Title:

A detailed assessment of the maxillary morphology of *Limnopithecus evansi* with implications for the taxonomy of the genus

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Abbreviations:

KNM – Kenya National Museums; SO – Songhor; BUMP – Boston University/Uganda Museum/Makerere University Paleontology Project; UMP – Uganda Museum, Paleontology; M – British Museum of Natural History (now The Natural History Museum, London); MD – mesiodistal; BL – buccolingual.

Abstract

Limnopithecus is a small-bodied catarrhine genus that is widespread throughout early Miocene sites in East Africa. Although two species of this genus have been described – *Limnopithecus legetet* (type species) and *Limnopithecus evansi* – they are poorly known anatomically and their systematic positions remain unresolved. Here, we provide detailed descriptions and comparisons for two well-preserved maxillary specimens that we attribute to *L. evansi*. These specimens come from the type locality of the species, Songhor in Western Kenya, and add greatly to our knowledge of its dentognathic morphology. Together, they preserve the entire unilateral upper dentition, with overlapping elements demonstrating conspecificity, and provide new information about I² morphology and aspects of the palate, nasal aperture, and maxillary sinuses.

Detailed morphological comparisons suggest that specimens referred to *Limnopithecus* from Songhor, Koru, and Rusinga share a unique I² morphology not found in any other early Miocene catarrhine. This argues in favor of congeneric status for *L. evansi* and *L. legetet*. Moreover, features such as a broad palate, premolar morphology, and the relative proportions of the premolars of *L. evansi* distinguish it from *Lomorupithecus harrisoni*, another early Miocene catarrhine from Napak, Uganda. This finding challenges a recently proposed taxonomic interpretation that *Lomorupithecus* and *L. evansi* are conspecific. Our results underscore the distinctiveness of *L. evansi* and *Lo. harrisoni*, thereby reaffirming the validity of the taxon *Lo. harrisoni* and indicating that the Songhor and Napak catarrhine communities were relatively distinct, despite their apparent contemporaneity.

Introduction

Excavations during the 1988-1996 field seasons at the early Miocene locality of Songhor in western Kenya uncovered many catarrhine specimens, including two maxillary fragments referred to *Limnopithecus evansi* (Nengo and Rae, 1992). As this species was previously known only from relatively incomplete material consisting largely of isolated teeth, the discovery of these specimens added greatly to our knowledge of the species' dentognathic morphology. They are the most complete maxillae of *L. evansi* found to date and together preserve the entire unilateral upper dentition, overlapping in P³⁻⁴. One specimen preserves an intact I², which was previously unknown in this species (Harrison, 1988). Here, we describe these maxillae in detail and use this information to evaluate the recent taxonomic proposal that *L. evansi* is generically distinct from *L. legetet* and instead conspecific with *Lomorupithecus harrisoni*, another early Miocene catarrhine known only from Napak, Uganda (Harrison, 2010, 2013; Pickford et al., 2010).

Background and history of the genus Limnopithecus

Hopwood (1933) erected the taxon *Limnopithecus legetet* for material from the Legetet Formation deposits at Koru. He assigned only two specimens to the species – the holotype, an adult mandible fragment with only two teeth, and the paratype, a juvenile mandible fragment preserving dC₁-dP₄ – emphasizing similarities to both *Pliopithecus* and to modern gibbons. MacInnes (1943), describing new material largely from Songhor and Rusinga, assigned additional specimens to *L. legetet* and also named a

second species, *L. evansi*, based on three mandibles and isolated lower teeth from Songhor. *L. evansi* is distinguished from *L. legetet* in exhibiting molars that are slightly larger overall yet relatively narrow for their length (length-breadth index < 90), a shallow mandible that decreases in depth posteriorly, and a slightly different arrangement of the lower molar cusps (MacInnes, 1943). Le Gros Clark and Leakey (1951) were unconvinced that these differences warranted species-level distinction, but it was Andrews (1978), in a larger study of East African fossil catarrhines, who formally synonymized *L. evansi* with *L. legetet*.

Following extensive fieldwork at both the Songhor and Koru localities that greatly expanded the small-bodied catarrhine collections, Harrison (1981) proposed that *Limnopithecus* from Songhor was truly distinct from the material from Koru (including Legetet Hill and Chamtwara). He resurrected *L. evansi* and provided a formal diagnosis differentiating it from *L. legetet* in exhibiting taller incisors, buccolingually expanded upper premolars and molars, relatively smaller M_3/M^3 , low rounded occlusal crests on the molars and premolars, and a taller mandibular corpus (Harrison, 1982, 1988).

To date, specimens from several early Miocene sites in Kenya and Uganda have been referred to *Limnopithecus* (Hopwood, 1933; MacInnes, 1943; Le Gros Clark and Leakey, 1951; Bishop et al., 1969; Harrison, 1981, 1982, 1988, 2002, 2010). The genus appears restricted to the early Miocene, except for possible middle Miocene occurrences at Kipsaramon (Pickford et al., 2010) and Fort Ternan (Andrews and Walker, 1976; Andrews, 1978; Harrison, 1982). In Kenya, *L. evansi* is known only from Songhor and the Mteitei Valley localities in western Kenya, whereas *L. legetet* is thought to be

present at the early Miocene localities Koru, Legetet, Chamtwara, Rusinga, and Williams Flat (Harrison, 2010). In Uganda, isolated teeth from both Napak and Bukwa have been referred to *L. legetet* (Harrison, 1981, 1982, 1988). Moreover, Harrison (1982) indicated that *L. evansi* might also be present at Napak localities IV and V, and noted that these would be the only known localities where *L. evansi* and *L. legetet* are found together. After further study, he reaffirmed the presence of *L. evansi* at Napak but without referring individual specimens to this taxon (Harrison, 2010, 2013). Pickford et al. (2010) likewise reported that *L. evansi* and *L. legetet* co-occur at Napak localities I, IV, V, and IX.

