

Distinctiveness of *Ugandapithecus* from *Proconsul*

La distinción entre Ugandapithecus y Proconsul

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ABSTRACT

The decision to create the genus *Ugandapithecus* by Senut *et al.*, 2000 has been criticised, either directly and in detail by MacLatchy & Rossie (2005b) who argued that it is a junior synonym of *Proconsul*, or indirectly without providing reasons, firstly by Harrison (2001) who wrote that he did not retain it as a genus distinct from *Proconsul*, and then by Suwa *et al.* (2007) who employed the name "*Ugandapithecus*" with inverted commas, implying some degree of doubt about its validity as a genus, but without providing details. More recently Harrison & Andrews (2009) have recognised the Meswa sample as a separate species but they argue that it should be maintained within *Proconsul*, despite the morphological differences that it has from other species of the genus. We here re-examine the question by comparing, on the one hand, the holotype maxilla of *Proconsul africanus*, the type species of the genus, with the upper dentition of *Ugandapithecus major*, and, on the other hand, the holotype mandible of *Ugandapithecus major* with the lower dentition and mandibles previously attributed to *Proconsul africanus*. We conclude that the differences between the known upper and lower dentitions of *P. africanus* and *U. major* are of such a degree that the two taxa warrant generic separation, and that the differences are not related to sexual dimorphism. Where *Proconsul africanus* differs from *Ugandapithecus major*, it approaches *Proconsul nyanzae* and *Proconsul heseloni* from Rusinga.

Furthermore, the range of morphometric variation within the fossil samples previously attributed to *Ugandapithecus major* is so great that it far surpasses variation in any other hominoid, fossil or extant. Previously this great amount of variation was interpreted to mean that *U. major* was extremely dimorphic, with huge males and small females, but if this is true, then *U. major* would be unique among hominoids in having females in which the cheek teeth fall completely outside the range of variation of male cheek teeth. All other known male and female hominoid species possess cheek teeth whose ranges of variation overlap strongly. Bivariate plots of the teeth attributed to *Ugandapithecus* reveal three consistent non-overlapping clusters of points among the Early Miocene specimens, which we interpret to represent three distinct species. A fourth species of the genus, *U. gitongai*, was previously defined at the Middle Miocene site of Kipsaraman, Kenya. We conclude that *Ugandapithecus* was a lineage of great ape distinct from *Proconsul*, and its main evolutionary trend was an increase in dimensions from basal Early Miocene *Ugandapithecus meswae* (21.5-19 Ma) to late Early Miocene species *Ugandapithecus leg-etetensis* nov. sp. (20-19 Ma) and *Ugandapithecus major* (19-18 Ma), and culminating in late Middle Miocene *Ugandapithecus gitongai* (ca. 14.5 Ma).

Key words: Hominoidea, *Ugandapithecus*, *Proconsul*, morphometric, East Africa, Lower & Middle Miocene

RESUMEN

La decisión de crear el género *Ugandapithecus* por Senut *et al.* (2000) ha sido criticada, tanto directamente y en detalle por MacLatchy & Rossie (2005b) que argumentan que es una sinonimia de *Proconsul*, o indirectamente sin ninguna argumentación, primero por Harrison (2001) que no lo considera como distinto de *Proconsul*, y después por Suwa *et al.* (2007) que emplean el nombre de "*Ugandapithecus*" entre comillas, implicando algún grado de duda sobre su validez como género. Recientemente Harrison & Andrews (2009) han reconocido la muestra de Meswa como una especie diferente, pero argumentando que debería ser mantenida en *Proconsul*, a pesar de las diferencias morfológicas que posee con

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respecto a otras especies del género. En este trabajo reexaminamos el problema, por un lado, comparando el maxilar holotipo de *Proconsul africanus*, especie tipo del género, con la dentición superior de *Ugandapithecus major* y, por otro lado, con la dentición inferior y mandíbulas previamente atribuidas a *Proconsul africanus*. La conclusión de estas comparaciones es que las diferencias entre las denticiones superiores e inferiores conocidas de *P. africanus* y *U. major* son de tal grado que los dos taxones necesitan una separación genérica, y que las diferencias no están relacionadas con dimorfismo sexual. Tanto como *Proconsul* difiere de *Ugandapithecus major*, se aproxima a *Proconsul nyanzae* y *Proconsul heseloni* de Rusinga.

Además, el rango de variación morfométrica en la muestra previamente atribuida a *Ugandapithecus* es tan grande que sobrepasa de lejos la variación conocida en cualquier hominoideo, fósil o actual. Previamente esta importante variación fue interpretada como debida a que *U. major* era extremadamente dimórfico, con enormes machos y pequeñas hembras, pero si esto fuese verdad, entonces *U. major* sería único entre los hominoideos al tener hembras cuya dentición cae completamente fuera del rango de variabilidad de la dentición de los machos. En todas las otras especies conocidas de hominoideos, machos y hembras poseen rangos dentarios cuyas dimensiones se solapan ampliamente. Los gráficos bivariantes de los dientes atribuidos a *Ugandapithecus* revelan tres agrupaciones independientes para los ejemplares del Mioceno inferior, que nosotros interpretamos como representantes de tres especies diferentes. Una cuarta especie del género *U. gitongai* fue previamente definida en el yacimiento Mioceno Medio de Kipsaraman, Kenia. Nosotros podemos concluir que *Ugandapithecus* constituyó una línea de grandes simios distintos de *Proconsul*, en los que su principal tendencia evolutiva fue el incremento en talla desde *Ugandapithecus meswae* de la base del Mioceno Inferior (21,5-19 Ma) hasta las especies final del Mioceno Inferior, *Ugandapithecus legetetensis* (20-19 Ma) y *Ugandapithecus major* (19-18 Ma), culminando en *Ugandapithecus gitongai* del final del Mioceno medio (ca. 14,5 Ma).

Palabras clave: Hominoidea, *Ugandapithecus*, *Proconsul*, morfometría, Africa del Este, Mioceno Inferior y Medio.

