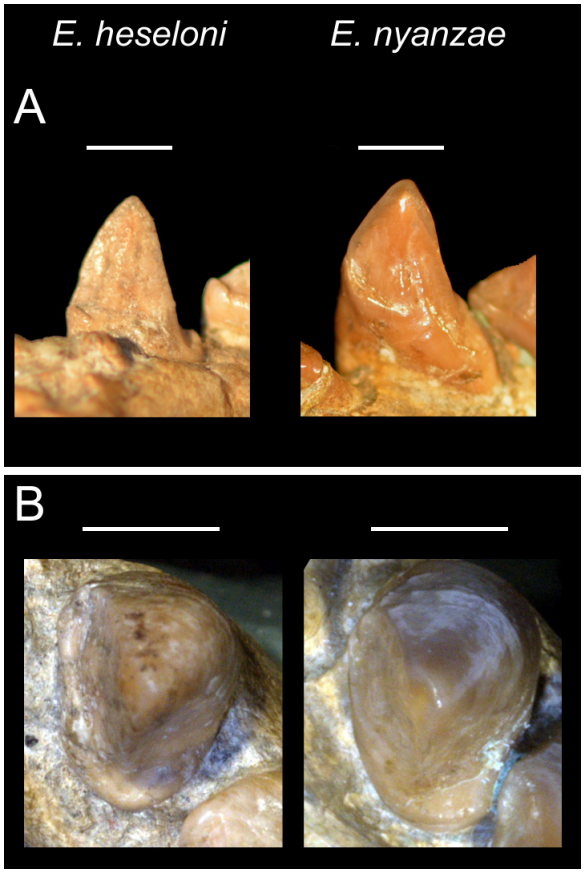

Figure 6. Differences in representative female lower left canines in the A) lingual cingulum, and B) basal outline, demonstrated by KNM-RU 2036 (left column: holotype of E. heseloni*) and KNM-RU 7290 (right column: referred in this study to* E. nyanzae*) (scale bars=0.5cm).*

p<0.0001)—*E. heseloni* has greater basal flare than does *E. nyanzae* in M_1 and M_2. Three isolated molars (KNM-RU 1959, 2000, 2032) could be statistically assigned to *E. heseloni* based on this index; none of the unassigned molars had a basal flare index beyond the prediction interval for that species and exclusively within the range of *E. nyanzae*.

A related difference that could be measured in additional specimens is the shape of the occlusal area, with *E. heseloni* exhibiting a relatively narrower occlusal area than that of *E. nyanzae* based on average breadth between mesial and distal cusp pairs divided by crown length (t-test: df=16.431, t= -7.95, p<0.0001)—*E. heseloni* has a narrower occlusal area than does *E. nyanzae* in M_1 and M_2. Four additional isolated molars (KNM-RU 1695, 1789, 1818, 17377) as well as the three that were referred based on basal flare (KNM-RU 1959, 2000, 2032) could be statistically assigned to *E. heseloni* based on the index of occlusal shape; the isolated molar KNM-RU 1780 was beyond the prediction interval for *E. heseloni* and within the range of *E. nyanzae* and thus assigned to the latter.

A final distinguishing feature is the relative size of M_1 to M_2 (Harrison 2002, 2010), specifically in the ratio of maximum crown breadths rather than occlusal or crown planar areas (see Figure 8). There is a greater difference between M_1 and M_2 breadths in *E. nyanzae* than in *E. heseloni* (t-test: df=5.6939, t=2.88, p<0.0299). Although most specimens that preserve these two molars can be assigned according to criteria presented above, two such specimens could not. One, KNM-RU 1710, measured in the overlap between the species' prediction intervals for the ratio of maximum crown breadths. Moreover, its corpus morphology appears to be pathological, which calls into question the usefulness of its morphological features for taxonomic assignment. The other specimen, KNM-RU 1676, fell in the prediction interval of *E. nyanzae* rather than *E. heseloni* for the ratio of maximum crown breadths, which is the opposite assignment suggested by the upper molars. Therefore, neither of these specimens was assigned to species.

Upper Central Incisors

Qualitative assessment of upper central incisors distinguished two groups according to crown (mesiodistal) and root (apical-cervical) lengths relative to overall tooth size. Placement of KNM-RU 7290 in one group, based on relative crown length, enabled us to identify *E. nyanzae* as having relatively shorter crowns and longer roots, whereas the opposite morphology is presumed to characterize *E. heseloni*. Shape indices comparing these two dimensions relative to labiolingual breadth support our qualitative sorting with significant differences in both relative crown length (t-test: df=5.9739, t=5.12, p=0.0022) and root length (t-test: df=6.9786, t= -3.92, p=0.0058). One specimen that could not be qualitatively assigned to species, M 47272, can be referred to *E. heseloni* based on its crown proportions; none of the unassigned I^1s had root lengths outside of the overlap in prediction intervals. We also assigned one additional specimen, KNM-RU 1979, to *E. heseloni* based on its association with that species' holotype. The specimen was discovered in 1950 from the R114 tree trunk deposit and was included by Napier and Davis (1959) among the elements belonging to KNM-RU 2036 though it was never formally accessioned with that specimen. Our analysis places it in the overlap between prediction intervals, but we accept the association identified by its discoverers.

BODY SIZE

Body mass estimates provided in Table 5 are based on upper and lower first and second molars. Estimates vary depending on the tooth type, and these variations also reflect differences in M_1:M_2 proportions noted above. Female body mass estimates for *E. heseloni* range from 13.1–14.4kg; those for *E. nyanzae* range from 14.3–17.4kg. Estimates for *E. heseloni* males range from 22.4–25.9kg; those for *E. nyanzae* males range from 24.6–31.4kg. These results reflect what is obvious from the larger set of dental measurements (see Table 4)—*E. nyanzae* was only modestly larger than *E. heseloni*, with a substantial amount of overlap between the species.

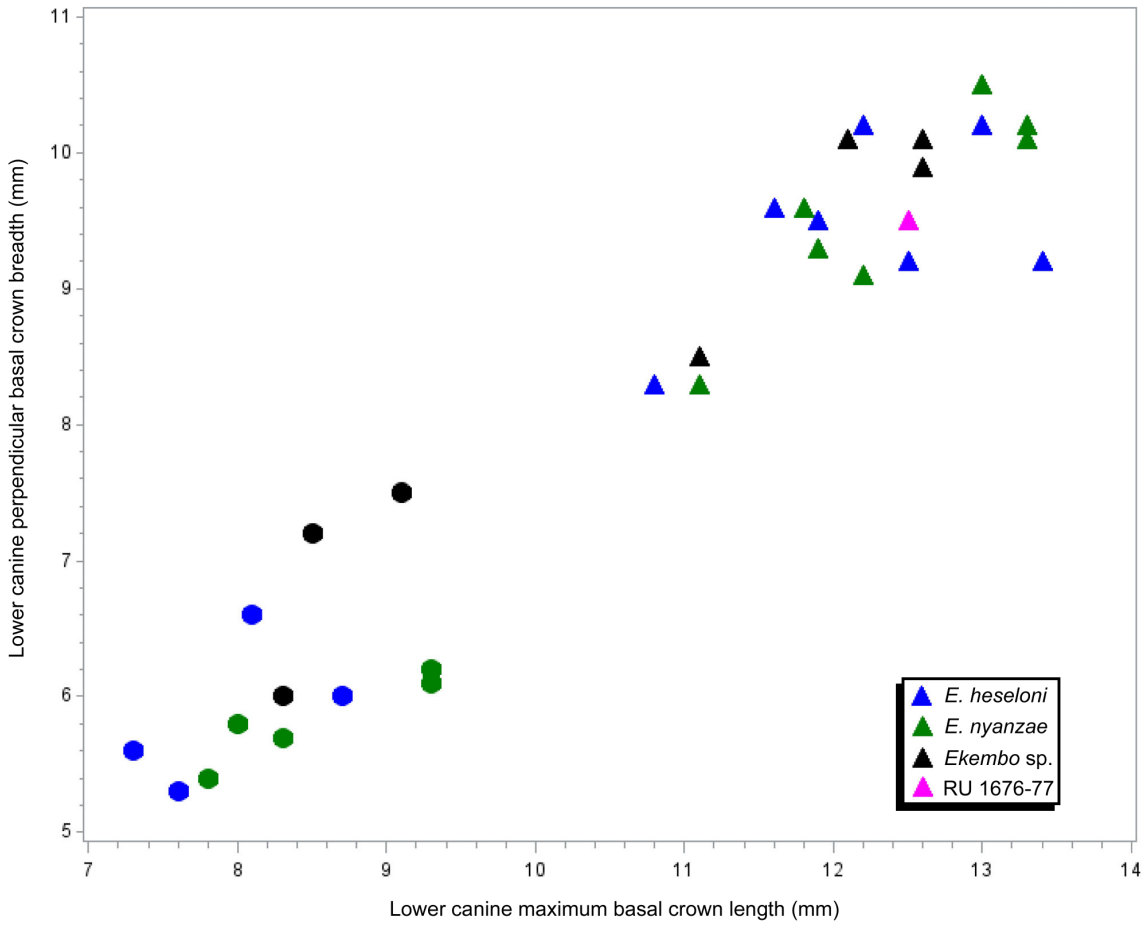

Figure 7. Bivariate plot of lower canine basal crown dimensions. Males are indicated by triangles and females by circles. Species identifications according to qualitative anatomical features (see text, Table 2).

DISCUSSION

The most revelatory outcome of the alpha-taxonomy presented here is the broad overlap in size of craniodental specimens attributed to *E. nyanzae* and *E. heseloni*. The diagnostic qualitative and quantitative features detailed above reveal that the slightly smaller *E. heseloni* includes larger individuals not previously recognized as belonging to this species, whereas *E. nyanzae* includes some small individuals well within the size range of *E. heseloni*. Although much of the extensive *Ekembo* postcranial sample cannot be confidently assigned to species at present, the craniodental sorting suggests with a high degree of probability that body size in the two species overlapped to a similar degree. This size relationship contrasts with the almost universal perception that the two species—under whichever nomenclature and however they were constituted—represented a nearly identical large and small species pair (e.g., Andrews 1978; Harrison 2010; Le Gros Clark and Leakey 1951; Pilbeam 1969; Walker et al. 1993). This perception was initially driven by the size distribution of craniodental remains, with the focus being almost exclusively on postcanine dentition and associated gnathic material.

Challenges to the conception of a large and small species pair were put forward by both Pickford (1986) and Kelley (1986), with the latter focused especially on the canine dentition, which displayed what appeared to be disproportionate representation of males and females in the traditional species hypodigms (Bosler 1981). Based on larger samples and more explicit morphological criteria for sexing canines, Kelley (1986) interpreted this unlikely representation as demonstrating that the entire Rusinga/Mfangano sample comprised a single species, since all the small canines were morphologically female whereas all the large canines were morphologically male.

Soon after, as a consequence of a dramatic increase in the postcranial sample from Rusinga (Beard et al. 1986; Begun et al. 1994; Rafferty et al. 1995; Ruff et al. 1989; Teaford et al. 1993; Walker and Pickford 1983; Ward et al. 1993), taxonomic arguments and characterizations of body size shifted away from craniodental remains to focus on postcrania. This led to the first estimates of body size that were not based on tooth size, with characterizations of the size ratio between *E. nyanzae* and *E. heseloni* estimated in the range of 3:1 to 4:1 (Rafferty et al. 1995; Ruff et al. 1989; Teaford et al. 1993). Although these estimates were always spuriously high, as they failed to account for a lack of what would be males of the smaller species (Kelley 1993)—acknowledged by Ruff et al. (1989)—they did reinforce the argument for

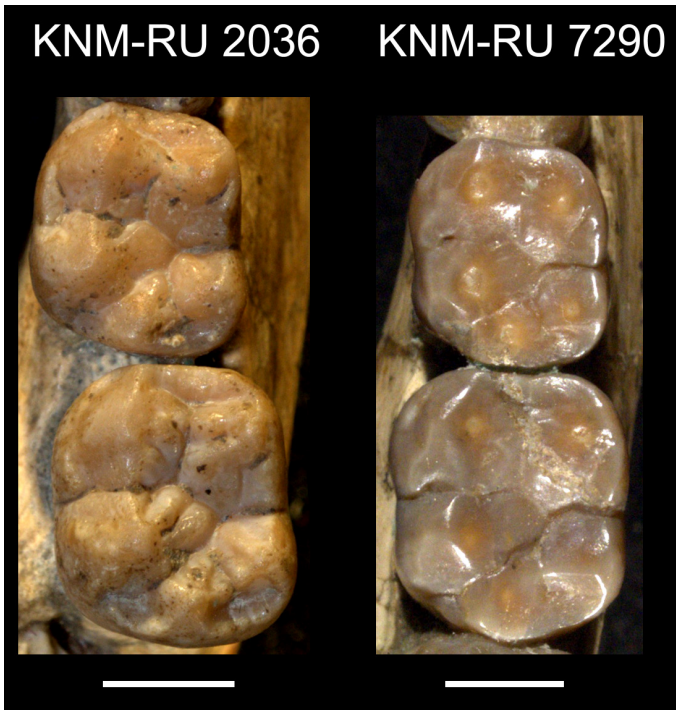

*Figure 8. Lower first and second molars of KNM-RU 2036 (*E. heseloni*) and KNM-RU 7290 (*E. nyanzae, *in this paper). Photos are scaled to approximately the same M_2 mesiodistal length. The difference in size (statistically significant with respect to crown breadth) between M_1 and M_2 is much greater in E. nyanzae compared to E. heseloni (scale bars=0.5 cm).*

the presence of two species, one substantially larger than the other.