Despite this wide distribution of *Limnopithecus* in the early Miocene, the phylogenetic affinities of the genus are poorly understood. Andrews (1978) provided character support demonstrating that *Limnopithecus* is more like *Proconsul* than *Dendropithecus*, and suggested that a common problem with previous studies of fossil catarrhines was the tendency to group species of similar size together. Harrison (2010, 2013) listed *Limnopithecus* as a stem catarrhine, but refrained from assigning it to a particular family. Several cladistic analyses have included *Limnopithecus* and are consistent in placing it among stem catarrhines. However, its exact placement relative to other stem taxa differs from study to study (Singleton, 2000; Rossie and MacLatchy, 2006; Rossie and Seiffert, 2006; Stevens et al., 2013).

Taxonomic status of Lomorupithecus harrisoni and Limnopithecus evansi

Lomorupithecus harrisoni is a small-bodied catarrhine known only from the holotype maxilla and facial fragment (BUMP 266) and a paratype juvenile mandible (BUMP 268), both discovered in ~20 Ma deposits at Napak IX, Uganda (MacLatchy et al., 2006; Rossie and MacLatchy, 2006). Rossie and MacLatchy (2006) presented *Lo. harrisoni* as a distinct catarrhine taxon with possible affinities to pliopithecoids, but Pickford et al. (2010) and Harrison (2010, 2013) have suggested instead that the type specimen of *Lomorupithecus harrisoni* is better referred to *L. evansi*. Whereas Rossie and MacLatchy (2006) differentiated *Lomorupithecus* from other early Miocene catarrhines based in part on its mesiodistally narrow upper premolars, ovoid P⁴ with central fovea, and platyrrhine-like contact between the premaxillae and nasal bones, Pickford et al. (2010) used these same characteristics to liken BUMP 266 to *L. evansi*, while at the same time differentiating both from *L. legetet* at the genus level. In that taxonomic scheme, *Lo. harrisoni* becomes a junior subjective synonym of *L. evansi*, but the available genus name *Lomorupithecus* results in the new combination "*Lomorupithecus evansi*." Harrison (2010) presaged that arrangement, and later incorporated it into a revised taxonomy (Harrison, 2013), wherein both *L. legetet* and *Lo. evansi* are listed as superfamily and family incertae sedis. Adding further complexity, Pickford et al. (2010) reassign the paratype (BUMP 268) to *L. legetet*, whereas Harrison (2010) instead attributes it to *Micropithecus clarki*.

It is important to recall that any taxonomic propositions with regard to the upper dentition of *Limnopithecus* – including those presented here – must be regarded as provisional given that the type specimens of *L. legetet* and *L. evansi* are both mandibles,

and that there are currently no published specimens preserving both the upper and lower dentition. Nevertheless, the new morphology described for these two maxillae adds considerably to our knowledge of *L. evansi* and underscores fundamental differences between *Limnopithecus* and the holotype palate of *Lomorupithecus*.

Materials and methods

In addition to the two partial maxillae described in detail and illustrated in Figures 1 and 2, we also attribute several isolated upper teeth from Songhor to *L. evansi* (Table 1). The latter specimens are not described in detail, but illustrations are provided in the supplementary information (Figure S1) and their morphology is consistent with the teeth in the two maxillary specimens. All of these specimens were collected between 1988 and 1996 during expeditions to Songhor led by one of us (ION) in partnership with the National Museums of Kenya. All specimens derive from the Redbed Member of the main Songhor fossil locality (Pickford and Andrews, 1981). The two maxillae were collected from the surface and the isolated teeth were found during wet screening of excavated sediments. K/Ar dating of the Biotite Tuff (part of the Calcified Tuff Member, and located stratigraphically below the Redbed Member) produced age estimates of 19.9 ± 0.6 and 19.7 ± 0.5 Ma (Bishop et al., 1969). When corrected for new radiometric constants (Ness et al., 1980), these dates are 20.2 ± 0.5 and 20.4 ± 0.6 Ma (A. Hill, pers. comm.), suggesting an approximate age of 20 Ma for the Songhor main fossil assemblage. Although updated Ar/Ar dating is currently being undertaken,

Bishop et al.'s (1969) approximate age is well supported by biochronological comparisons to other localities in the region (Pickford, 1981; Cote, 2008).