Introduction

The holotype of *Ugandapithecus major*, M 16648, is a right mandible with deeply worn cheek dentition from Songhor, Kenya. It is not possible to compare the holotypes of the species, *Ugandapithecus major* and *Proconsul africanus*, because the latter species has a maxilla as its holotype (M 14084) and its mandible is unknown (a specimen, KNM SO 1112 was for a while attributed to *P. africanus*, after having been classified as *Rangwapithecus gordonii*, but we consider that it belongs to the small species of *Ugandapithecus*, *U. meswae*).

Collections from Songhor, Koru, Chamtwara, and Legetet in Kenya and Napak I, IV, V, IX XV and CC in Uganda contain several dozen specimens of large hominoid teeth, many of which are isolated, but with a significant number *in situ* in mandibles, for there to be little doubt about correctly attributing upper and lower teeth either to *Ugandapithecus* (Pilbeam, 1969; Martin, 1981; Senut *et al.*, 2000; MacLatchy & Rossie, 2005b; Uchida, 1996; Harrison & Andrews, 2009) or to *Proconsul africanus* (Bosler, 1981, Martin, 1981). Of particular value for this analysis is a set of upper cheek teeth (P3/-M3/) from Chamtwara, Kenya (Martin, 1981) and a newly reassembled partial set of upper cheek teeth (C1/-M1/) from Napak V both of which are attributed to *Ugandapithecus*.

The maxilla of *Ugandapithecus* is poorly known, the only known fragments (KNM SO 418 and KNM CA 1855) (Martin, 1981) being too fragmentary and poorly preserved to reveal any morphology of value for this kind of analysis. They do however show more robust and inflated maxillary morphology in the vicinity of the canine jugum than occurs in *P. africanus*. Upper teeth of *Ugandapithecus* are now well enough represented in the fossil deposits at Koru, Legetet, Chamtwara and Songhor in Kenya and Napak in Uganda, for informative comparisons to be made with the teeth in the type specimen of *P. africanus*.

The lower jaw of *Proconsul africanus* is poorly known, but some isolated teeth collected from Koru, Legetet and Chamtwara, have been reasonably attributed to the species (Martin, 1981). A mandible from Songhor (KNM SO 1112) first identified as *Rangwapithecus gordonii*, then as *Proconsul africanus* does not belong to either genus, but to a small species of *Ugandapithecus* which is also known from Meswa Bridge, Kenya. We are therefore in a position to compare the type specimens of the two litigious species with specimens that can be attributed to each of them with a reasonable degree of confidence.

The case made by MacLatchy & Rossie (2005b) that *Ugandapithecus* is a synonym of *Proconsul* was unsatisfactory because the holotype of *P.*

africanus barely figured in their analysis, nor did the mandibular teeth of the latter species receive adequate comparison to the dentition in the holotype mandible of *U. major*. In this contribution, we therefore re-examine the question of the status of these two genera, taking into account all the available dental data, focussing in particular on the type specimens of the two species.

This paper is organised into seven parts, the first being an introductory background to the problem, the second is a demonstration that *Ugandapithecus* is indeed morphologically distinct from *Proconsul*, the third is a metric analysis of all the fossil material that we could study, the fourth is a systematic revision of the genus, the fifth is a reassessment of the Rusinga fossils attributed to *Proconsul*, and the sixth is the discussion which is followed by the seventh, the conclusions.

Methods

In previous studies of variation in *Proconsul* from Rusinga (Walker, *et al.*, 1993) use was made of statistics for analysing samples, without bivariate plots. The outcome of this study was that *P. nyanzae* ended up being represented almost exclusively by males and *P. heseloni* only by females, an unlikely and biologically unrealistic result. Bivariate plots of the data used in this paper, show, in contrast, overlapping clouds of points, which we interpret to represent two taxa, both of which contain males and females, an interpretation that straightforward statistical treatment does not reveal. For this reason, we prefer to focus on bivariate plots of data, rather than on statistical treatment of the data, which has serious limitations where two taxa are close in dimensions to each other.

Summary statistics for *Pan* and *Gorilla* were published by Pilbeam (1969). In our comparisons, we use bivariate plots of the dimensions published by him.

Introductory background to the *Ugandapithecus* question

Of direct relevance to this paper is proper identification of the Songhor mandible, KNM SO 1112. MacLatchy & Rossie (2005b) accepted Bosler's (1981) removal of this specimen from *Rangwapithecus gordonii* (Andrews, 1978) and its re-identifi-

cation as the only known mandible of *Proconsul africanus*. They stressed its similarity to that of *Ugandapithecus major* from Songhor and its differences from mandibles from Rusinga attributed to *Proconsul heseloni* and *Proconsul nyanzae*. On this basis they concluded that the mandibular morphology of this supposed specimen of *P. africanus* meant that if anything, it is the Rusinga material that needs to be renamed rather than *Proconsul major*. However, the presence of the small species *Ugandapithecus meswae* at Meswa Bridge which is close in dimensions, but not in morphology to *P. africanus*, suggests that KNM SO 1112 is not a specimen of the latter species, but belongs instead to *Ugandapithecus*. Canine and cheek tooth morphology of SO 1112 confirm this identification, as does the lingual aspect of the lower canine, which, although incomplete, shows morphology close to that of *Ugandapithecus*, and different from that of *Proconsul*. Bosler (1981) wrote that the p/3 morphology in KNM SO 1112 was not similar to that of *Proconsul africanus* (as observed in material from Rusinga and another specimen from Songhor [KNM SO 377]). This difference is confirmed by a newly discovered specimen of p/3 from Koru which differs from that in KNM SO 1112. The p/3 in the Songhor mandible is morphologically close to those of *Ugandapithecus major*, as well as to specimens of the new species *Ugandapithecus legetetensis* from Legetet, collected in the 1930's (Hopwood, 1933a, b). We adopt the identification of KNM SO 1112 as a small species of *Ugandapithecus*, which as a result reinforces the distinctiveness of *Ugandapithecus* from *Proconsul*, rather than weakening it as was concluded by MacLatchy & Pilbeam (1999), MacLatchy *et al.* (2000) and MacLatchy & Rossie (2005b).