The single-species scheme of Pickford (1986) and Kelley (1986) ultimately proved incorrect but what was largely overlooked in subsequent taxonomic treatments of *Ekembo* was that a satisfactory explanation for the unusual distribution of canines—with one species preserving only morphologically male canines and the other almost exclusively morphologically female canines—was still lacking. Three possible explanations exist: 1) that the distribution reflects correct species and sex assignments, with a sample of more than 70 canines preserving, by chance, mostly males of a large species and females of a smaller one; 2) that both species had monomorphic canines, with the larger species' canines all morphologically male and the smaller species' canines all morphologically female; or 3) that the two species of *Ekembo* broadly overlap in size, with the sample of larger specimens including males of both species and the sample of smaller specimens including females of both. What should have been clear is that the only alpha-taxonomy that can fully accommodate all the sample characteristics of *Ekembo*, both craniodental and postcranial, without recourse to highly unusual and unlikely species characteristics and/or sampling, is the third explanation in which the two species broadly overlap in size.

The diagnostic features identified in this study flip the narrative of *E. heseloni* and *E. nyanzae* being craniodentally similar, size-differentiated species to being craniodentally distinct, similarly-sized species. Further, as a consequence

TABLE 5. MEAN BODY MASS ESTIMATES (kg) IN BOLDFACE FOLLOWED BY 95% CONFIDENCE INTERVALS COMPUTED FROM UPPER AND LOWER MOLARS AS IN GINGERICH (1982) (numbers in parentheses are sample sizes used to compute means).

Species	Sex	M^1	M^2	M_1	M_2
E. heseloni	F	(5) **14.3**, 12.7–16.2	(6) **13.1**, 11.6–14.7	(2) **13.6**, 12.4–15.0	(4) **14.4**, 13.2–15.8
	M	(5) **24.1**, 20.7–28.0	(8) **25.9**, 22.2–30.3	(11) **22.4**, 19.9–25.2	(9) **25.6**, 22.9–28.5
E. nyanzae	F	(2) **14.3**, 12.7–16.2	(2) **15.6**, 13.7–17.7	(4) **14.8**, 13.4–16.4	(3) **17.4**, 15.8–19.1
	M	(2) **24.8**, 21.3–29.0	(2) **26.9**, 22.9–31.5	(3) **24.6**, 21.7–27.7	(2) **31.4**, 27.9–35.3

of the allocation of craniodental specimens to species hypodigms based on these distinguishing features, all prior characterizations of species attributes derived from size-based taxonomies—including degrees of canine and postcanine sexual dimorphism, and tooth size:body size relationships (postcanine megadontia versus microdontia)—must be reconsidered.

Likewise, the relative simplicity of assigning specimens to one species or the other based on size, which has resulted in the vast majority of *Ekembo* specimens having species attributions, can no longer be trusted. Closely related, similar-sized species are not expected to differ in all aspects of their anatomy, nor is every specimen—even in elements for which average species morphotypes differ—expected to be diagnosable. In such cases, the prudent course is not to assign specimens simply because they fall within the range of one fossil sample and not the other, but rather to assign them only when they fall within the range of one and would be a statistical outlier in the other (cf. Simpson and Roe 1939). This conservative approach results in fewer specimen assignments but is based on, we propose, a more biologically sound justification—differences between congeneric species are likely to be subtle, and therefore the ranges exhibited in small samples are unlikely to adequately characterize the magnitude of those differences or the degree of overlap. Our methodology also reflects a desire not to unintentionally increase the uncertainty inherent to all taxonomies, which are provisional by nature and always subject to change with additional discoveries or novel analyses.

The complicated taxonomic history of *Ekembo* illustrates well that provisional nature but also prevents a straightforward summary of all the characteristics, apart from size, that researchers have used to differentiate the two species. Studies prior to the naming of *P. heseloni* (Walker et al. 1993) necessarily differentiated *P. nyanzae* from a mixed *P. africanus* sample comprising both *Ekembo* and *Proconsul*; taxonomic treatments since then have been based on size (e.g., Teaford et al. 1993; Walker et al. 1993), have lacked diagnostic descriptions (Pickford et al. 2009), or did not elaborate hypodigms (Harrison 2002, 2010). Because Harrison (2002, 2010) provides the most recent comprehensive descriptions of the two species, it is worth comparing his diagnostic craniodental traits to those emerging from this project. Both studies identified relatively broader lower molars and a greater size difference between M_1 and M_2 as distinguishing *E. nyanzae* from *E. heseloni*. Other differences, however, were not supported in our specimen sorting: lack of an inferior transverse torus; greater height difference between paracone and protocone of P^3; more secondary wrinkling on upper and lower molars; greater size difference between M^1 and M^2 and both teeth relatively narrower with hypocone subequal to metacone, a better developed lingual cingulum, and a more pronounced distal transverse crest; M^3 larger and M_3 with a larger entoconid and well-developed crest connecting it to hypoconulid as characteristics of *E. nyanzae* (Harrison 2010). These were all found to vary in both species, as constituted by our hypodigms, and we could not obtain a specimen sorting in which that variation was eliminated (i.e., sorting specimens by one trait did not resolve the variation in others). We also did not observe the reduced bilateral compression in lower canines of *E. nyanzae* noted by Harrison (2010), and we found the opposite pattern in the upper canines (see Table 2). Finally, oft-cited differences in enamel thickness based on small samples of sectioned or CT-scanned teeth (Beynon et al. 1998; Harrison 2010; MacLatchy et al. 2019; Smith et al. 2003) were not supported here because none of the five specimens for which data are available can be referred to *E. nyanzae* according to our sorting.

NOTABLE SPECIMENS

KNM-RU 7290

Among those who have recognized two species within the *Ekembo* sample, almost all have referred the 1948 skull discovered by Mary Leakey to the smaller species, initially *P. africanus* then later *E. heseloni* (e.g., Andrews 1978; Le Gros Clark 1950; Le Gros Clark and Leakey 1950, 1951; Pickford et al. 2009; Walker et al. 1983, 1993; but see Begun 2004, 2015; Begun and Kordos 2004; Walker 1992). Here, we assign it to *E. nyanzae* based on a large number of diagnostic characteristics that it shares with the *E. nyanzae* holotype but considering as well dentognathic differences between KNM-RU 7290 and the *E. heseloni* holotype and hypodigm. Reliance on size to distinguish the two species certainly played a role in forming the consensus opinion that KNM-RU 7290 belongs in *E. heseloni*, but other features, such as a highly reduced M^3, were also used to support this assignment (Le Gros Clark and Leakey 1950, 1951; Walker et al. 1993). As noted above, we found that some features previously used to distinguish *E. heseloni* and *E. nyanzae* vary substantially even within their attendant hypodigms. Third molar morphology in particular is quite variable in *Ekembo*, *Proconsul*, and many other mammalian groups (see McNulty et al. 2015 and references therein). The diagnostic traits identified in this study, however, consistently place KNM-RU 7290 in *E. nyanzae*.

KNM-RU 16000

Teaford et al. (1988) described the difficulties in assigning this specimen to either species because of a postcanine dentition that is intermediate in size between those of *E. heseloni* (then *Proconsul africanus* but conceptually much the same) and *E. nyanzae*. Although not definitively assigned in the original description (Teaford et al. 1988), KNM-RU 16000 was tentatively assigned by Walker et al. (1993) to *E. nyanzae*, since doing so produced lower measures of species dental variability than an assignment to *E. heseloni*. A confounding factor, however, was the lack of a reliably identified male specimen of *E. heseloni* to which KNM-RU 16000 could be compared (Teaford et al. 1988; Walker et al. 1993).

Here, we identify several male specimens of *E. heseloni* and assign KNM-RU 16000 to this group based on cranial and dental anatomy. In this comparative sample, individual teeth of RU 16000 no longer plot as outliers of *E. heseloni*.

Likewise, adding its estimated canine dimensions (Teaford et al. 1988: MD=14.5, BL=11.7) to Figure 5 would make the range of *E. heseloni* males more similar to that of *E. nyanzae* males. Nevertheless, we acknowledge that the relative canine (estimated):postcanine crown sizes are problematic (see Teaford et al. 1988). The alveoli of RU 16000 suggest canines at the large end of the *Ekembo* range, but its molar planar occlusal area estimates (length x breadth) are among the smallest for putative males (Teaford et al. 1988), a pattern of discrepant proportions also observed in a few specimens attributed to *P. major* Le Gros Clark and Leakey, 1950 (Bosler 1981; Pilbeam 1969). However, the canine:postcanine ratio is problematic no matter which species KNM-RU 16000 is assigned to, and in the several facial and dental traits shown here to be diagnostic of *Ekembo* species, this specimen clearly aligns with *E. heseloni*.

Kaswanga Primate Site

At least ten individuals of *Ekembo* from the Kaswanga Primate Site (Walker and Teaford 1988) have been referred by many authors to *E. heseloni* (e.g., Begun et al. 1994; Daver and Nakatsukasa 2015; Walker 1997; Walker et al. 1993; Ward et al. 1995; but see Harrison 2002, 2010). Although most individuals are represented by multiple elements, including several partial skeletons, there are scant craniodental remains. Based on the few preserved adult teeth, we support the assignment of Individuals I, II, III, IV, and VI to *E. heseloni*. The teeth of Individuals V and X are not diagnostic; individuals VII, VIII, and IX do not have sufficiently preserved or associated adult dentitions that can be assigned to species. Hence, none of the *Ekembo* teeth from the Kaswanga Primate Site could be exclusively assigned to *E. nyanzae*, nor is there compelling craniodental evidence that two species are represented in this sample. The number of species present might be better assessed from the abundant postcranial remains (cf. Beard et al. 1986; Begun et al. 1994; Rafferty et al. 1995; Ruff et al. 1989; Teaford et al. 1993; Walker 1992) but doing so would require the identification of size-independent, species-specific morphologies for each postcranial element as well as consideration of ontogenetic changes. With so little of the overall sample being diagnostic by the craniodental criteria presented here, we cannot rule out the possibility that *E. nyanzae* is also represented in this assemblage (Harrison 2002, 2010).

KNM-RU 1676/1677

The challenges of assigning to a genus the associated dentition comprising KNM-RU 1676 (lower teeth) and 1677 (upper teeth) were discussed by McNulty et al. (2015) (see Figure S1). Within the *Ekembo* sample, these teeth more than others bear some resemblance to *Proconsul* (in I^1 lingual tubercle development and M^2 occlusal shape) but lack the strongest diagnostic features of that genus (McNulty et al. 2015). They also exhibit a few characteristics reminiscent of *Afropithecus* Leakey and Leakey, 1986 (cf. Rossie and MacLatchy 2013), but are demonstrably different from that taxon as well (McNulty et al. 2015). Considering the entire dentition, this individual is more similar to *Ekembo* than to other named taxa but does not fit comfortably in this genus either. It is one of the largest individuals in the collection and therefore has been assigned by previous researchers to *P. nyanzae* (Andrews 1978; Greenfield 1972, 1973; Le Gros Clark and Leakey 1951; Pickford et al. 2009; Walker et al. 1993). In this study, however, it variously shows affinities to one or the other *Ekembo* species or to neither, depending on the characteristic being analyzed. An important epistemological consideration is that, had these teeth been discovered individually rather than in association, there would be much less difficulty in assigning them to a species—likely to different species, however, depending on the tooth. This underscores the possibility that other individuals referred to *Ekembo* had similarly chimeric character suites that go unappreciated among specimens known from only few or individual elements. Because of the unique set of features in the dentition of KNM-RU 1676/1677, we refer this specimen to aff. *Ekembo*.