All specimens listed in Table 1 are stored in the Paleontology Section of the Earth Sciences Department at the National Museums of Kenya, Nairobi. Descriptions and comparisons were made from original specimens housed in the National Museums of Kenya, Uganda Museum, and The Natural History Museum (London), as well as to published photographs of specimens from Napak that were not available for study (Pickford et al., 2010). All measurements were made with sliding digital calipers on original specimens, except where noted, and recorded to the nearest 0.1 mm (Table 1; Figure S2, S3). Dental terminology follows Harrison and Gu (1999) except that we distinguish the distal fovea as separate from the talon basin.

[Table 1 positioned roughly here]

[Figure 1 positioned roughly here]

[Figure 2 positioned roughly here]

Results

Morphological Descriptions - KNM-SO 22259

This specimen preserves most of the anterior lower face on the right side including about one third of the nasal aperture, the external premaxillo-maxillary surface from I^2 back to P^4 and extending superiorly above the canine root, the anterior portion of the maxillary sinus, and some of the palatine process from the incisive

fenestra back to the first molar position and extending medially almost to the intermaxillary suture. The I^2 , canine with broken tip, P^3 , and P^4 are preserved in place (Figure 1).

The premaxilla is demarcated from the maxilla by what appears to be a patent premaxillary suture extending from the superior-most extent of the specimen down into the I^2 -canine diastema and medially toward the incisive fenestra. We cautiously interpret this as a suture rather than a break because the external superior aspect follows a sigmoid pattern into the diastema whereas a break would be expected to propagate straight through the weaker bone surrounding the I^2 alveolus. Moreover, it is continuous onto the palate surface where it exhibits a slightly oscillating morphology typical of this suture in catarrhines. The suture is lateral and superolateral to the nasal aperture as it travels superiorly, and based on its preservation above alare (the most lateral point on the nasal aperture margin) it would likely have extended up to the nasal bone; the superior extent of the suture, however, cannot be determined. There is a small break running from the inferolateral nasal aperture to the premaxillary suture, just above the I^2 root, but this appears to have occurred after fossilization and without causing any distortion. A small bit of distortion can be observed on the palate surface, where the posterior premaxilla has been warped inferiorly resulting in a small ridge near the I^2 alveolus.

Approximately 8 mm of the nasal aperture is preserved, from just above a superiorly placed alare (at the level of the canine root apex) down nearly to the midline. Although the alveolus for I^1 is completely absent, making the precise midline difficult to

ascertain, it is still possible to determine that this specimen would have exhibited a narrow elliptical aperture characteristic of other *Limnopithecus* specimens (Harrison, 2010). The I^2 root is lateral to the nasal aperture, and internally the atrioturbinal ridge extends anteriorly onto the premaxilla. A small segment of the nasolacrimal duct is visible at the apex of the inferior meatus, which exhibits lateral hollowing similar to other specimens of *L. evansi* (KNM-SO 443, KNM-SO 539) and to *Kalepithecus* (KNM-SO 417). The damaged palatal premaxilla obscures the morphology in the region of the incisive fenestra, and it is unclear whether any of the fenestra margin is intact. A large break in the maxillary palatine process gives the appearance of a very large incisive fenestra, but this is too posteriorly placed to be the posterior margin, as indicated by the position of the premaxillary suture.

The transition from the premaxilla to the maxilla on the external face is a flat region terminating posteriorly at the canine jugum. A very shallow canine fossa is posterior to this and the specimen is broken just where the face begins to widen into the inferior malar region above P^3/P^4 . Superiorly, the specimen is preserved to approximately 5 mm above the apex of the canine root, at which point the external facial surface becomes more vertical. There is no evidence of an orbital margin. An extensive maxillary sinus protrudes into the alveolar region between P^3 and P^4 , and superiorly reaches nearly to the line of the canine ridge well above the canine root apex. Inferiorly, the sinus penetrates below the level of the premolar root tips almost to the root bifurcation. Viewed inferiorly, the maxillary palatine process has a slight superior slope toward the midline, conveying the impression of a generally shallow anterior

palate. It is preserved posteriorly to the position of M¹ although the tooth itself is not preserved. Medially it is broken before reaching the intermaxillary suture.

The I² is highly asymmetric and expanded labiolingually. An exceptionally tall mesiolingual cingulum forms a thick 'heel,' which is approximately 50% of the crown height at the mesial shoulder, angling steeply toward the root as it runs distally (Figure 3A). Correspondingly, the distolabial shoulder is very low. Contact wear from the lower canine is observable under magnification only on the distal-most side of the crown whereas the mesial two-thirds of the cingulum appear unworn. There is no lingual pillar and no distal marginal ridge. Overall, the crown is relatively small compared to the size of the postcanine dentition.

The canine is broken ~ 5 mm from the cervix. Therefore its full height cannot be determined, although we estimate that at least half of the original crown height is gone. Its basal dimensions measure at the highest end of the *Limnopithecus* range (Harrison, 1988), suggesting that this is a male specimen. There is a ~2.5 mm diastema between the canine and I², and the crown is moderately bilaterally compressed. The mesial and distal ridges are sharp, and there is a strong honing facet for P₃ on the distolingual aspect of the tooth despite only a small degree of wear on other teeth. Only the base of the mesial groove is preserved, but it exhibits a slight degree of wear from the lower canine and appears to have been relatively shallow. A lingual cingulum is present, running from the mesial groove to the distal ridge. This is more strongly developed than that in *Kalepithecus* males (cf. KNM-SO 417), and is situated higher on the crown than in *Dendropithecus*, although whether it continued distally or was stepped down toward

the cervix cannot be determined because of the intruding honing facet.