In the paper in which the genus *Ugandapithecus* was created, Senut *et al.* (2000) paid particular attention to the species *U. major*, and pointed out a number of dentognathic and post-cranial differences between it and material attributed to *Proconsul africanus* from Koru on the one hand, and the Rusinga species attributed to *Proconsul* (*P. nyanzae*, *P. heseloni*) on the other (Gommery *et al.*, 1998, 1999).

Senut *et al.* (2000) pointed out that the post-cranial skeleton of *Proconsul africanus* is so poorly known that almost nothing can be said about it. Unfortunately this is still the case. Because of this, the postcranial differences between *Ugandapithecus* and *Proconsul* evoked by Senut *et al.* (2000) were based on comparisons between *U. major* and the

two species of *Proconsul* from Rusinga (*P. heseloni* and *P. nyanzae*), where the post-cranial skeleton is well known (Walker 1997; Walker & Pickford, 1983). It could be argued, as has been done by MacLatchy & Rossie (2005b) that *Proconsul africanus* might have had post-cranial bones similar to those of *U. major*, and different from those of *P. nyanzae* and *P. heseloni*, in which case it would be the Rusinga species that would require a new generic name, rather than the species *U. major*. This is a valid criticism, but it detracts attention away from the dentognathic evidence that Senut *et al.* (2000) marshalled in their paper. The decision to erect the genus *Ugandapithecus* was not based solely on the post-cranial evidence, but was based primarily on dentognathic evidence (Senut *et al.*, 2000).

MacLatchy (2009) described additional postcranial bones of *Ugandapithecus major*, found at Napak, Uganda (distal humerus, proximal radius). She reported that the specimens differ morphologically and metrically from the other species of *Proconsul* (*P. africanus*, *P. nyanzae*, *P. heseloni*), but she did not consider the possibility that this might support the generic distinctiveness of *U. major* from *Proconsul*. In contrast, we take this additional postcranial material as providing further evidence that *U. major* is indeed generically distinct from other species of *Proconsul*, not only in its dentognathic parts, but also in its femora, tibia, scapula and, now, its elbow joint. We agree with her main conclusion that “*P. major*... may have had a different locomotor repertoire than (sic) the smaller *Proconsul* species”, a suggestion that reinforces its distinctive generic status.

We here re-examine the available fossils, taking into account new discoveries at Napak, Uganda, and the Koru succession (Kenya) which greatly augment the available samples (Table 1). We include fossils from Napak attributed by MacLatchy & Rossie (2005b) to *Proconsul major*, as well as undescribed fossils collected by the Uganda Palaeontology Expedition between 1985 and 2009, and the Kenya Palaeontology Expedition in 2004 and 2005 totalling 54 specimens. In the new collections from Koru, Kenya, there are several teeth of *Proconsul africanus* which provide valuable evidence, because the species, in particular its mandible and lower dentition, still remains poorly known. In contrast, the mandible and lower dentition of *Ugandapithecus* are better represented in the fossil record, but it is the maxilla which is poorly known, and apart from a single partial set of upper

teeth found at Chamtwara by the senior author (Martin, 1981) and a partial set of upper cheek teeth from Napak V, Uganda, the upper dentition of the genus is represented by isolated teeth. Recent finds of upper cheek teeth at Napak V include a specimen belonging to an individual of *U. major* (UMP 69.01) which was described by Pilbeam (1969). The undescribed Napak V fossils help to fill out the upper cheek tooth row of *U. major*, as it comprises the second known partial set of upper teeth of this species. There are still some limitations to the fossil record, but we consider that the available samples now reveal enough to confirm that *Ugandapithecus* is indeed a genus distinct from *Proconsul*.

As a separate issue, we contribute to the debate about the generic status of the Rusinga species traditionally classified as *Proconsul*, and note that where *Proconsul africanus* differs dentognathically from species of *Ugandapithecus*, it approaches the Rusinga species *P. nyanzae* and *P. heseloni*. The debate about the presence of a single species or two species of *Proconsul* at Rusinga (Pickford, 1986a; Senut, 1986, 1987, 1989; Walker *et al.*, 1993) has a long pedigree (Leakey L.S.B., 1963, 1967, 1968, 1970, 1971, Simons & Pilbeam, 1965; Walker *et al.*, 1983), and we attempt to clarify it in this paper. However, it is not particularly germane to solving the issue of the validity of the generic name *Ugandapithecus*, although an understanding of the degree of sexual dimorphism in the Rusinga *Proconsul* species is relevant for addressing the role of variability in *Ugandapithecus*.

A note about the holotype of Proconsul africanus

The maxilla of the type specimen of *Proconsul africanus* from Koru is broken at the level of the P4/, and the two halves of the maxilla have drifted apart in an antero-posterior direction, leaving the P4/ floating in red limestone matrix between the two fragments of maxilla (fig. 1, 2, 3). Although the damage is immediately discernible to the naked eye, it gives the false impression that the tooth row is longer and more buccally recurved than it really is. We have digitally repaired the damage in order to have a better idea of the original palatal morphology and tooth row dimensions. It would be better to scan the fossil and repair it in three dimensions, but for the time being we consider that the reconstruction done with the digital camera is accurate enough