SIZE, SCALING, AND SEXUAL DIMORPHISM

Body mass estimates for both species underscore the minor size differences between them, but the degree and, in one case, the direction of the inferred difference varies depending on which tooth is used (see Table 5). When sexes are considered separately, overlap between species estimated body mass ranges is fairly narrow. Among females, mean molar areas predict that *E. heseloni* was ca. 14kg (estimates from 13.1–14.4kg) and *E. nyanzae* was slightly larger (estimates from 14.3–17.4kg); among males, mean molar area estimates predict 22.4–25.9kg in *E. heseloni* and from 24.6–31.4kg in *E. nyanzae*. If it is assumed that relationships between tooth size and body mass in these two closely related species were basically the same, the relative differences in the body mass estimates between them should be reasonably accurate, regardless of inaccuracies in actual predicted values.

Concordance between dental and postcranial estimates of body size cannot be established without inclusion of postcranial elements in species hypodigms. However, a comparison between our estimates based on tooth size and estimates from talar and long bone diaphyseal and articular dimensions (Rafferty et al. 1995; Ruff 1989) suggests that dental specimens identified in this study as females from both species produce higher body mass estimates than those derived from the grouping of small postcranial bones (9.3–13.9kg), whereas dental specimens identified as male produce lower estimates than those derived from the grouping of large postcranial bones (25.6–46.3kg). This result, suggesting some level of megadontia among females of the two species and microdontia among males, mirrors the findings of Teaford et al. (1993) and Rafferty et al. (1995), but in this case with different implications. Rather than reflecting species differences in tooth size/body mass relationships, our results reflect expected differences between males and females in moderately to highly size-dimorphic species, where the percentage difference in tooth size between sexes is substantially less than that in body mass (e.g., Scott et al. 2009). In such species, females gen-

erally appear somewhat megadont and males somewhat microdont. Body masses estimated separately from tooth sizes in males and females will also reflect this relationship and differ from estimates based on postcrania in a predictable fashion. Fully documenting how dental versus postcranial elements predict body mass in *Ekembo*, however, will require many more specimens with associated teeth and postcrania.

Dental sexual size dimorphism in both species appears to be similar. Considering only specimens that are reliably assigned to sex based on association with a canine, the average male to female ratios of upper and lower P4-M3 tooth crown lengths and breadths is about 1.2 in both species (*E. heseloni*: mean=1.20, range=1.09–1.38; *E. nyanzae*: mean=1.18, range=1.07–1.28). Assessing dimorphism measurement-by-measurement is probably not meaningful since the number of specimens that can be reliably assigned to sex is low for most teeth. However, this average across P4-M3 measurements probably does reflect substantial dimorphism in both species, as indicated by values for canine dimorphism, which are based on the largest reliably assigned samples. Lower canine crown height dimorphism in *E. heseloni* (1.53) is greater than in both species of *Pan*, less than in both species of *Gorilla* and *Pongo abelii*, and similar to dimorphism in *Pongo pygmaeus*; in *E. nyanzae*, lower canine crown height dimorphism (1.67) is greater than in all extant great ape species, but only marginally so compared to both species of *Gorilla* and to *Po. abelii.* None of the upper canines attributed to *E. heseloni* males is sufficiently complete for reliable crown height measurements, but upper canine crown height dimorphism in *E. nyanzae* (1.66) is greater than in both species of *Pan*, less than in both species of *Gorilla* and *Po. abelii*, and similar to that in *Po. pygmaeus* (see Kelley 1995a for extant ape values).

One notable outcome of this study concerns mandibular proportions in the two species. Le Gros Clark (1950) and others (Le Gros Clark and Leakey 1950, 1951; Pilbeam 1969) highlighted differences in mandibular proportions and robusticity as important for distinguishing what were then regarded as *P. africanus* and *P. nyanzae*. However, whereas they saw increased mandibular proportions as characteristic of the larger *P. nyanzae* (comprising a mixture of *E. heseloni* and *E. nyanzae* males according to our taxonomic sorting), we find the slightly smaller *E. heseloni* to have greater mandibular corpus dimensions relative to tooth size (see also Andrews 1978). For example, although crown lengths and breadths in KNM-RU 1947 (*E. nyanzae* male) exceed those of KNM-RU 2087 (*E. heseloni* male) for every preserved tooth, the latter specimen has an absolutely and relatively thicker mandibular corpus (see Figure 3), creating the impression of a 'larger' individual than might be predicted from its dental dimensions (cf. Greenfield 1972, 1973).

BIOGEOGRAPHY

Our revised alpha-taxonomy provides a new basis for interpreting temporal and geographic distributions of *Ekembo* and its two closely related species, and a few preliminary observations can be made based on data presented here. Both *E. nyanzae* and *E. heseloni* are present at all major mammal collecting areas on Rusinga including R4 (Nyamsingula), which records the youngest known presence of the genus (Peppe et al. 2009). Although the precise contemporaneity of species at any one site cannot be conclusively established, this study does rule out the possibility that *E. nyanzae* replaced *E. heseloni* in time-successive strata (e.g., Retallack et al. 1995). Whether one species gave rise to the other or both evolved via cladogenesis of an earlier species is not discernible in the current record, and more work in the oldest deposits is needed to test these alternatives.

Both species are also present on Mfangano Island, but the degree to which they overlap at different sites or within the same strata is uncertain due to the much smaller number of fossils found there and to the poor provenance of some specimens in the historic collections. The majority of Mfangano fossils derive from beds that are stratigraphically lower than Rusinga's Hiwegi Formation (the most fossiliferous unit) (Pickford 1984), and hence it may be that Mfangano localities offer the best chance for documenting lineage evolution in *Ekembo* (cf. Michel et al. 2023). Although interesting variations among Mfangano specimens hint at more primitive morphology (McNulty 2019; McNulty et al. 2015), the paucity of remains prohibits a rigorous assessment of the significance of these differences.

A single upper female canine (NHMUK-P-M 32309) from the Chianda North site on the Uyoma peninsula is referred here to aff. *Ekembo.* Though most similar to *E. heseloni* in its crown cross-section near the cervix, this is one of the smallest specimens associated with *Ekembo* and exhibits a strong shelf-like lingual cingulum (Andrews 1978) and slight concavity in the distolingual portion of that shelf that is unique. In this latter feature, it bears some resemblance to KNM-MB 70 (McNulty et al. 2024), referred initially to *Victoriapithecus* (Von Koenigswald 1969) then later to *Equatorius africanus* (Kelley et al. 2002; Pickford 1982, 1985). However, its size and curved mesiolingual margin are more consistent with *Ekembo*. If that association is correct, M 32309 would be the only evidence of this genus outside of Rusinga/Mfangano. Only two other primate fossils are known from Uyoma. One is too small to be assigned to *Ekembo*; the other, an edentulous mandible, is within the size range of female *Ekembo* but morphologically consistent with *Nyanzapithecus* (McNulty et al. 2018).

Ekembo cannot be reliably identified from fossil outcrops near Karungu. Of five potential *Ekembo* craniodental specimens in the historic collections, one (KNM-KA 5) is a suid incisor, three others (KNM-KA 7, 163, 164) are too badly preserved to assign, and KNM-KA 6 is not currently available for study (see Table 3). A photograph of the latter, kindly provided by Peter Andrews (cf. Andrews 1973), suggests that KA 6 is also insufficiently preserved to assign to *Ekembo*. New fieldwork at Karungu has resulted in more than a dozen additional, as yet unpublished, catarrhine specimens of the appropriate size range (Lehmann et al. 2014), but these also are insufficiently preserved to diagnose (McNulty unpublished data).

As have others, we regard previous identifications of *E. nyanzae* at other Early and Middle Miocene localities (Songhor, Koru, Maboko Island, Fort Ternan) as spurious. The so-called 'Koru mandible' (M 14086) was assigned to *P. nyanzae* by Le Gros Clark and Leakey (1951) along with an edentulous mandible, a maxillary fragment, and several isolated teeth, all from Koru and Songhor. The mandible is particularly interesting in that its canines and premolars are larger than expected based on $M_{2\text{-}3}$ size (Bosler 1981; Pilbeam 1969), similar to the pattern in the upper teeth of KNM-RU 16000. Nonetheless, these specimens are consistent with Tinderet species of *Proconsul* (Andrews 1978; Martin 1981; see also Pickford et al. 2009) and were not transferred to *Ekembo* (McNulty et al. 2015). Andrews (1978; Andrews and Walker 1976) referred several specimens from Fort Ternan to *E. nyanzae*, but most of these have since been assigned to *Kenyapithecus wickeri* Leakey, 1962 (e.g., Harrison 1992; Kelley et al. 2002; Pickford 1985; Ward et al. 1999;); the upper molar KNM-FT 16, assigned by several authors to *P. africanus* (Andrews 1978; Harrison 1992; Pickford 1985), has unclear affinities but is not considered by us to belong to *Ekembo*. Likewise, a few specimens from Maboko Island assigned to *P. nyanzae* (Andrews 1978) are now referred to *Equatorius africanus* Ward et al., 1999 (Kelley et al. 2002; Pickford 1985). Specimens from Rusinga Island that have at times been assigned to *P. major* (e.g., Andrews 1978; Bosler 1981) are included here in *Ekembo* (McNulty et al. 2015). Finally, two specimens purportedly from Rusinga (M16649, RU 1681) have been shown to be from Maboko Island (Andrews and Molleson 1979; Foecke et al. 2022), with the former specimen the holotype of *Equatorius africanus* and the latter now referred to that species (Foecke et al. 2022). In all of these cases, earlier attributions were reevaluated by the referenced authors and we concur with those latter assessments.

SPECIES ABUNDANCES

The revised alpha-taxonomy for *Ekembo* provides a basis for estimating the relative abundances of the two species. Looking just at the number of identified specimens, the ratio of *E. heseloni* to *E. nyanzae* is about 1.6:1 (see Table 1). However, the distribution of canines between species suggests more equitable representation. Upper canines are one of the most common elements in the *Ekembo* sample, and 93% of them can be assigned to species based on criteria presented here. Our results found upper canines split evenly between species, suggesting that, when a large portion of an element's sample can be allocated to species, the species abundances aggregated across the Kisingiri complex of sites are approximately equal. Whether that proportion holds across different outcrops, habitats, and strata is an important direction for future studies.

FUTURE RESEARCH: ECOLOGICAL IMPLICATIONS

One important question that emerges from this study is: if *E. heseloni* and *E. nyanzae* were similar in size, living contemporaneously and possibly sympatrically, and shared the same basic anatomy, how did these species partition ecological resources in a way that enabled both to thrive for millions of years in the Kisingiri environs? Interspecific differences identified in this study suggest potential directions for answering this. For example, mandibular differences between *E. heseloni* and *E. nyanzae* might point to differences in regular, seasonal, or fallback dietary strategies. An interesting comparison is to extant capuchins, *Cebus* and *Sapajus*, which are similar in body size but differ in dietary behavioral ecology and masticatory anatomy—tufted capuchins consume harder food items and exhibit a variety of associated anatomical correlates including more robust mandibles (e.g., Polvadore et al. 2025). The broader, deeper mandible of *E. heseloni* may point to the possibility that it consumed tougher foods than *E. nyanzae*. Likewise, a dorsally rotated premaxilla and procumbent incisors have been linked to hard-object feeding in *Afropithecus* (Leakey and Walker 1988), though these features are more subtle in *E. heseloni* and not obviously accompanied by the other functionally related mandibular and dental features found in *Afropithecus*.