The P³ is subtriangular in occlusal outline, with light apical wear on both the protocone and paracone. The buccal profile is nearly symmetric owing to pre- and postparacristae of similar length and slope. The cusps are roughly equal in occlusal area, but the protocone is more mesially positioned and lower than the paracone. A moderately developed postprotocrista runs distally to terminate at the junction of the lingual cingulum and distal marginal ridge. A strong preprotocrista initiates a well-developed mesial marginal ridge, which, together with a weak mesial crest, demarcates a small but distinct mesial fovea. The lingual cingulum is very well developed for a premolar, reaching around the mesial aspect of the protocone and then becoming a moderately developed distal marginal ridge. A weak buccal cingulum is also present, rising to pre- and postparastyles and continuous with a central buccal pillar, giving the buccal surface a trefoil appearance. The tooth lacks a distal transverse crest or central fovea.

The P⁴ is more oval in occlusal outline than the P³, owing to a mesiodistally narrower buccal face and correspondingly smaller distal fovea. The buccal profile is symmetric due to similar pre- and postparacristae, but these are shorter than those observed in the P³ as a result of a paracone that is more similar in height to the protocone. The protocone is large and mesially positioned but less so than the condition observed in the P³. Both cusps are lightly worn with dentine visible only on the tip of the paracone. Strong pre- and postprotocristae are distinct from the cingulum, which is very well developed and continuous with the mesial and distal marginal ridges around the

lingual surface of the protocone. The postprotocrista is angled slightly distobuccally rather than distally as in the P^3 , but likewise terminates at the junction of the cingulum and distal marginal ridge. The buccal face exhibits well developed pre- and postparastyles connected by a weak buccal cingulum and continuous with a small central buccal pillar. A mesial transverse crest is present, but there is no distal transverse crest or central fovea.

[Figure 3 positioned roughly here]

KNM-SO 22736

This specimen is a right maxilla that preserves the complete P^3 through M^3 , part of the palate including the midline opposite $C-M^1$, and the base of the zygomatic process of the maxilla (Figure 2). The teeth in this specimen are slightly more worn than those of KNM-SO 22259. KNM-SO 22736 is also smaller, with dental measurements near the mean values for *L. evansi* (Table 1; Harrison, 1988).

The specimen terminates anteriorly near the premaxillary suture of the palate; the external maxillary surface is sheared off anterior to P^4 between the maxillary sinus and incisive fenestra leaving only a small portion of the canine alveolus. A thickening of the palatine process in the region of P^{3-4} results in a gradual incline of the anterior nasal cavity floor, which then narrows into a chute sloping down into the incisive fenestra. An extensive maxillary sinus persists anteriorly as far as the roots of P^4 , posteriorly past M^3 , and penetrates the zygomatic process of the maxilla. Adhering matrix makes it

impossible to determine the inferior extent of the sinus. The zygomatic root arises low on the face, approximately 2.5 mm superior to the alveolar plane above M^1/M^2 .

In inferior view, a small portion of the premaxillary suture is patent, extending to the incisive fenestra, and exhibits an oscillating or “jagged” border. The fenestra breadth is estimated to be approximately 4.1 mm based on extending the preserved midline anteriorly. The palate is shallow as far posteriorly as it is preserved to the midline (mid- M^1), and exhibits a slight ridge at the intermaxillary suture. Only the most lateral aspect of the palate is preserved from mid- M^1 to M^3 . A large, well-excavated gutter leading into the greater palatine foramen begins at M^1 and deepens out to distal- M^3 where a small lateral portion of the foramen is preserved. Approximately 1-2 mm of the left palatine process is preserved beyond the midline ridge, exaggerating the apparent breadth of the palate. Nevertheless, the palate is quite broad relative to its dental size, measuring approximately 8.5 mm horizontal distance from the lingual margin of M^1 to the midline. For comparative purposes, we plotted this measurement (scaled for size by the geometric mean of: this measurement plus the MD and BL dimensions of P^3 , P^4 , M^1) in KNM-SO 22736 and in nine other well-preserved early Miocene specimens (Figure 4). Only *Ekembo* from Rusinga Island (material formerly attributed to *Proconsul* [McNulty et al., 2015]) and *Micropithecus* from Napak have similarly broad palates.

[Figure 4 positioned roughly here]

The teeth of KNM-SO 22736 are lightly worn, with small dentine pits exposed on

all teeth, but only on the lingual cusps of the molars. In contrast with KNM-SO 22259, however, which exhibits larger dentine pits on the cusp tips, the occlusal faces on the cusps and in the basins of this specimen are more heavily worn. KNM-SO 22736 has a P³ that is subtriangular in outline but the lingual margin is rounded rather than angular. The buccal profile is somewhat more asymmetric than in the P³ of KNM-SO 22259, with a preparacrista that is longer than the postparacrista. The mesiobuccal portion of the crown extends well onto the buccal root, a trait that is variable in the samples referred to *L. evansi* (compare KNM-SO 443 and KNM-SO 421). The protocone has a smaller occlusal area relative to the paracone, and is also more mesially positioned on the crown. The paracone is taller than the protocone. The pre- and postprotocristae initiate the mesial and distal marginal ridges, respectively, but unlike in KNM-SO 22259 the lingual cingulum is only weakly developed. The postprotocrista appears less well developed than in KNM-SO 22259, but is somewhat obliterated by wear. It is oriented distally from the protocone and then curves buccally near the distal marginal ridge. Both mesial and distal marginal ridges are thin but sharp. The buccal cingulum is weakly present only adjacent to the pre- and postparastyles, the latter of which is more strongly developed. The mesial transverse crest is quite distinct but low and rounded; there is no evidence of a distal transverse crest or central fovea.