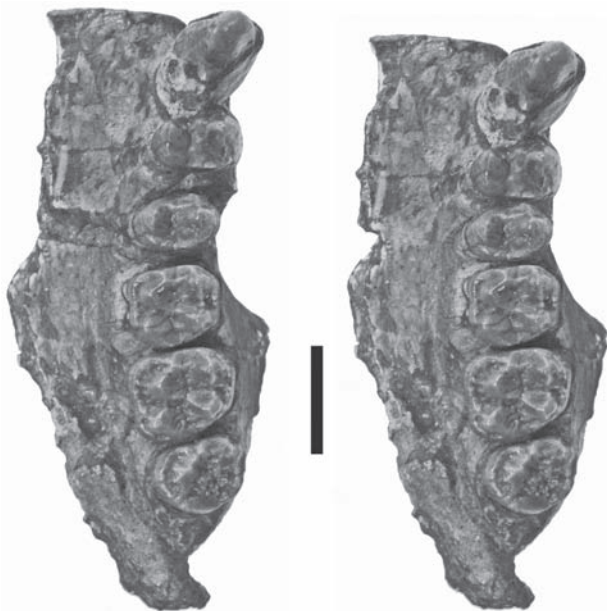


Fig. 1.—Palatal view of M 14084, the holotype maxilla of *Proconsul africanus*, from Koru, A) as preserved, and B) after digital reconstruction removing matrix from the break at the level of P4/, and realigning the two pieces of the maxilla and the P4/. The result is a 6% reduction in the apparent length of the specimen, and a straightening of the tooth row (scale: 10 mm).

for the purposes of this paper. The differences between the fossil as preserved and the digital reconstruction is provided in figure 1.

The enigma of mandible KNM SO 1112

In view of the small dimensions of the Meswa Bridge specimens of *Ugandapithecus*, it is necessary to re-examine the status of KNM SO 1112, a mandible originally identified as *Rangwapithecus gordonii* by Andrews (1978) and subsequently as a male individual of *Proconsul africanus* (Bosler, 1981; Martin, 1981; Pickford, 1986a; Walker *et al.*, 1993). The reason this mandible was attributed to *Proconsul africanus* by Martin (1981) is that it was considered to be too small to belong to *Proconsul major* or *Proconsul nyanzae* (recall that, at that time, *Proconsul heseloni* had not been differentiated from *P. nyanzae*). Faute de mieux, it ended up in *Proconsul africanus* as a large male individual, a solution which has persisted despite the morphological awkwardness produced by its inclusion in the species, and by extension, to the genus as a whole. Andrews (1978) had good reason to consider that



Fig. 2.—Unreconstructed lingual view of M 14084, holotype left maxilla of *Proconsul africanus* (scale: 10 mm).



Fig. 3.—Buccal stereo view of M 14084, holotype left maxilla of *Proconsul africanus*, unreconstructed (scale: 10 mm).

this mandible did not belong to *Proconsul*, but his attribution of it to *Rangwapithecus gordonii* was incorrect, as was realised by Bosler (1981) who attributed it to *Proconsul africanus*, but with the qualification that its third lower premolar differed



Fig. 4.—Buccal view of cast of KNM SO 1112 with the occlusal surface of the cheek teeth oriented approximately horizontally, showing the marked degree of distal shallowing of the ramus, a feature typical of *Ugandapithecus*. This jaw is attributed to *Ugandapithecus meswae* (scale: 10 mm).

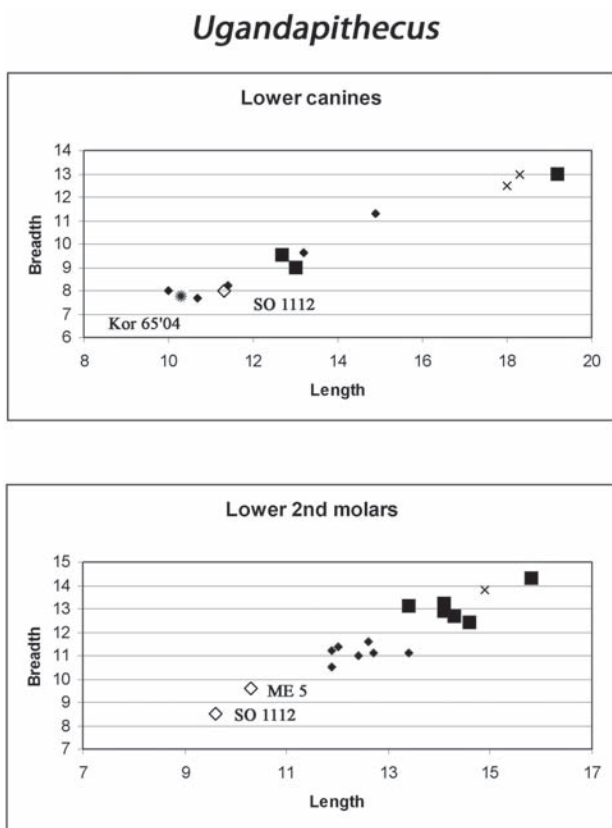


Table 1.—Unpublished specimens of *Proconsul africanus* and *Ugandapithecus* species