Recent and ongoing research on dental microwear (Shearer et al. 2015), isotopes (Garrett 2016), and topographic variables (Cicak 2023) in *Ekembo* has thus far failed to illuminate strong differences between the species, even when analyses are updated to reflect the alpha-taxonomy presented here (McNulty unpublished data). However, two findings do hint at adaptations for processing tough foods specifically in *E. heseloni*. Molar relative enamel thickness data published by Beynon et al. (1998) and MacLatchy et al. (2019) position *Ekembo* at the upper limit or exceeding values in extant apes, and notably all of their sampled specimens are referred in our study to *E. heseloni*. Again, a comparison to capuchins is instructive—the durophagous *Sepajus* has relatively thicker molar enamel than the non-durophagus *Cebus capucinus* (Dumont 1995; Pampush et al. 2013). Second, dental topographic analysis of *Ekembo* specimens found a subtle connection to extant hard-object frugivores, with *E. heseloni* comprising the majority of that sample—and hence the bulk of the dietary signal—and only a single specimen (KNM-RU 1780) representing *E. nyanzae*, according to our allocations (Cicak 2023). Speculation about niche differentiation based on these results is far from conclusive, however, particularly without proper representation of both species.

In further consideration of the possible sympatry of the two *Ekembo* species, monkeys (*sensu lato*) may be better analogs than apes since, on the whole, they are more similar to *Ekembo* in anatomy and body size, despite the small number of mostly incipient features that position *Ekembo* in the hominoid clade and notwithstanding the derived features of cercopithecoid anatomy. It is likely that *Ekembo* is still more like primitive catarrhines than it is even later Miocene hominoids in terms of its overall biology. Sympatry among extant, frugivorous monkeys of similar size and craniodental morphology is not uncommon. Dietary niche differentiation in such cases is often more subtle than having fundamentally different diets, and we anticipate that

differences between *Ekembo* species will be similarly understated. Nevertheless, more explicit sampling and testing, grounded in the revised alpha-taxonomy presented here, stands a better chance of revealing the ecological differences between these closely related apes than when they were perceived as differing greatly in body size.

Expanding the present hypodigms to include postcranial specimens would also be a major advancement toward differentiating the ecologies of *E. heseloni* and *E. nyanzae*, but doing so based solely on associations with craniodental remains will be difficult; specimens in this study that have associated postcrania and can be referred to species are placed primarily in *E. heseloni*. Yet, if consistent differences that distinguish two postcranial morphotypes could be identified, associating one with *E. heseloni* based on our study and the other (by default) with *E. nyanzae* would provide a good basis for hypotheses about certain aspects of ecological differentiation.

CONCLUSIONS

We have reassessed the hypodigms of *Ekembo heseloni* and *Ekembo nyanzae* based on cranial and dentognathic differences in morphological shape rather than size, which has been central to all prior attempts to sort *Ekembo* specimens into species. Consistent species differences were found in the cranium, mandible, upper and lower canines, upper and lower first and second molars, and upper central incisors. In the cranium, *E. heseloni* differs from *E. nyanzae* in having a broad inferior nasal aperture with shallowly sloping margins and sharply defined inferolateral borders, a dorsally rotated subnasal clivus and corresponding elongated rostrum, a broader and rounded zygomaticoalveolar crest positioned anterior to the inferior orbital margin relative to an alveolar horizontal, and a shallower palate with a strong ridge along the intermaxillary suture and deep grooves anterior to the incisive foramen. In the mandible, *E. heseloni* has a taller and thicker corpus relative to first molar length, broad extra-molar and retro-molar spaces, and an anterior ramus that crosses the alveolar plane distal to M_3. Dentally, *E. heseloni* has upper central incisors with relatively longer crowns and shorter roots, less compressed upper canines with distinct male and female basal cross-sectional shapes, lower canines with relatively shorter roots and a distinct crown morphology in females, upper and lower molars with greater basal flare, and lower molars with a relatively narrower occlusal area and more similar buccolingual breadths between M_1 and M_2.

Based on these differences, 119 out of 239 specimens referred here to *Ekembo* were assigned to species; a further 28 specimens often referred to *Ekembo* were not assigned to that genus. Notable differences from previous allocations include assigning KNM-RU 7290 to *E. nyanzae* and KNM-RU 16000 to *E. heseloni*. Five of the ten Kaswanga Primate Site individuals were assigned to *E. heseloni*; specimens of the other five individuals could not be positively assigned to either species based on the preserved anatomy. The resulting hypodigms for *E. heseloni* and *E. nyanzae* differ markedly from those based on sorting according to size (e.g., Andrews 1978; Pickford et al. 2009; Walker et al. 1993), and they permit several observations about the paleobiology of *Ekembo*. Overlap in dental measurements is substantial; hence, new body mass estimates based on teeth indicate that the species were similar in size, with *E. nyanzae* only modestly larger than *E. heseloni*. Estimates of sexual dimorphism in tooth crown dimensions are about 1.2 in both species. Evidence from the most diagnostic elements suggests that species frequencies were approximately equal across the geologic sequence, and that both species appear at all major collecting areas on Rusinga, indicating that *E. heseloni* and *E. nyanzae* were not time-successive phyletic species. Finally, a single tooth from the nearby Uyoma peninsula provides the only potential evidence of *Ekembo* outside of Rusinga and Mfangano Islands.

ACKNOWLEDGMENTS

We dedicate this study to Alan Walker, in honor of his work in the paleontology of the Kisingiri region and in eastern Africa, and for his contributions to the broader paleoanthropology community. We also acknowledge and thank generations of collaborators in the Kisingiri area who have participated in, facilitated, encouraged, and supported the field projects that enabled this research. This work was conducted under the authority, and adhering to the guidelines, of Kenya's National Commission for Science, Technology, and Innovation, with research permits granted to the authors over multiple years (e.g., NACOSTI/P/15/9092/4745, NACOSTI/P/18/9092/23264). We thank Fredrick Manthi, Emma Mbua, and Job Kibii for providing access to specimens in their care, and Tom Mukhuyu, Samuel Muteti, Faith Wambua, James Yatich, and Cliff Ochieng for their assistance working in the collections. Niki Garrett, Abbey Hall, Penina Kadalida, Risa Luther, Francesca Socki, and Madelaine Walker are gratefully acknowledged for their assistance compiling and validating data. We especially thank Andrea Taylor, Eric Delson, Laura MacLatchy, James Rossie, and two anonymous reviewers for their enthusiasm and insightful comments on drafts of this manuscript. D.R.B. first started working on this project from 1987–1989 thanks to support from the Johns Hopkins School of Medicine and a grant from the Wenner-Gren Foundation. Our recent efforts were supported by grants from the National Science Foundation (BCS 0852609, 1241807), the Leakey Foundation, the McKnight Foundation, and the Leverhulme Foundation to K.P.M, who also acknowledges Phi Pi and Perkins New Brighton for their support of his work. D.R.B. acknowledges support from the Alexander Humboldt Stiftung and NSERC, and J.K. gratefully recognizes support from the Institute of Human Origins, Arizona State University. This manuscript is publication #8 supporting Research on Eastern African Catarrhine and Hominoid Evolution (REACHE).

AUTHOR CONTRIBUTIONS

Conceptualization and Ideas: D.R.B. had the earliest conceptualization of this project, with K.P.M. and J.K. later helping to conceive of the final research goals and aims. Ef-

forts toward Funding Acquisition, Methodology, Investigation, and Writing (Original and Editing) were contributed by all authors. Data Curation, Formal (statistical) Analysis, and Visualization were done by K.P.M.

DATA STATEMENT

All data used to support the analyses in this study are available from the University of Minnesota's University Digital Conservancy at https://hdl.handle.net/11299/271539 (https://doi.org/10.13020/b0bz-ze90).

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Supplement 1: The Alpha-Taxonomy of *Ekembo*

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SUPPLEMENT 1

SUPPLEMENTARY FIGURE S1

Figure S1: Occlusal views of KNM-RU 1676 (lower dentition) and RU 1677 (upper dentition), referred in this manuscript to aff. *Ekembo*.

SUPPLEMENTARY FIGURE S2

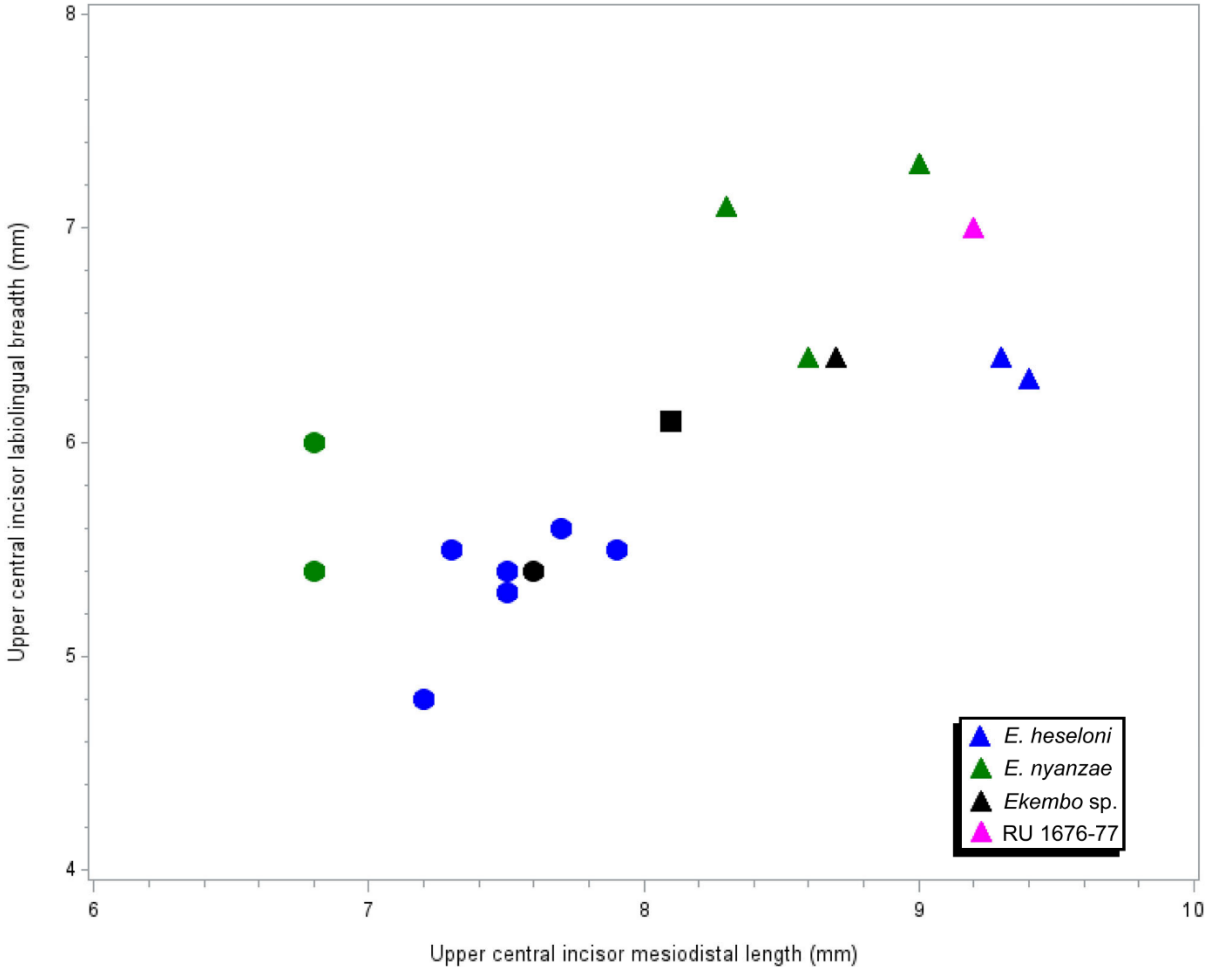

Figure S2: Bivariate plot of I^1 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S3