The P⁴ is ovoid in outline, with a symmetric buccal profile that is shorter than that of the P³. The protocone is larger in occlusal area than the paracone, and slightly more mesial in position; the two cusps are nearly equal in height. A strong lingual cingulum extends lingually from the mesial face of the protocone, wraps distally around

that cusp and terminates near the lingual margin of a small distal fovea. A small but distinct mesial fovea is demarcated mesiolingually by a weak preprotocrista and distally by a weak mesial transverse crest. A strong postprotocrista is slightly angled distobuccally from the protocone to intersect the lingual cingulum and distal marginal ridge. The buccal cingulum is more clearly visible than on P^3 with small pre- and postparastyles. There is no central fovea and no distal transverse crest.

The molars are lightly worn and well preserved. Overall, they are relatively square in shape, but somewhat wider (BL) than long (MD); $M^2 > M^3 > M^1$. The M^1 has a strong lingual cingulum from the mesial side of the protocone back to the distolingual aspect of the hypocone. Mesial and distal marginal ridges are very weak and only present on the buccal half of the crown. There is only a faint trace of a buccal cingulum, most evident between the paracone and metacone. There is a slight but distinct swelling in the area of the paraconule, but it is far less developed than on M^2 or M^3 . The trigon crests are clearly developed, and there is a strong mesiobuccally oriented preprotocrista. The paracone and metacone are of equal height and size. The hypocone is clear and distinct, well separated from the much larger protocone, and lacks a prehypocrista. There is a poorly developed hypocone-metacone crest present. The protocone is not buccally displaced relative to the hypocone (as is seen in *Kalepithecus*). The mesial fovea is small but distinct and there is an expansive talon basin.

Compared to the M^1 , the M^2 is larger and the mesial cusps in particular are taller and larger relative to the distal cusps. Development of cingula and the mesial and distal marginal ridges are similar to the M^1 . A large paraconule forms the lingual border of a

small mesial fovea, but the distal fovea is indistinct. Occlusal crests are low and blunt, and there is no sign of a hypocone-metacone crest, unlike on the M¹. There is a strong shelf-like lingual cingulum that wraps around from the mesial side of the protocone back to the distolingual aspect of the hypocone.

The M³ is not reduced in overall size, but both distal cusps are small compared to their counterparts in the first two molars and the hypocone is distobuccally displaced making the crown more mesiodistally elongate. The mesial half of the tooth is generally similar to M², but the paraconule is less developed and the mesial fovea is larger. The trigon crests are very weakly developed, and therefore the trigon and talon basins essentially form a single occlusal basin. The lingual cingulum forms a wide beaded shelf along the entire lingual face, connecting mesially with the mesial marginal ridge and then transitioning to a faint buccal cingulum. The distal marginal ridge is strong, but discontinuous with the buccal cingulum. There is no proper distal fovea but the talon basin is well developed.

Attribution to Limnopithecus evansi

The attribution of specimens KNM-SO 22259 and KNM-SO 22736 to *Limnopithecus* is rather straightforward. Although the holotype specimens of both *Limnopithecus* species are mandibles, and no known specimens currently referred to this genus preserve associated upper and lower dentitions, both of these maxillae are consistent with specimens attributed to *L. evansi* by Harrison (1982, 1988). They share several cranial features with other referred specimens, such as a tall and narrow nasal

aperture, a premaxillary component of the atrioturbinal, an expansive maxillary sinus that extends from P³ to beyond M³ and also into the zygomatic root, an orbital rim positioned anteriorly above the canine root (inferred from the position of the nasolacrimal duct [cf. Rossie and Smith, 2007]), and a shallow canine fossa. Dentally, these specimens can be attributed to *Limnopithecus* based on the following features: the canine is moderately bilaterally compressed, the upper premolars are broad with only slight cusp height heteromorphy, the molars have a rectangular occlusal outline with a broad lingual cingulum and large hypocone, and M³ is not reduced in size. Finally, the crown dimensions of each tooth are within the range of other specimens referred to *L. evansi* (Harrison, 1988: Table 5).

Although both specimens fit comfortably within the referred sample of *L. evansi*, they differ from each other in P³ morphology, particularly in the development of the lingual cingulum, which is faint in KNM-SO 22736 but strong in KNM-SO 22259. Harrison (1982) noted that *L. evansi* P³s show variable development of the lingual cingulum, with some, but not all, specimens possessing a shelf-like lingual cingulum. This corresponds well with our own observations of P³s referred to *L. evansi* as well as for other early Miocene catarrhine species. Hence, we interpret the difference in P³ cingular development between KNM-SO 22736 and KNM-SO 22259 as consistent with intraspecific variation.