Locality abbreviation	Catalogue N.º	Year of collection	Figure	Specimen	Length (mm)	Breadth (mm)	Locality	Identification
Kor	2	04	23 A	Right c/1	7.9	10.9	Legetet	<i>U. legetetensis</i>
Kor	251	04	23 C	Right c/1	7.8	10.2	Juma's Red Bed	<i>U. legetetensis</i>
Kor	252	04	33 C	Left m/2	12.8	11.7	Juma's Red Bed	<i>U. legetetensis</i>
Kor	253	04	33 E	Left m/3	14.9	12.0	Juma's Red Bed	<i>U. legetetensis</i>
Kor	254	04	17 C	Left I1/	—	6.5	Juma's Red Bed	<i>U. legetetensis</i>
Kor	255	04	33 D	Left M1/	9.8	10.9	Juma's Red Bed	<i>U. legetetensis</i>
Kor	90	04	33 H	Right m/3	13.2	10.2	Legetet	<i>U. legetetensis</i>
Kor	140	05	33 G	Right m/3	18.4	15.0	Chamtware	<i>U. major</i>
Kor	141	05	17 B	Right I1/	9.5	7.1	Chamtware	<i>U. legetetensis</i>
Kor	159	05	17 A	Right i/2	5.7	7.0	Chamtware	<i>U. legetetensis</i>
Kor	278	05	17 D	Left I1/	9.6	6.6	Legetet	<i>U. legetetensis</i>
Kor	280	05	33 F	Right p/4	9.1	11.5	Brook's Quarry	<i>U. major</i>
Kor	283	05		Left i/1	4.6	8.0	Chamtware	<i>U. major</i>
Nap I	49	00	29 G	Left m/3	—	13.4	Napak I	<i>U. major</i>
Nap I	28	01	15 G	Left D4/	8.9	10.0	Napak I	<i>U. major</i>
Nap I	181	02	8 A	Right I1/	11.3	8.6	Napak I	<i>U. major</i>
Nap I	2	99	29 A	Left p/4	8.6	9.7	Napak I	<i>U. major</i>
Nap I	1	09	21 A	Right I2/	8.6	10.7	Napak I	<i>U. major</i>
Nap V	1	99	9 A	Left dC1/	8.6	7.5	Napak V	<i>U. major</i>
Nap V	4	01	34	Right mandible	—	—	Napak V	<i>U. major</i>
Nap V	36	02		Right I1/ broken	—	—	Napak V	<i>U. major</i>
Nap V	1	03	15 C	Right M1/	11.5	14.0	Napak V	<i>U. major</i>
Nap V	50	06		Right i/1	4.8	7.0	Napak V	<i>U. major</i>
Nap V	140	08	20 I	Right I2/	8.5	10.4	Napak V	<i>U. major</i>
Nap V	169	08	8 C	Right I1/	9.0e	7.6	Napak V	<i>U. major</i>
Nap V	4	09	35	Right i/1 (root)	4.9e	5.7e	Napak V	<i>U. major</i>
Nap V	4	09	35	Right i/2 (root)	5.3e	9.8e	Napak V	<i>U. major</i>
Nap V	5	09	21 B	Right M2/	13.0	14.7	Napak V	<i>U. major</i>
Nap V	88	09	21 E	Right m/1	12.6	11.2	Napak V	<i>U. major</i>
Nap V	95	09	21 D	Left p/3	10.0	7.4	Napak V	<i>U. major</i>
Nap V	179	09		Right c/1	15.3	—	Napak V	<i>U. major</i>
Nap V	220	09	14A	Right P3/	10.0	14.5	Napak V	<i>U. major</i>
Nap IX	7	98	22	Left c/1	12.4	9.7	Napak IX	<i>U. major</i>
Nap XV	60	07	18 D	Left m/3	18.9	14.0	Napak XV	<i>U. major</i>
Nap XV	61	07	18 C	Left p/3	10.8	13.4	Napak XV	<i>U. major</i>
Nap XV	62	07	18 B	Left c/1	19.2	13.0	Napak XV	<i>U. major</i>
Nap XV	116	07	18 A	Right I2/	7.5+	—	Napak XV	<i>U. major</i>
Nap XV	117	07	18 E	Left m/3	18.7	13.6	Napak XV	<i>U. major</i>
Nap XV	8	08	20 G	Left m/2	12.9	11.5	Napak XV	<i>U. major</i>
Nap XV	62	08	20 C	Right p/3	16.3	10.6	Napak XV	<i>U. major</i>
Nap XV	62	08	20 C	Right p/4	9.0	10.0	Napak XV	<i>U. major</i>
Nap XV	62	08	20 C	Right m/1	12.3	11.4	Napak XV	<i>U. major</i>
Nap XV	63	08	20 E	Left p/4	9.3	11.6	Napak XV	<i>U. major</i>
Nap XV	100	08	20 D	Left m/1	12.4	11.5	Napak XV	<i>U. major</i>
Nap XV	174	08	20 F	Right m/3	12.4	11.3	Napak XV	<i>U. legetetensis</i>
Nap XV	184	08	20 A 22 A-B	Right i/1	7.4	7.0e	Napak XV	<i>U. major</i>
Nap XV	270	08	20 H	Right i/1	7.0	9.6	Napak XV	<i>U. major</i>
Nap XV	394	08	20 J	Right d/3	8.3	6.0	Napak XV	<i>U. major</i>
Nap XV	33	09	21 C, 22 A-B	Right i/2*	8.0	12.6	Napak XV	<i>U. major</i>
Mor II	10	08	56 B	Left m/3	16.1	13.4	Moroto II	<i>U. cf gitongai</i>
Kor	65	04	23 C	Right c/1	7.8	10.0	Legetet	<i>Proconsul africanus</i>
Kor	158	05	34 A	Right d/4	6.1	5.0	Chamtware	<i>Proconsul africanus</i>
Kor	284	05		Left C1/	8.0	6.6	Chamtware	<i>Proconsul africanus</i>
Kor	292	05	34 B	Left p/3	5.4	6.7	Chamtware	<i>Proconsul africanus</i>
Kor	303	05		Right I2/	—	4.8	Chamtware	<i>Proconsul africanus</i>

+ = Means that the tooth is broken and the measurement should be greater than the figure given.

* Nap XV 33'09 includes the apical part Nap 35'08, found in 2008.



Fig. 6.—Left lateral view of cast of the 1942 mandible of *Proconsul nyanzae* (KNM RU 1674) from Rusinga Island, Kenya, with the occlusal surface oriented approximately horizontally, showing the characteristic distal deepening of the ramus, the opposite of the situation in *Ugandapithecus meswae*, *U. leg-etetensis* sp. nov., and *U. major*, in which the ramus shallows distally (scale: 10 mm).



Fig. 7.—KNM RU 1947, lateral view of cast of left ramus of a complete but crushed mandible of *Proconsul nyanzae* from Rusinga showing slight distal shallowing of the ramus followed by slight deepening at the gonial angle. The right mandible has been digitally removed for the sake of clarity; the complete specimen is shown in miniature at the top (scale: 10 mm).