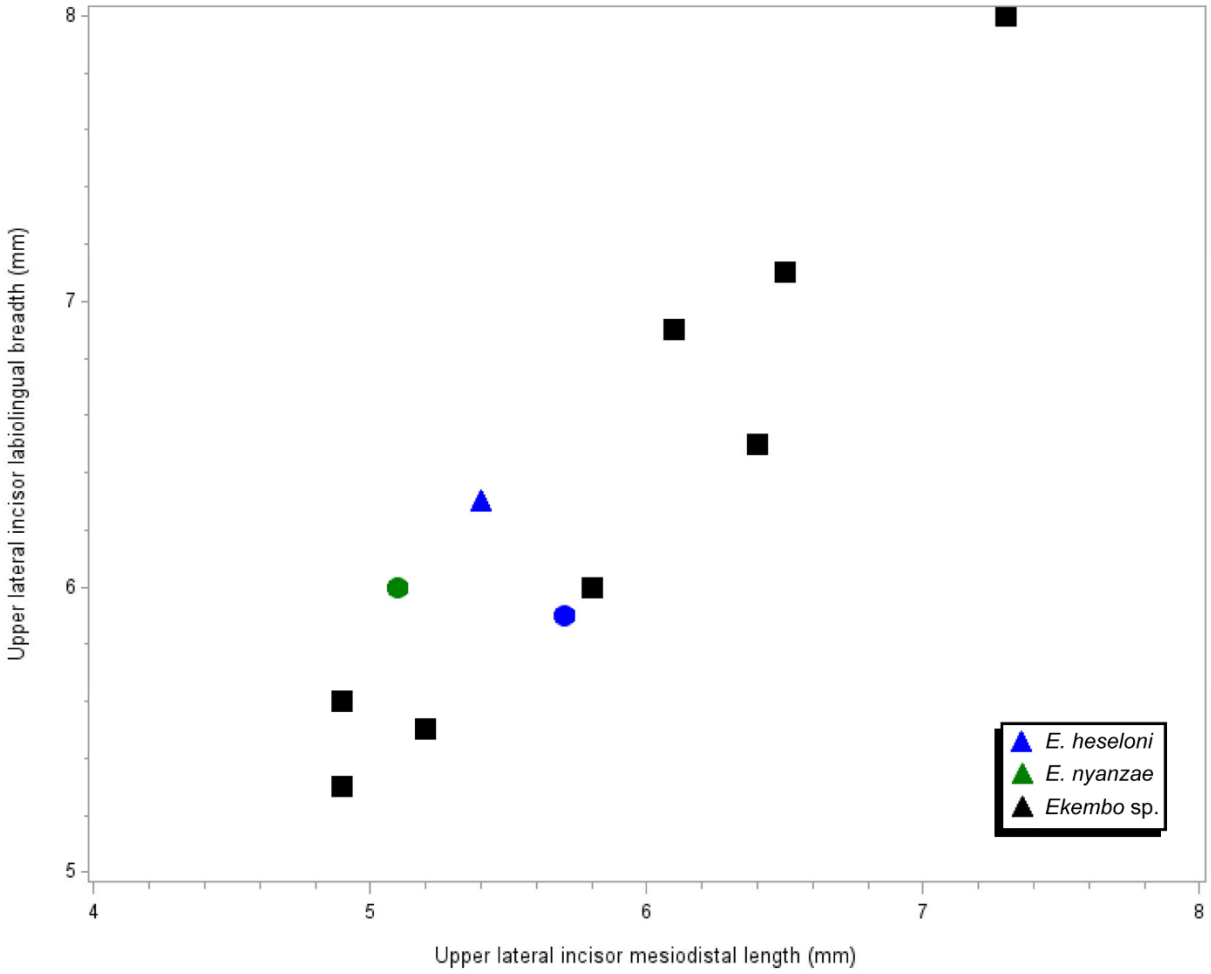

Figure S3: Bivariate plot of I^2 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S4

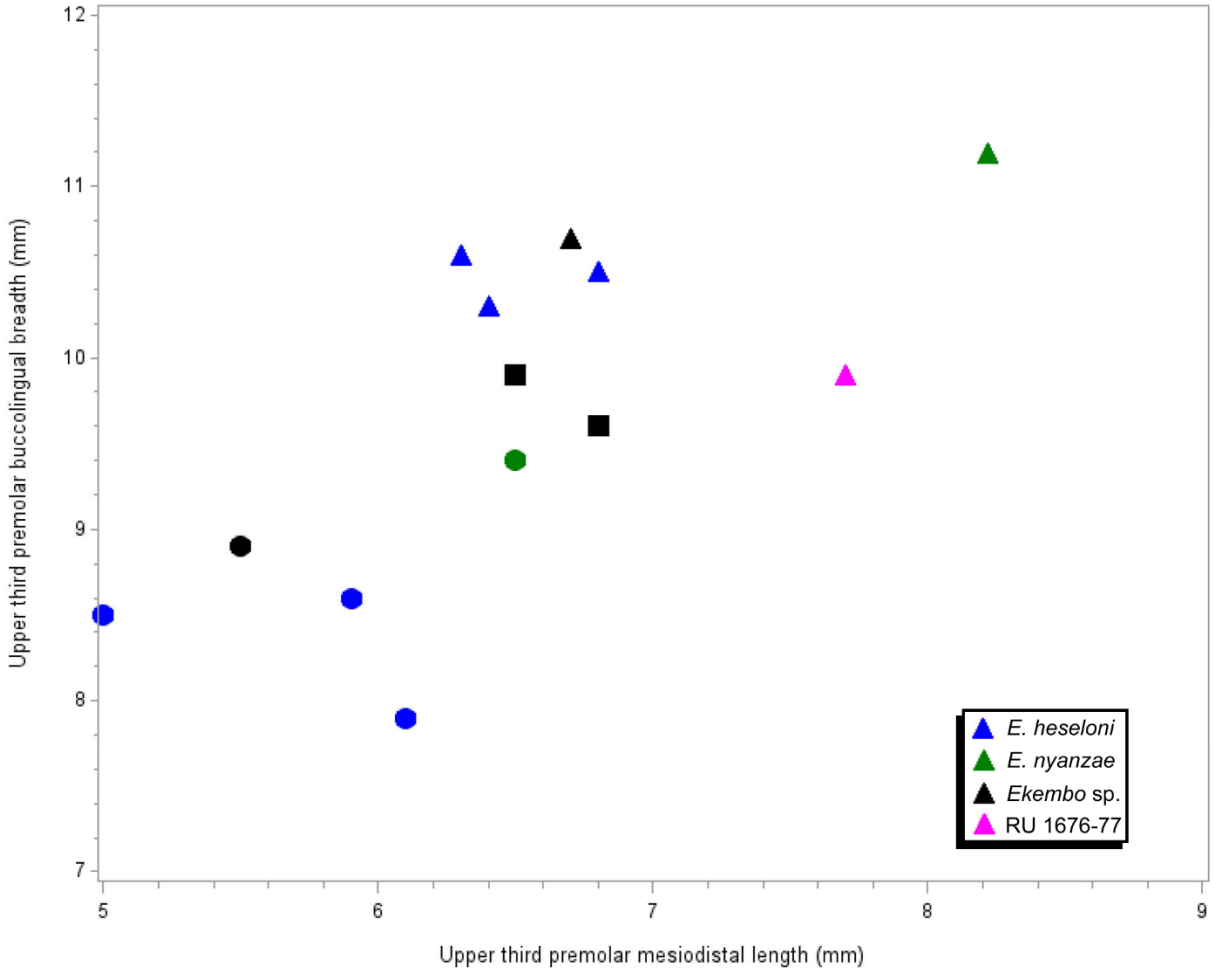

Figure S4: Bivariate plot of P^3 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S5

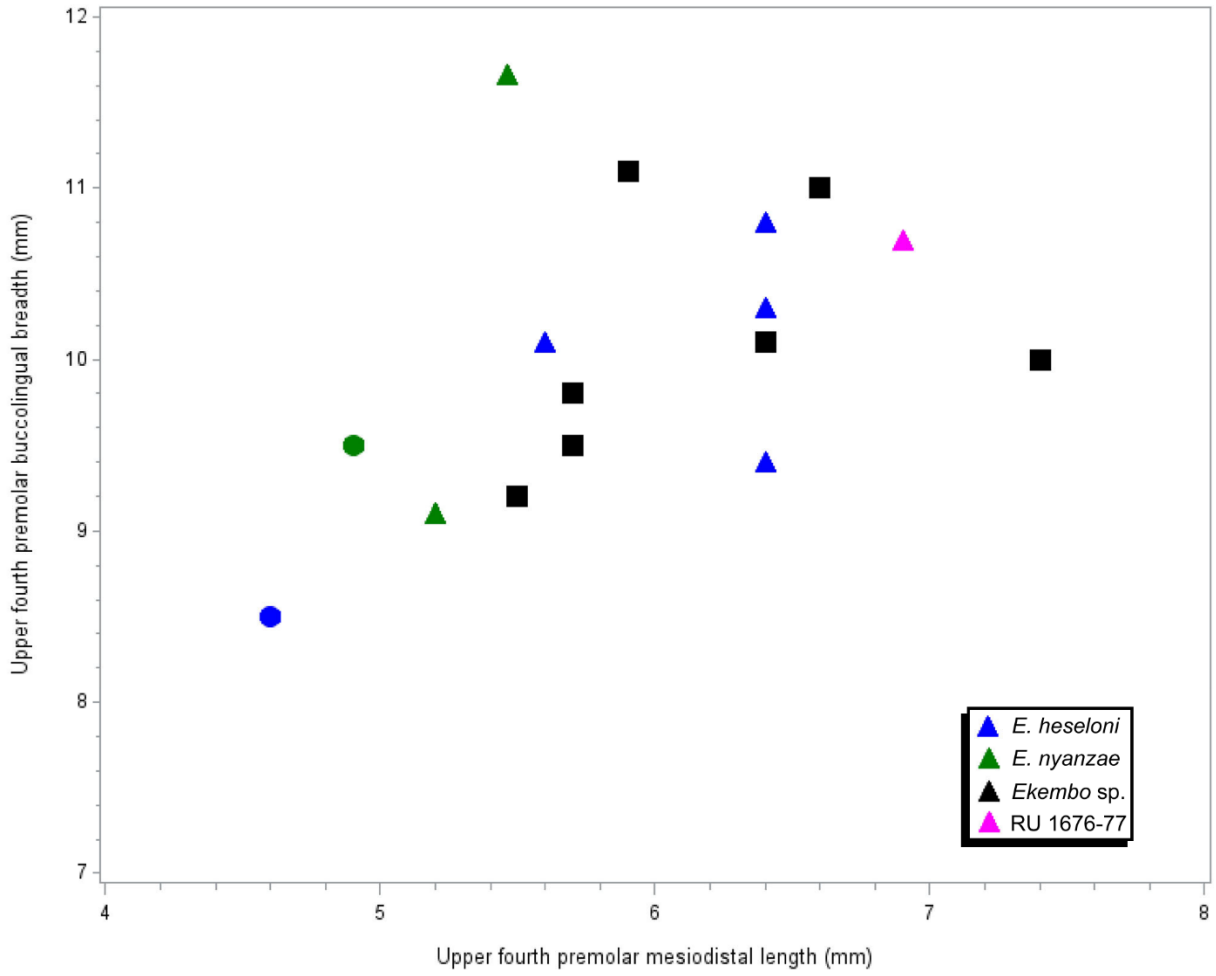

Figure S5: Bivariate plot of P^4 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S6