Both specimens can reasonably be excluded from *Proconsul* and *Rangwapithecus* based on size alone. Likewise, these specimens are too small for *Dendropithecus* and lack the well-developed crests on the molars and premolars associated with that genus.

In addition the canine is less bilaterally compressed, the P³ is substantially less heteromorphic in cusp height, and the M¹ is squared rather than rectangular in outline. *Micropithecus*, which has never been documented at Songhor, can also be excluded because it possesses smaller teeth than these specimens and exhibits substantial cusp height heteromorphy in the premolars and ovoid molar occlusal outlines. *Kalepithicus* is the closest match in size for these specimens, after *Limnopithecus*, but is characterized by less compressed canines, absolutely larger premolars, and a buccally displaced protocone on the molars.

Within *Limnopithecus*, we refer these specimens to *L. evansi* based on diagnostic criteria provided by Harrison (1988, 2002, 2010). These include the overall weak development of occlusal crests on the premolars and molars and mesiodistally broad upper premolars. The distal cusps of the M³ in KNM-SO 22736 are underdeveloped, which is consistent with the diagnosis of *L. evansi* (Harrison, 1988), but the tooth is not reduced in size. We remain skeptical about the use of third molar reduction as a taxonomically meaningful feature given the high degree of variation in this feature among at least some early Miocene catarrhines (McNulty et al., 2015). The two species of *Limnopithecus* have also been separated geographically, with *L. evansi* typically recognized from localities along the Mteitei Valley – Songhor, Kapurtay, Mteitei Valley – and *L. legetet* more broadly at other Tindaret sites (Koru, Chamtwara), Kisingiri localities (Rusinga and Mfangano Islands), and at Napak, Uganda (Pickford, 1986; Harrison, 1988, 2002, 2010; Nengo and Rae, 1992; Pickford et al., 2010; McNulty, unpubl. data). Although these geographic distinctions may not hold up under further scrutiny,

attribution of these Songhor specimens to *L. evansi* is both morphologically justified and consistent with our current understanding of species distributions.

Discussion

Morphology of Limnopithecus evansi

Nengo and Rae (1992) noted the importance of specimens KNM-SO 22259 and KNM-SO 22736 in revealing for the first time the morphology of the I^2 , the relative proportions of the upper teeth, and the morphology and relative sizes of the upper molars, which are particularly helpful in distinguishing *L. evansi* from *Kalepithecus songhorensis*. In addition, these specimens also demonstrate that the upper dentition of *L. evansi* is generally characterized by strong lingual cingula on both the premolars and molars, although this varies in the P^3 , as described above; a broad palate relative to most other early Miocene catarrhine taxa (Figure 4), and an unusual I^2 morphology not seen in any other early Miocene catarrhines.

The I^2 morphology preserved in KNM-SO 22259 adds important new information about *L. evansi* and potentially about the cohesion of the genus *Limnopithecus*. Prior to the discovery of this specimen, the I^2 morphology was unknown in *L. evansi* and represented by only a few isolated specimens of *L. legetet* (Harrison, 1988). The distinctive I^2 morphology in KNM-SO 22259 – an exceptionally tall and thick mesiolingual cingulum that forms a ‘heel’ on the mesial aspect, slopes steeply toward the cervix as the cingulum runs distally, and results in a highly asymmetric incisor that is remarkably labiolingually thick – provides a clear criterion for referring specimens to this taxon

(Figure 3A). No other early Miocene taxon displays this cingular configuration, although the middle Miocene *Equatorius* has a spiral cingulum on its I² that slopes at a similar angle (Ward et al., 1999: Figure 4d). In that taxon, however, the cingulum is angled across the entire lingual aspect of the tooth rather than forming a distinct ‘heel’ on the mesial half of the lingual surface, as is seen in *Limnopithecus*. In addition, the cingulum in *Equatorius* is not as labiolingually broad, relative to crown dimensions, as that of *Limnopithecus*.

An additional isolated I² (KNM-SO 37964; Table 1) is broken just at the cingulum, but vestiges of the broken ridge nevertheless indicate a similar configuration to KNM-SO 22259. Importantly, this distinctive cingular morphology is also found in two of the three I²s assigned to *L. legetet* by Harrison (1982, 1988): KNM-CA 1871 from Chamtwara and KNM-RU 1938 from Rusinga (Figure 3B and 3C), although the latter specimen is relatively poorly preserved. This morphology is unique to *L. legetet* and *L. evansi* among known early Miocene catarrhines, and reinforces the unity of this genus (*contra* Pickford et al., 2010; Harrison, 2010). Pending further discoveries, an alternative interpretation – that the I² morphology is autapomorphic of *L. evansi*, and that species is found at Koru and Rusinga – is not warranted based on our current understanding of catarrhine taxonomic distributions (Harrison, 1988, 2002, 2010; Pickford et al., 2010). The Chamtwara specimen is particularly compelling in this regard given that nearly 100 specimens from this locality have been referred to *L. legetet* (Harrison, 1988: Table 2) but molars resembling *L. evansi* have yet to be documented.