1963; Gommery, 2006; Gommery *et al.*, 1998, 1999, 2002; Senut *et al.*, 2000; MacLatchy & Rossie, 2005a) but are not reliably reported from Rusinga, Kenya. *Proconsul* fossils in contrast are abundant at Rusinga, but rare at other sites (Keith, 1932; Leakey, L.S.B., 1943, 1948, Leakey, M.D., 1948; Teaford & Walker, 1993; Teaford *et al.*, 1988, 1993; Walker & Pickford, 1983; Walker & Teaford, 1988, 1989; Walker *et al.*, 1986).

Continued collecting at Napak and Moroto in Uganda and Koru in Kenya, has led to the discov-

ery of a significant quantity of new material of *Ugandapithecus* and a few specimens of *Proconsul africanus*. We add the following observations on the new specimens, which in our view confirm the taxonomic and morpho-functional differences between the genera *Proconsul* and *Ugandapithecus* proposed by Senut *et al.* (2000), supported by Uchida's (1996) findings and criticised by MacLatchy & Rossie (2005b).

Dentognathic morphological analysis

Upper incisors

Central upper incisors of *Ugandapithecus*, six of which are now known, tend to be broad and squat with well developed central lingual swelling and raised mesial and distal ridges, and there is a low concavity on the labial surface (fig. 8). In *Proconsul* in contrast, the I1/ tends to be taller relative to the mesio-distal diameter, the basal pillar is better developed and the marginal ridges sharper than in *U. major* (fig. 8). But perhaps the most marked difference between upper central incisors of *Ugandapithecus* and *Proconsul* resides in the more extensive surface distal to the median ridge that characterises incisors of the latter genus, imparting a more curved distal margin to the tooth than occurs in *Ugandapithecus*. The interproximal wear facet in Nap I 181'02, a lightly worn upper central incisor of *U. major*, is large enough to provide a good idea of the orientation of the tooth by mirror imaging. This reveals that the upper central incisors roots in *Ugandapithecus* are relatively further apart than in *Proconsul heseloni*, with the consequence that the angle between the mesial margins of the two central incisors make a wider angle (fig. 8A3) than in species of *Proconsul*. Nap V, 169'08 is a heavily worn right I1/ (fig. 8C) which shows a well developed central lingual pillar and well developed mesial and distal marginal ridges on the lingual side.

Upper second incisors of *Ugandapithecus major* are rare, but an unworn specimen (Nap V 140'08) found in August, 2008 at Napak V (fig. 20 I) is interesting as it reveals that there is no lingual cingulum, unlike *Afropithecus turkanensis* which does have one (observable in the holotype, and in the Moroto snout), a character also present in *Proconsul heseloni* from Rusinga (fig. 8B). Furthermore the lingual expansion of the base of the crown is greater in *Ugandapithecus major* than it is in *Pro-*

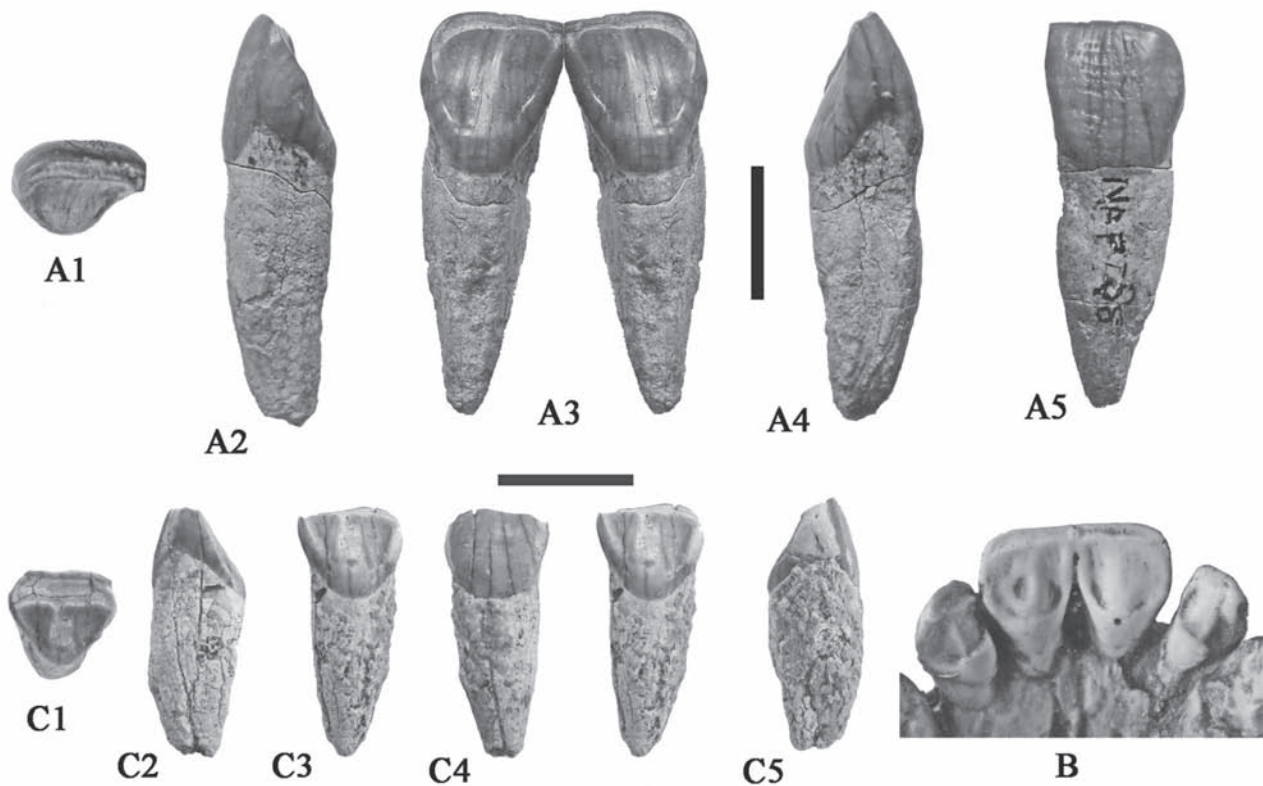


Fig. 8.—Upper central incisors of A) Nap I 181'02 + Nap I'58, (crown collected by the UPE in 2002 and root collected by W.W. Bishop in 1958) of right I1/ of *Ugandapithecus major* (A1 - occlusal view, A2 - distal view, A3 - lingual view with mirror image aligned parallel to the planar interproximal facet, which is extremely flat in this individual, A4 - mesial view, A5- labial view) and B) cast of KNM RU 7290, *Proconsul heseloni*, lingual view; C) Nap V, 169'08, right I1/ (C1 - occlusal view, C2 - distal view, C3 - stereo lingual view, C4 - labial view, C5 - mesial view) (scales: 10 mm).