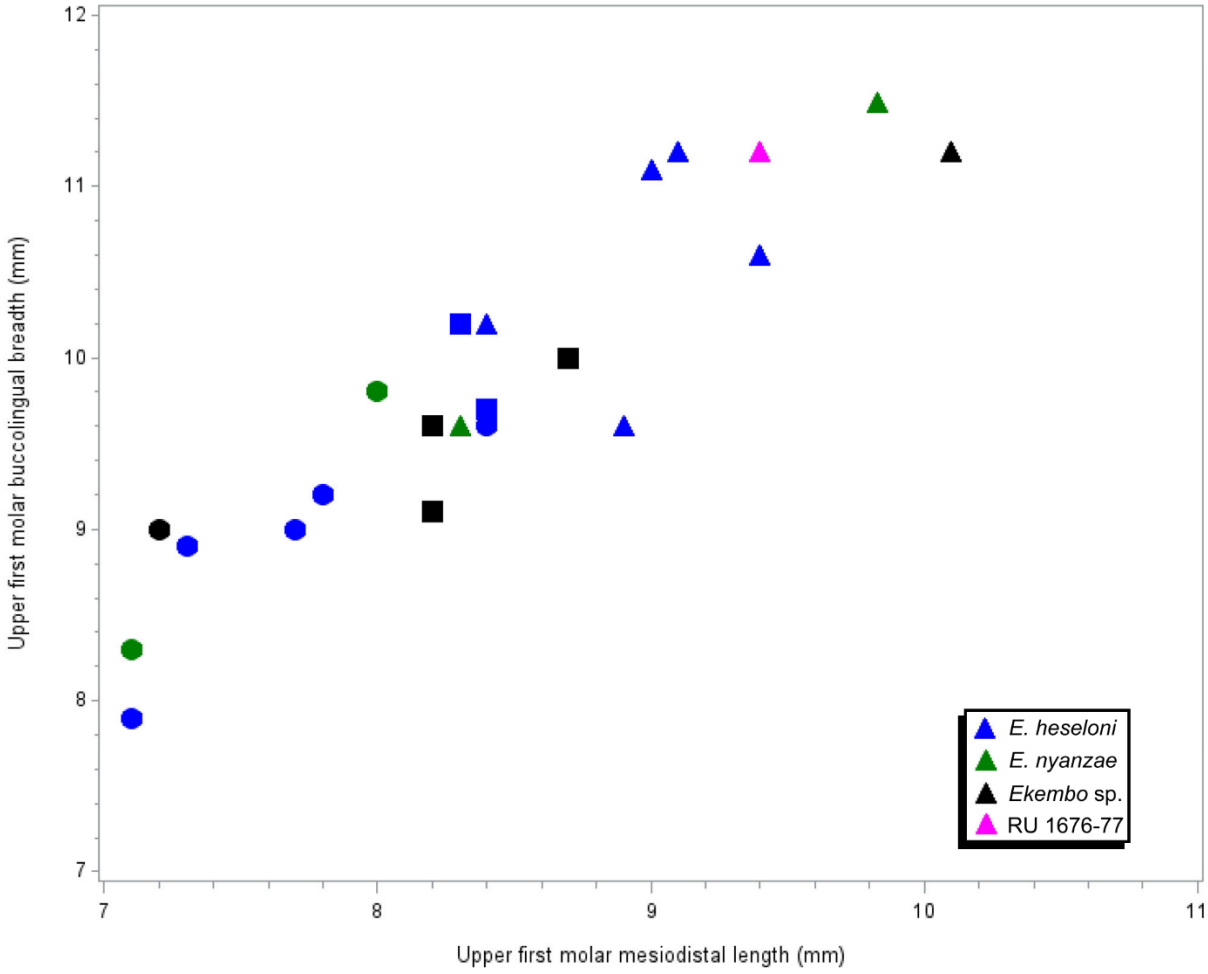

Figure S6: Bivariate plot of M^1 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S7

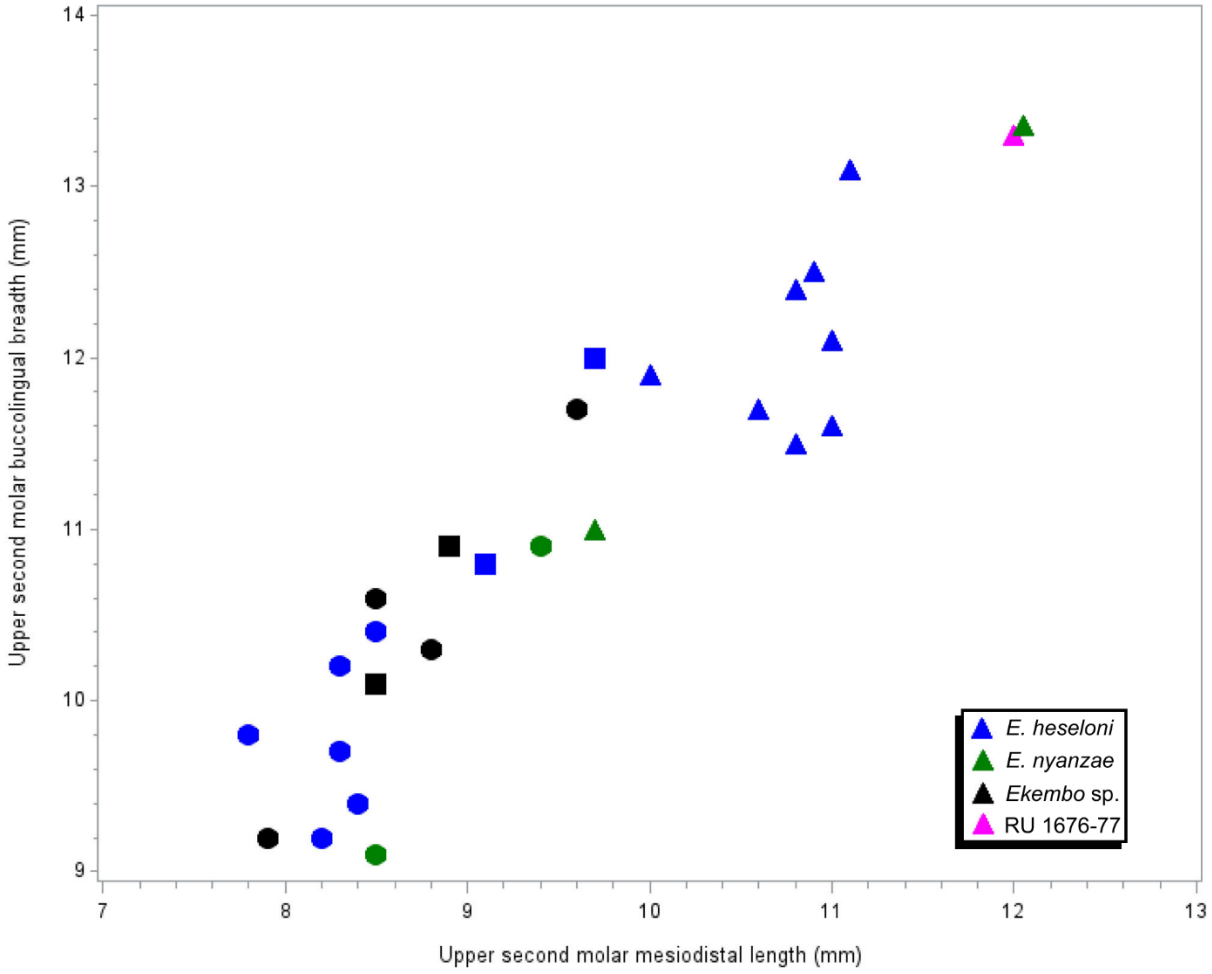

Figure S7: Bivariate plot of M^2 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S8

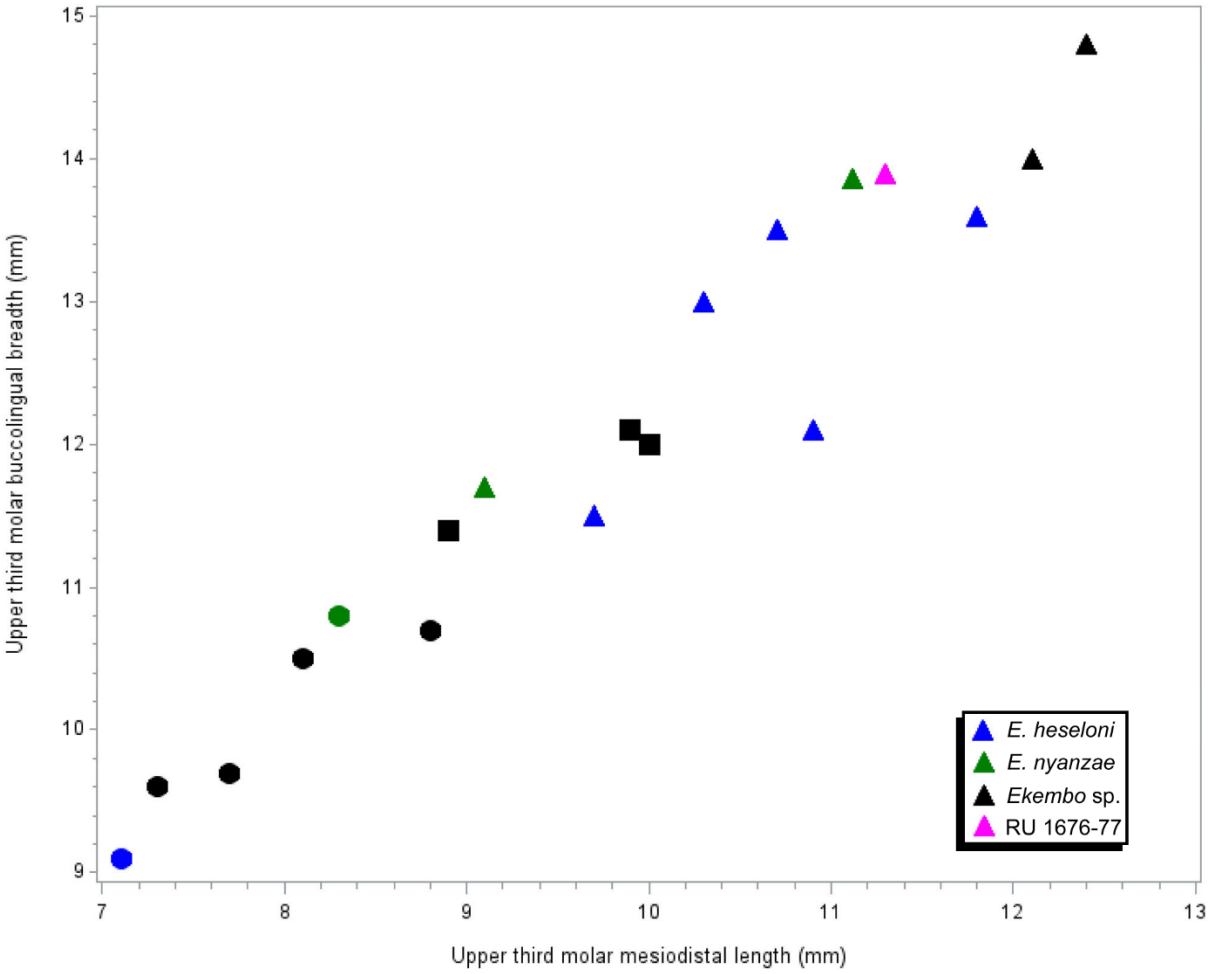

Figure S8: Bivariate plot of M^3 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S9

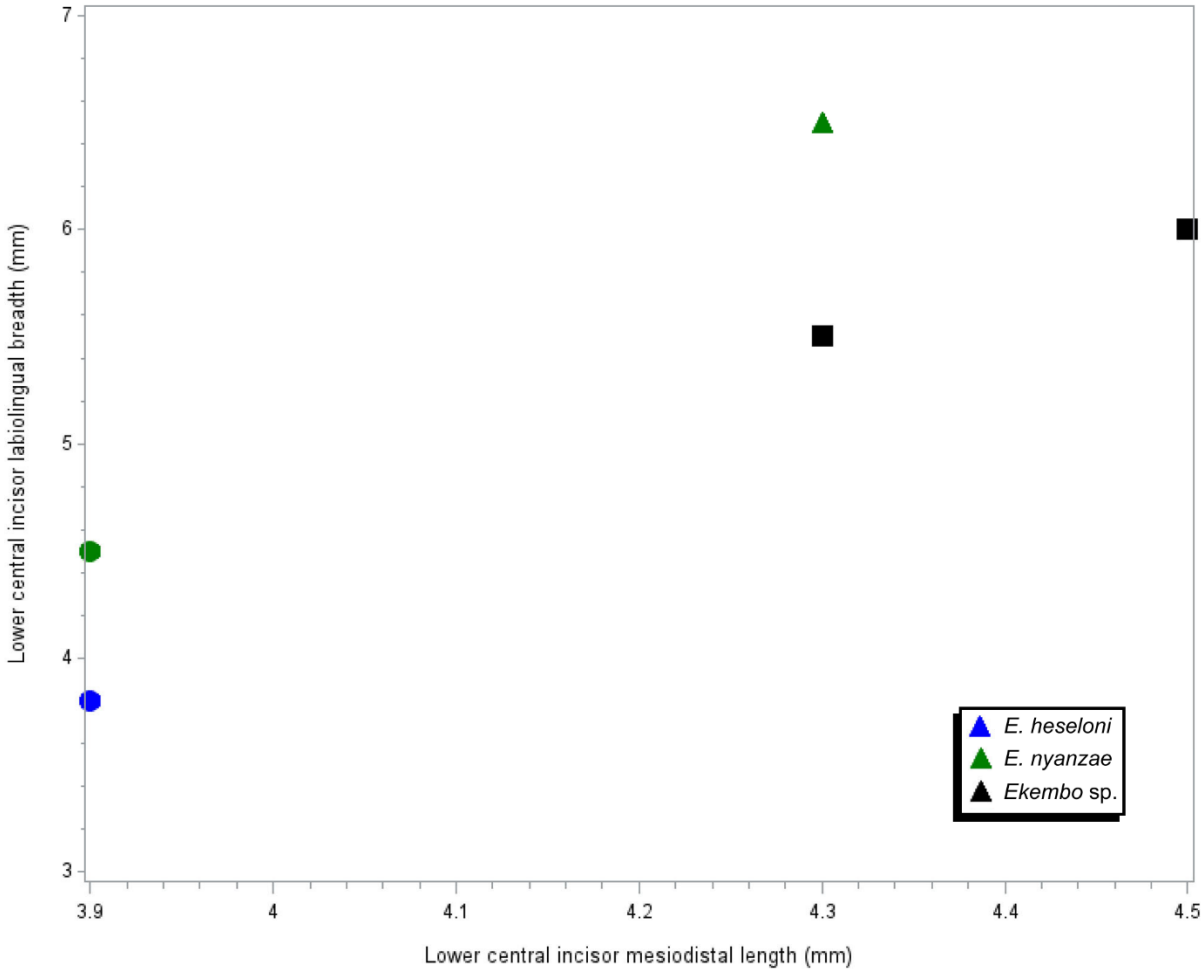

Figure S9: Bivariate plot of I_1 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S10