One additional specimen (KNM-CA 1823; Figure 3D) identified by Harrison (1988)

as an I² of *L. legetet* does not exhibit the characteristic *Limnopithecus* cingular morphology, hence we exclude it from this taxon. Likewise, an isolated I² (UMP 66-33a) from Napak IV that was referred to “*Lo.*” *evansi* by Pickford et al (2010: 64, Figure 94) lacks the distinctive cingular morphology present in KNM-SO 22259 and in other *Limnopithecus* incisors. Instead, the cingulum is relatively low and is not sloped distally. Fleagle and Simons (1978) and Harrison (1982) both referred the Napak specimen to *Micropithecus*, which we believe is the correct attribution. An alternative explanation is that I² morphology varies substantially within *Limnopithecus* – as does, for example, development of the P³ cingulum – and hence this feature is not taxonomically meaningful. While we acknowledge this possibility, we do not favor this interpretation. The total morphological pattern of the I² morphology observed in KNM-SO 22259 and other specimens referred to *Limnopithecus* (Figure 3A, B, and C), including not only the height of the cingulum, but its thickness and strong distally oriented slope, in addition to the overall asymmetric construction of the tooth and labiolingual thickness, is distinctive from all other early Miocene catarrhines.

Another important feature revealed by these new specimens is the palate of KNM-SO 22736, which is preserved to the midline and therefore provides the first opportunity to directly assess palatal breadth in *L. evansi*. When compared to other early Miocene specimens, the KNM-SO 22736 palate is most similar to *Ekembo* from Rusinga Island and to the *Micropithecus* holotype from Napak (Figure 4). In contrast, palates of *Afropithecus* (which is deformed but nevertheless narrow [Leakey and Leakey, 1986a]), *Dendropithecus*, *Rangwapithecus*, *Morotopithecus*, *Turkanapithecus*, and the

purportedly congeneric *Lomorupithecus* are much narrower for their dental size. This result recalls Andrews' (1978) conclusion that *Limnopithecus* and *Ekembo* (then *Proconsul* from Rusinga) are in many ways similar once differences in body size are taken into account.

Results of our comparisons of palate breadth at M¹ differ in some ways from those obtained by Rae (1997, 1999) for the internal breadth between canines – a measurement that cannot be properly taken or estimated on KNM-SO 22736 since the midline is not preserved that far anteriorly. Where he found general similarity among several “proconsulids,” our assessment permits inclusion of a greater number of specimens and provides greater differentiation among taxa. Based on a cladistic analysis of facial characters, Rae (1997, 1999) concluded that successive broadening of the anterior palate was important in the differentiation of both hominoids and hominids. We do not suggest that this single character should be used for grouping *Limnopithecus*, *Micropithecus*, and *Ekembo* in Hominoidea (or even with each other), but new data about the morphology of *Limnopithecus* – including palate breadth, lateral hollowing of inferior meatus, and I² cingular configuration – will hopefully lead to better resolution among early Miocene catarrhines in future phylogenetic analyses. Some of these features may also provide insight into patterns of correlated shape change that may be associated with processes of facial shortening, a topic relevant to many aspects of hominoid evolution, including that of hominins.

Limnopithecus and Lomorupithecus

Recently, Pickford and colleagues (2010) and Harrison (2010, 2013) have suggested that the holotype specimen of *Lomorupithecus harrisoni* should be considered conspecific with *L. evansi*. We contend that the morphology of the *L. evansi* specimens described in this paper provides evidence against that attribution and clarifies differences between *Lomorupithecus* and *Limnopithecus*. First, palate breadth, both relative and absolute, distinguishes KNM-SO 22736 from the *Lomorupithecus* type BUMP 266. Second, *Lomorupithecus* has upper premolars that are readily distinguished from those of *L. evansi*. *Lomorupithecus* has a distinctive central fovea on P⁴ (Rossie and MacLatchy, 2006) that is not present in either of the well-preserved and only lightly worn P⁴s of the *L. evansi* maxillae. The *Lomorupithecus* P³ occlusal outline exhibits a distinct lingual point, which broadens rapidly on the distal edge and then becomes boxy toward the buccal margin (Rossie and MacLatchy, 2006: Figure 1c). In contrast, *L. evansi* has a more rectangular lingual margin that broadens equally on both mesial and distal edges. Finally, Rossie and MacLatchy (2006: Figure 4) showed that *Lomorupithecus* upper premolars are mesiodistally narrower than those observed in any other East African Miocene catarrhine. The two maxillae described here have premolar proportions similar to those previously described for *L. evansi* (Harrison, 1988), thereby reinforcing this difference between *L. evansi* and *Lo. harrisoni*.

We interpret this suite of anatomical differences, based on an expanded sample of *L. evansi*, as further evidence of the distinctiveness of the BUMP 266 maxilla. Our results strongly indicate that the holotype of *Lomorupithecus* represents a distinct genus and species of catarrhine, as originally proposed by Rossie and MacLatchy (2006). To

date, *Lo. harrisoni* has been reported only from Napak, reinforcing previous observations that the Napak catarrhine community appears distinct from the roughly contemporaneous communities at Tinderet. Napak samples a cercopithecoid (Pilbeam and Walker, 1968), *Lomorupithecus* (Rossie and MacLatchy, 2006), and perhaps several additional small catarrhine taxa recently described by Pickford et al. (2010), none of which has yet been reported from Kenya, despite the roughly similar ages of many of the Kenyan sites (Bishop et al., 1969; MacLatchy et al., 2006). Our findings support the distinctiveness of the Napak catarrhine community, perhaps due to habitat differences between Napak and Tinderet during the early Miocene (e.g., Harrison 1982, 1988; Pickford, 1983, 1986; Cote, 2008). Further research aimed at understanding the chronology and environmental settings at both Napak and Tinderet may help to clarify why catarrhine communities in eastern Africa appear to possess such high levels of endemism during the early Miocene.