consul and *Afropithecus*. Two other specimens are known from Napak, Nap I 1'09, a complete specimen showing a rapidly tapering root, and a strong angle between the axis of the crown and that of the root (fig. 21 A), and Nap XV 116'07, the apex of a crown (fig. 18 A).

Upper canines

The upper canine in the holotype maxilla of *Proconsul africanus* is pointed with a slight hint of a burin-like form apically (fig. 1, 2, 3). The tip of the tooth extends far beyond the level of the occlusal surface of the premolars. For this and other reasons the type specimen has usually been interpreted as representing a male individual (Kelley, 1986a, b, 1995). Because of the degree of projection of the upper canine in *P. africanus*, a large concave wear facet is produced in the disto-buccal part of the lower canine against which the upper canine rubs

during honing and chewing. The basal concavity in the wear facet of the lower canine is produced by the apex of the upper canine, which therefore shows an apical wear facet accompanied by a large lingual facet. Male upper canines of *Ugandapithecus major*, in contrast, do not project greatly beyond the occlusal surface of the premolars and as a result the lower canines do not develop a concave wear facet from contact with the upper canine, but do develop a flat facet on its distal surface (fig. 9, 10). The honing mechanism and occlusal relationships of the canines in *P. africanus* and *U. major* are thus divergent.

A striking difference between the upper canines of *P. africanus* and *U. major* is the presence in the latter, of a prominent rounded distal ridge on the root in line with the distal crest and basal tubercle of the crown (fig. 9D2). This radicular ridge fits into the space between the anterior roots of the P3/ allowing the canine and P3/ to lie close together, as seen in the Chamtwara maxilla (fig. 12A) and the Napak upper dentition (fig. 14A). In *P. africanus*, in

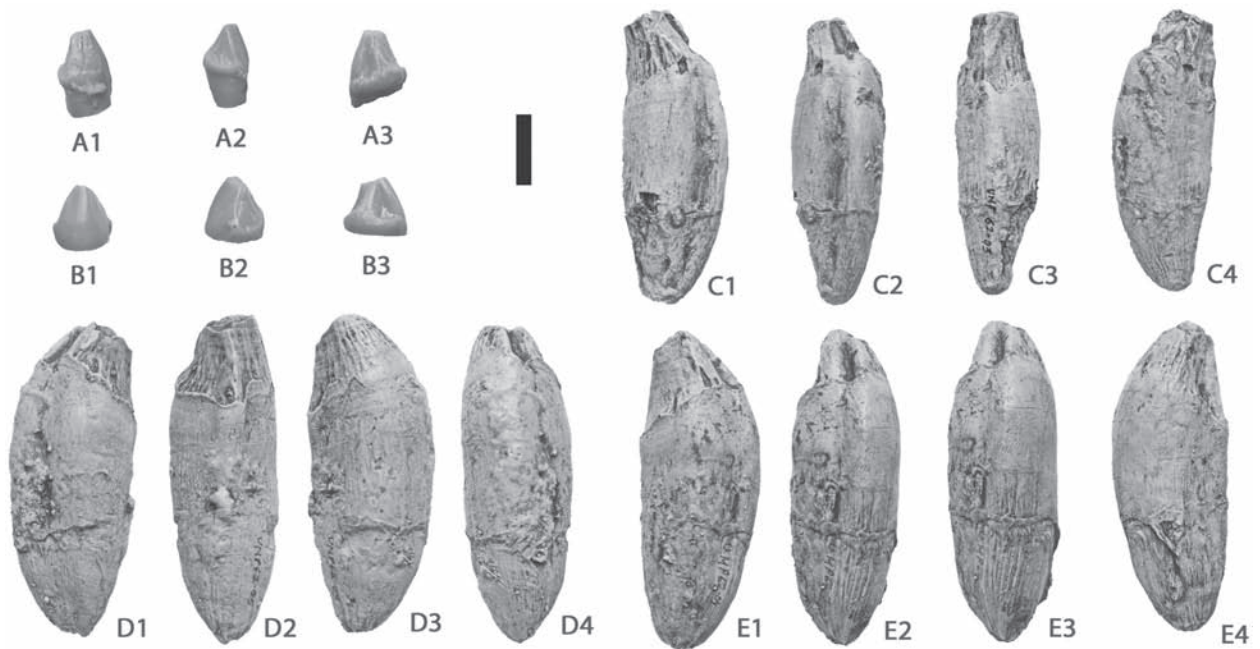


Fig. 9.—Lingual, distal and labial views of casts of upper canines of A) Nap V 1'99, left DC1/, (A1 - labial, A2 - distal, A3 - lingual views); and B) Nap IV UMP 62.20, right DC1/, (B1 - labial, B2 - distal B3 – lingual views); C) Nap I, UMP 62.03, right canine, (C1 - lingual, C2 - distal, C3 - mesial, C4 - labial views); D) Nap I, UMP 62.05, left canine, (D1 - lingual, D2 - distal, D3 - labial, D4 - mesial views); and E) Nap V, UMP 62.04, right canine of *Ugandapithecus major*, (E1 - lingual, E2 - distal, E3 - labial, E4 - mesial views). Note that in all three permanent canines of *U. major*, in line with the distal tubercle of the crown there is a strongly developed distal crest on the root bordered by grooves, a morphology that does not occur in *Proconsul africanus* (scale bar: 10 mm).