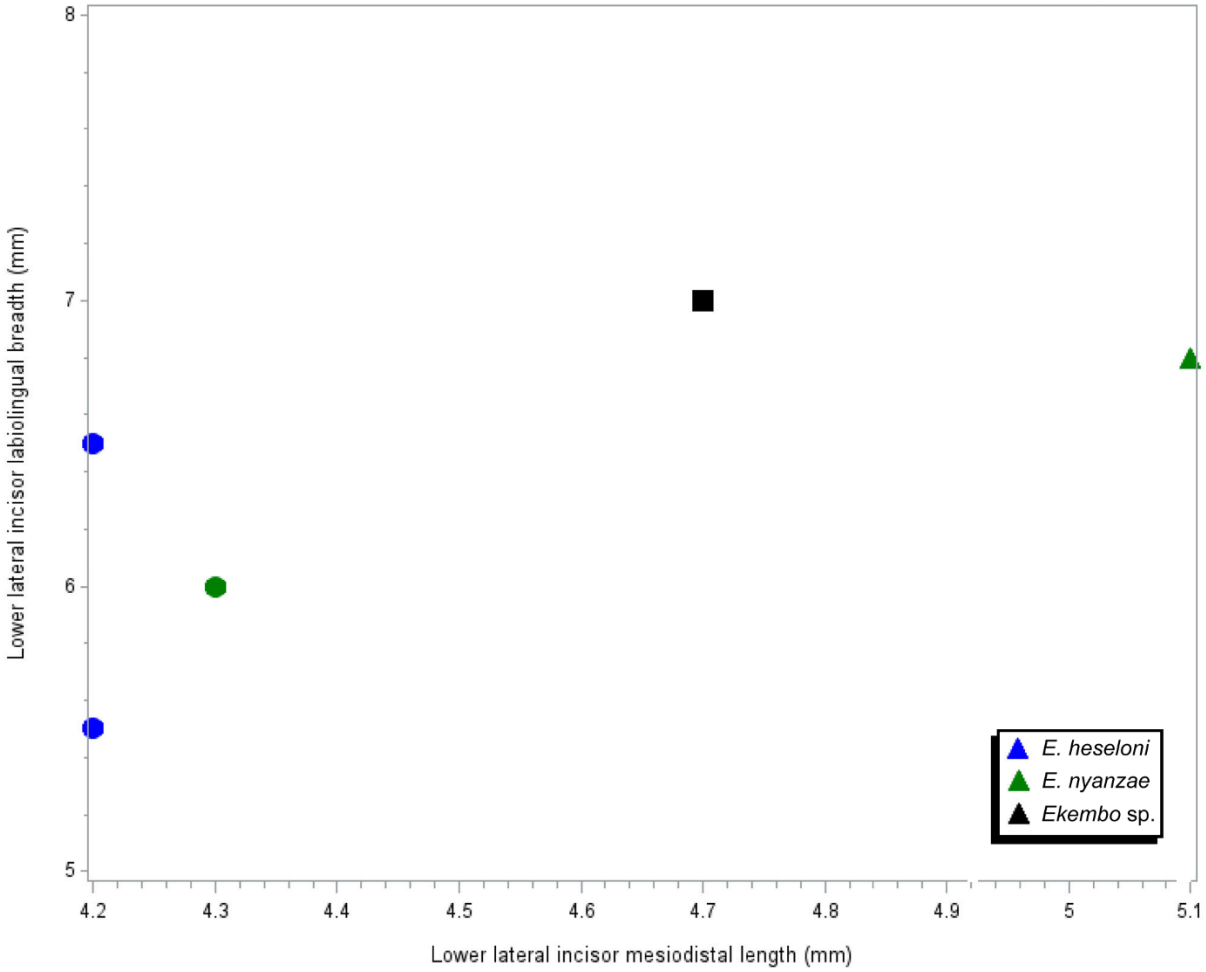

Figure S10: Bivariate plot of I_2 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S11

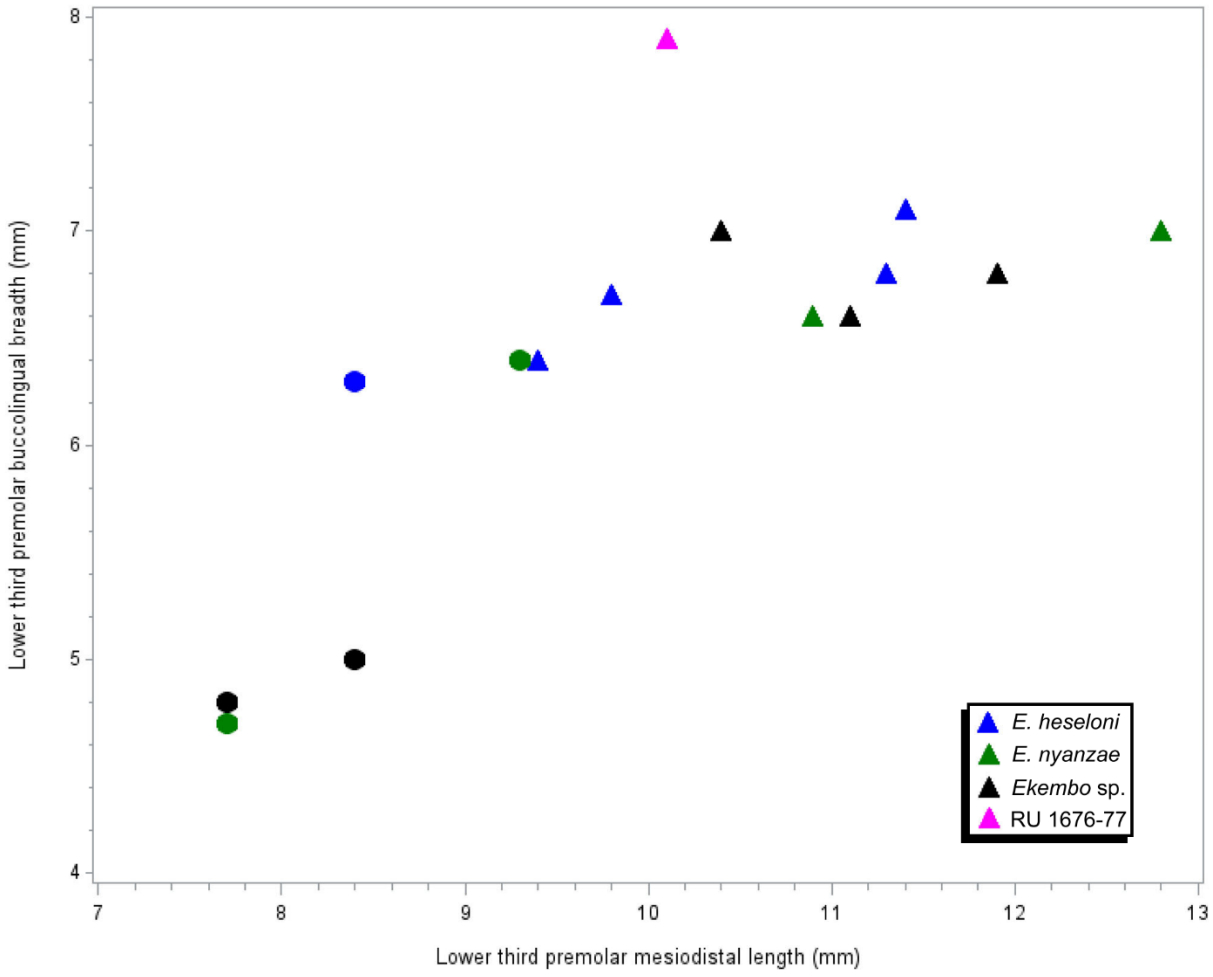

Figure S11: Bivariate plot of P_3 mesiodistal and labiolingual dimensions. Circles represent female specimens and triangles represent male specimens.

SUPPLEMENTARY FIGURE S12

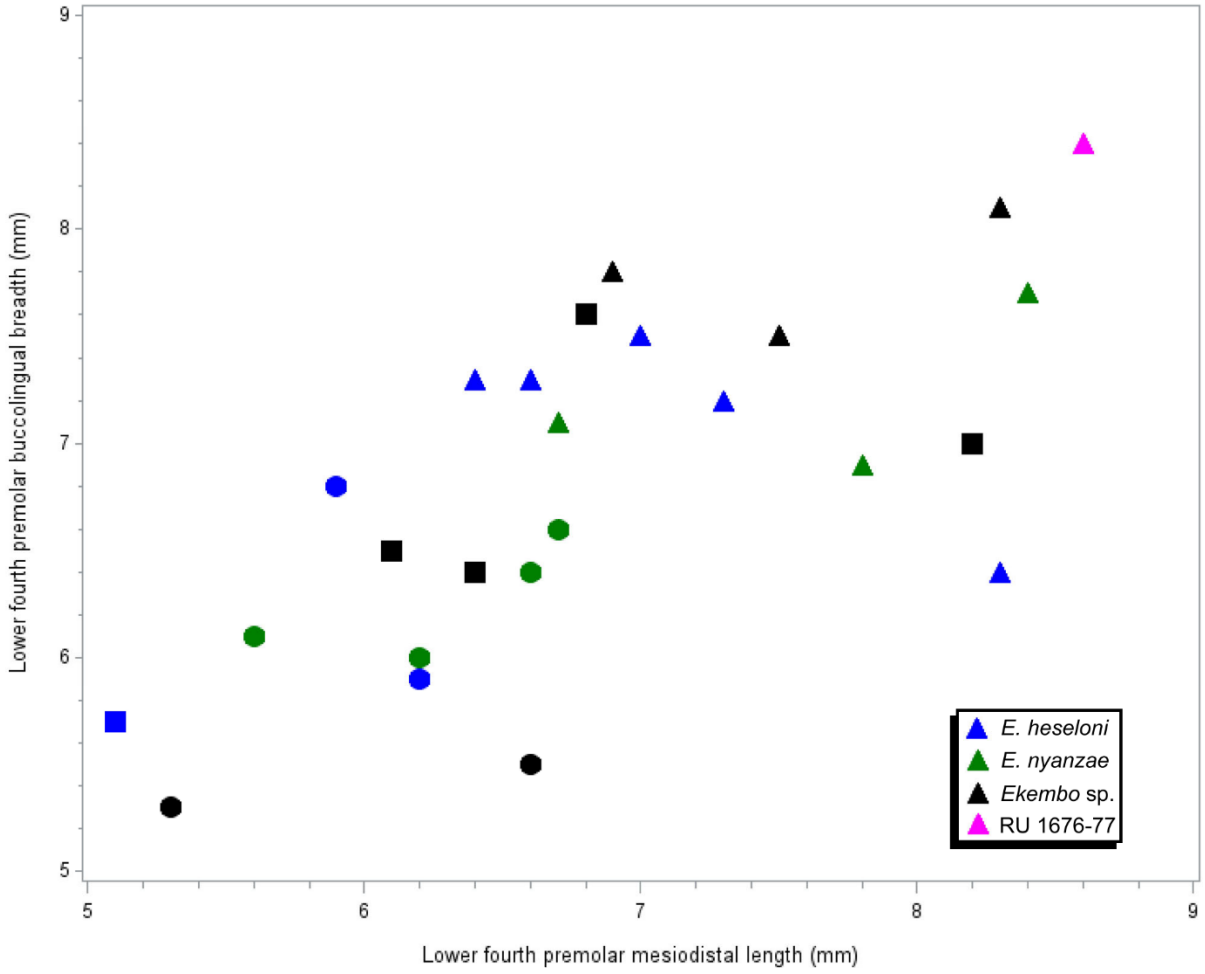

Figure S12: Bivariate plot of P_4 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S13