Conclusions

Two maxillae discovered at the type locality for *Limnopithecus evansi* are confidently referred to that species. These maxillae add substantially to our understanding of the upper dentition and maxillary morphology of *L. evansi*, revealing details of the upper second incisor, maxillary sinus, palate, and nasal region not previously known.

These specimens provide important insights into two current taxonomic debates about *L. evansi*. First, the unusual morphology of the I^2 is shared with isolated

specimens attributed to *L. legetet* and may be a synapomorphy linking the two species and supporting the traditional taxonomic arrangement whereby they are sister taxa. Second, details of the upper premolars and lower facial anatomy distinguish *Lo. harrisoni* and *L. evansi*. *Lomorupithecus* is hence a valid taxon that, to date, has only been found at Napak IX.

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Figure Captions

Figure 1. *Limnopithecus evansi* maxilla KNM-SO 22259. A) occlusal, B) lateral, C) anterior, and D) medial views.

Figure 2. *Limnopithecus evansi* maxilla KNM-SO 22736. A) occlusal and B) lateral views.

Figure 3. Upper lateral incisors. A) KNM-SO 22259, referred here to *L. evansi*, demonstrating the distinct lingual cingulum that exceeds half the crown height mesially and angles sharply toward the cervix at the distobuccal margin. B-D) Specimens referred to *L. legetet* by Harrison (1988). B) KNM-CA 1871 is very similar to KNM-SO 22259 including the distinct cingular morphology; C) KNM-RU 1938 is heavily damaged but nevertheless preserves the mesially tall and steeply angled lingual cingulum; D) KNM-CA 1823 (image reversed for comparison) exhibits a lingual cingulum more typical of other stem catarrhines and is distinct from *Limnopithecus*. Photographs courtesy of Thomas Lehmann.

Figure 4. Internal palate breadth at M^1 to midline, scaled by geometric mean of: this measurement and MD and BL dimensions of P^3 , P^4 , M^1 . Poor preservation results in two estimates for BUMP 266. Dental dimensions taken from the literature for KNM-WK 16999 (Leakey and Leakey, 1986a), KNM-WK 16950 (Leakey and Leakey, 1986b), and UMP 62-11 (Andrews, 1978), Palate breadth for UMP 64-02 was calculated from photographs and verified with published measurements (Fleagle, 1975) as this specimen

was unavailable for study.

Supplemental Figure Captions

Figure S1. Isolated upper teeth newly attributed to *Limnopithecus evansi* and listed in Table 1. All specimens are from Songhor. Incisors are figured in labial (left) and lingual (right) views, whereas the premolar is shown in buccal (left) and occlusal (right) views; molars are shown in occlusal view.

Figure S2. Scatter plots of the mesiodistal and buccolingual dimensions for the P³ and P⁴ of early Miocene small-bodied catarrhine primates. Data from Harrison (1982), Rossie and MacLatchy (2006) and Table 1 (this paper).

Figure S3. Scatter plots of the mesiodistal and buccolingual dimensions for the M¹, M², and M³ of early Miocene small-bodied catarrhine primates. Data from Harrison (1982), Rossie and MacLatchy (2006) and Table 1 (this paper).

Table 1. Newly described maxillae and maxillary dentition attributed to *Limnopithecus evansi* in this paper. Measurements (mm) are included for all teeth.

Specimen Number		Element	MD	BL
KNM SO 22259	Right maxilla with I ² , broken C, P ³ , P ⁴	I ²	3.6	3.7
		C	6.1	5.1
		P ³	4.3	6.5
		P ⁴	4.1	6.4
KNM SO 22736	Right maxilla with P ³ , P ⁴ , M ¹ , M ² , M ³	P ³	3.8	5.7
		P ⁴	3.7	5.8
		M ¹	5.4	6.3
		M ²	5.7	6.9
		M ³	5.9	6.6
KNM SO 22236	Right I ¹	I ¹	5.2	3.8
KNM SO 22237	Left M ²	M ²	5.8	7.1
KNM SO 22247	Left I ¹	I ¹	4.3	3.0
KNM SO 22248	Right M ¹	M ¹	5.3	6.4
KNM SO 22250	Right M ²	M ²	5.7	--
KNM SO 22748	Right M ²	M ²	5.9	7.1
KNM SO 22751	Right I ¹	I ¹	5.0	4.0
KNM SO 37961	Left P ⁴	P ⁴	3.5	5.8

KNM SO 37964	Left I ²	I ²	3.3	3.5
KNM SO 37977	Left I ¹	I ¹	5.3	--
KNM SO 38017	Right I ¹	I ¹	4.8	3.9
KNM SO 38022	Left M ¹	M ¹	5.5	6.7

Figure 1_REVISED

Figure 2

Figure 3

Figure 4