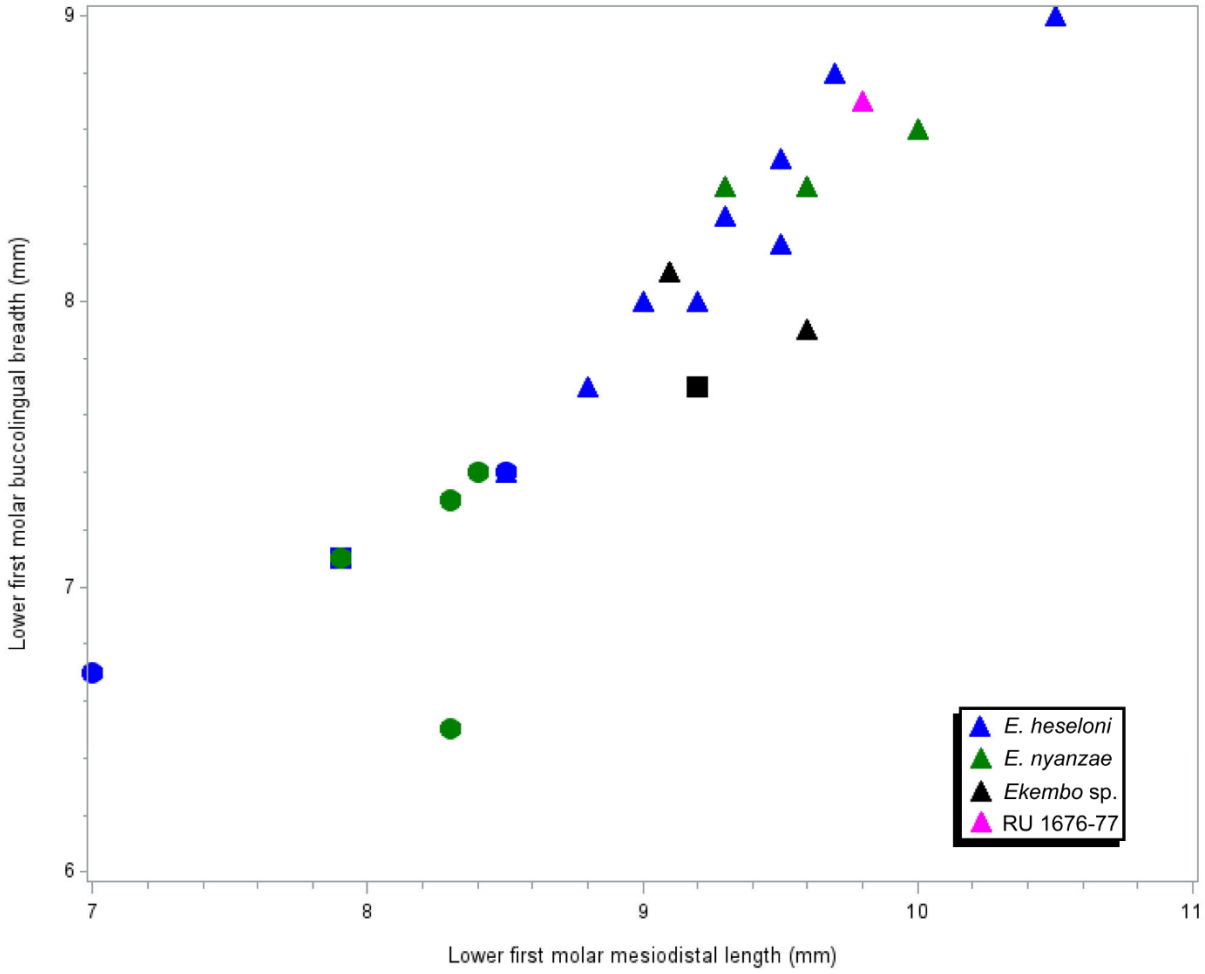

Figure S13: Bivariate plot of M_1 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S14

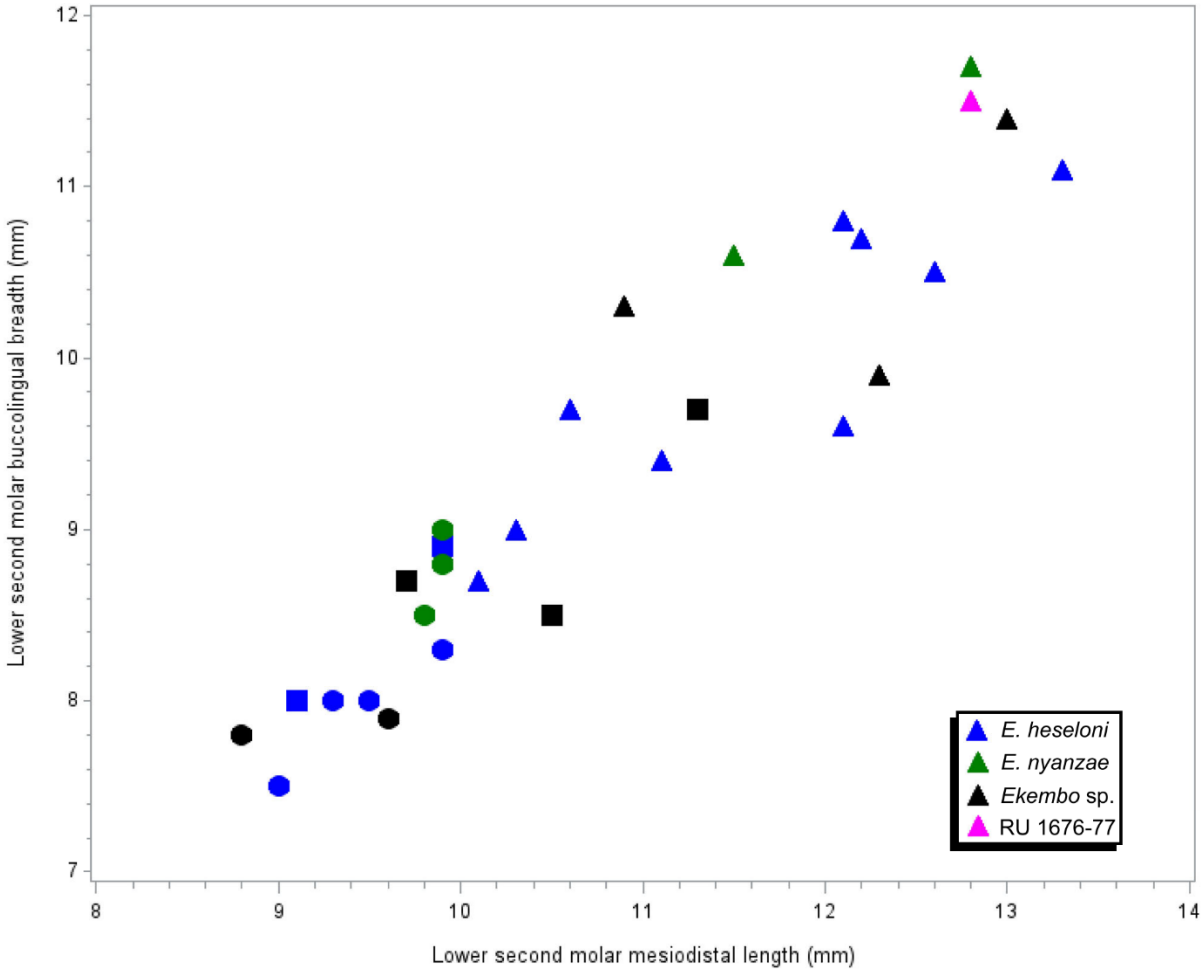

Figure S14: Bivariate plot of M_2 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.

SUPPLEMENTARY FIGURE S15

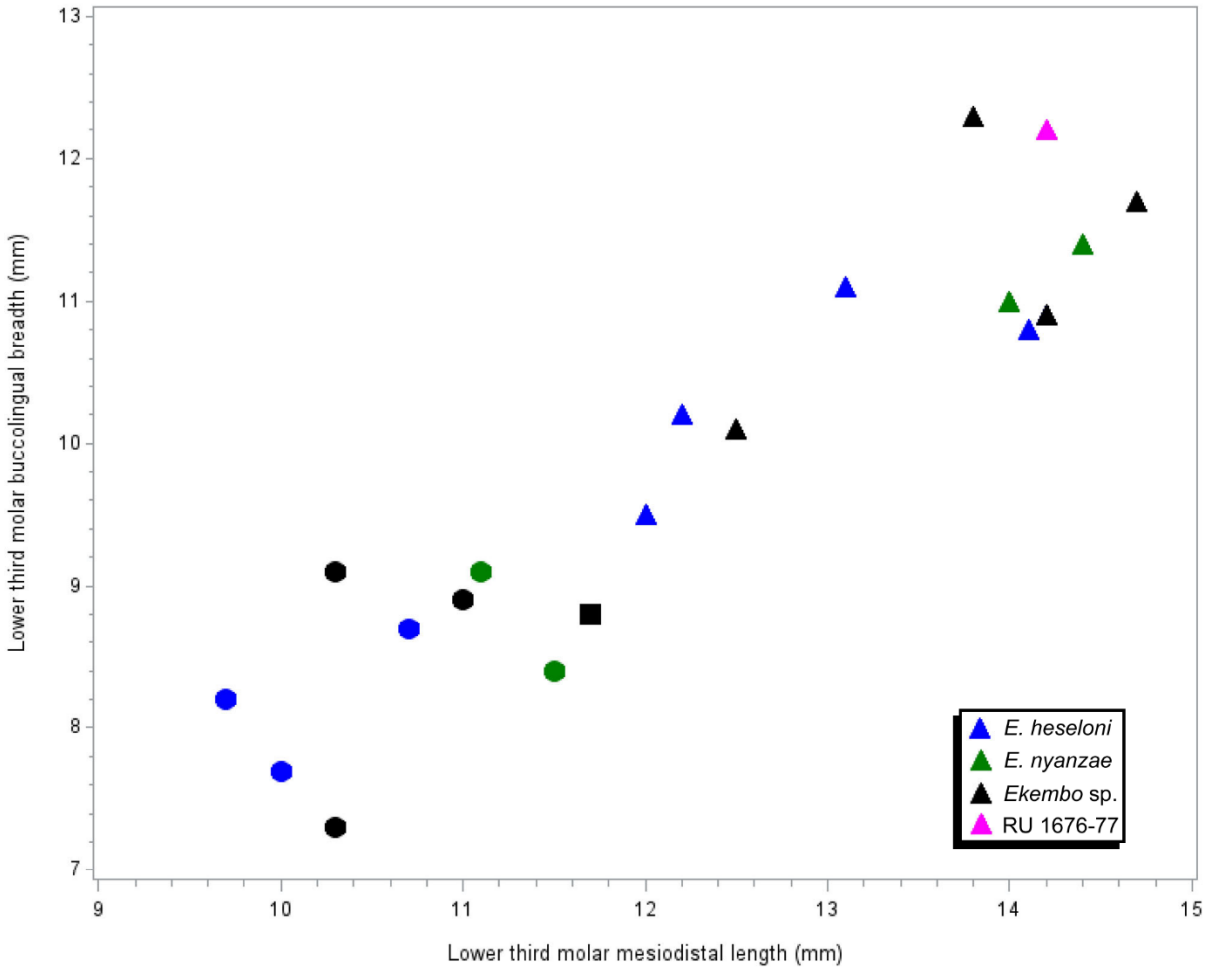

Figure S15: Bivariate plot of M_3 mesiodistal and labiolingual dimensions. Circles represent female specimens, triangles male specimens, and squares are specimens not assigned to sex.