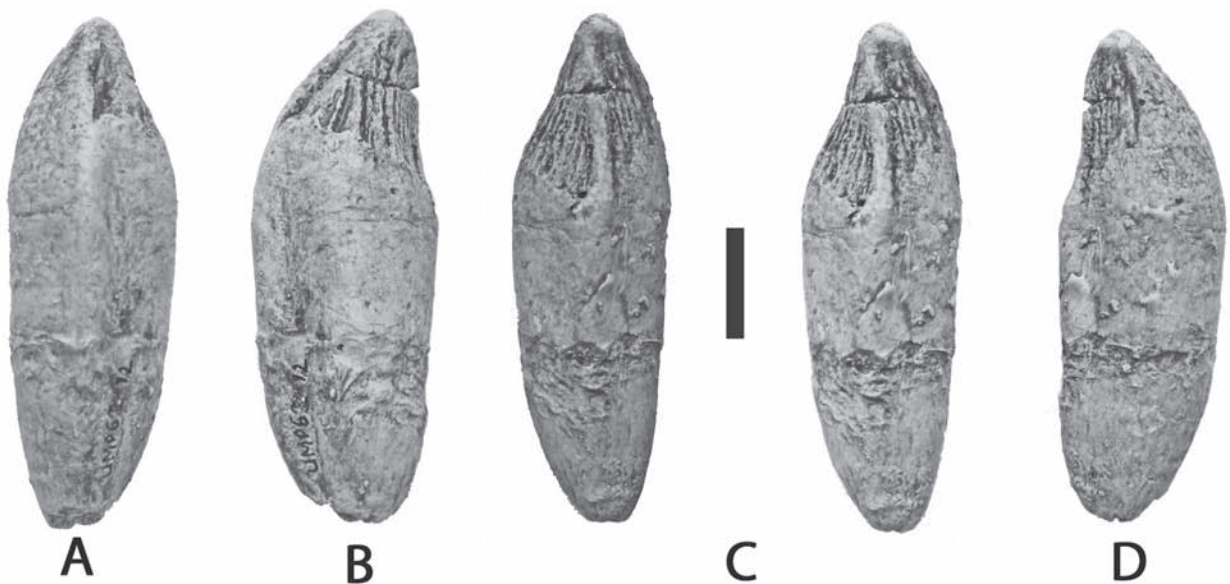


Fig. 10.—UMP 62.12, from Moroto II, left upper canine, (A - mesial, B - lingual, C - distal stereo view, D - labial view) (scale 10 mm).

contrast, the root shows no signs of a comparable ridge, but only an open angulation between the labial and distal surfaces of the root. Furthermore, upper canines of *U. major* possess a substantial anterior

radicular groove in line with the mesial groove of the crown which extends from just above the cervix to the apex of the root. Upper canines of *Proconsul africanus* do not possess a comparable groove.

A further difference in the upper canines of *U. major* and *P. africanus* resides in the relative dimensions of the crown and root. In *U. major*, the crown is low and stubby and is posed on a root that is substantially more massive than it (Pilbeam, 1969). In contrast, the upper canines of *P. africanus* have taller and more pointed crowns, which are broader at the base than the root (fig. 16).

Upper P3/

The upper third premolar in the type specimen of *P. africanus* is lightly worn, leaving the protocone and paracone almost unaltered by wear (fig. 11). The main points about this tooth are that the buccal and lingual cusps are markedly different in height, the buccal cusp projecting occlusally considerably more than the lingual one. In addition, the buccal cusp has a low degree of buccal flare, such that in distal view, the postparacrista is vertical with respect to the cervix of the tooth. Because of this, the apices of the protocone and paracone are relatively far apart from each other measured in relation to the total breadth of the crown. The preparacrista extends rootwards in an almost straight line, curving slightly as it reaches the anterior root. In occlusal view the distal margin of the P3/ in *P. africanus* is gently curved, and slightly overhangs the roots and, as a consequence, interstitial wear soon results in a straight posterior margin to the crown.

In *U. major*, in contrast, the buccal cusp of the P3/ is not as exaggeratedly taller than the lingual one and the apex of the paracone is closer to the

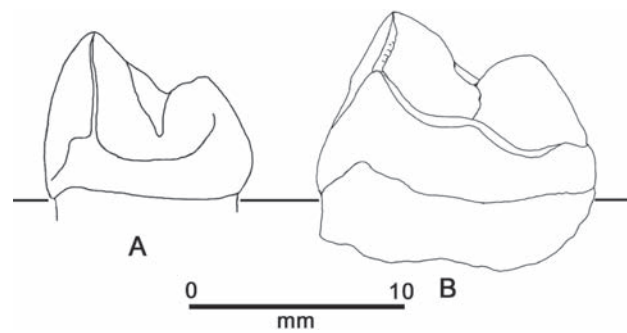


Fig. 11.—Distal views of unworn right P3/s of A) M 14084, *Proconsul africanus* (holotype reversed) and B) M 14331, *Ugandapithecus major* from Koru. The teeth are aligned with the buccal and lingual cervix at the same level (scale: 10 mm).

centre of the tooth than in *P. africanus*, due to its greater degree of buccal flare, and as a consequence the tips of the protocone and paracone are relatively closer together than they are in *P. africanus* (fig. 11, 12). Furthermore, the preparacrista is strongly curved from the apex of the paracone to its termination on the anterior root (fig. 12, 16D3) this curvature being related to the more central position of the paracone in this species when compared to the more peripheral position in *P. africanus* (fig. 1, 14). The strong curvature of the P3/ preparacrista in *U. major* gives the impression that the mesial side of the tooth wraps around the rear of the canine, whereas in *P. africanus*, the mesial edge of the P3/ is straighter and the wrap around the canine is less marked. Finally, the distal margin of the P3/ of *U. major* is strongly curved, the rear shelf largely overhanging the roots.

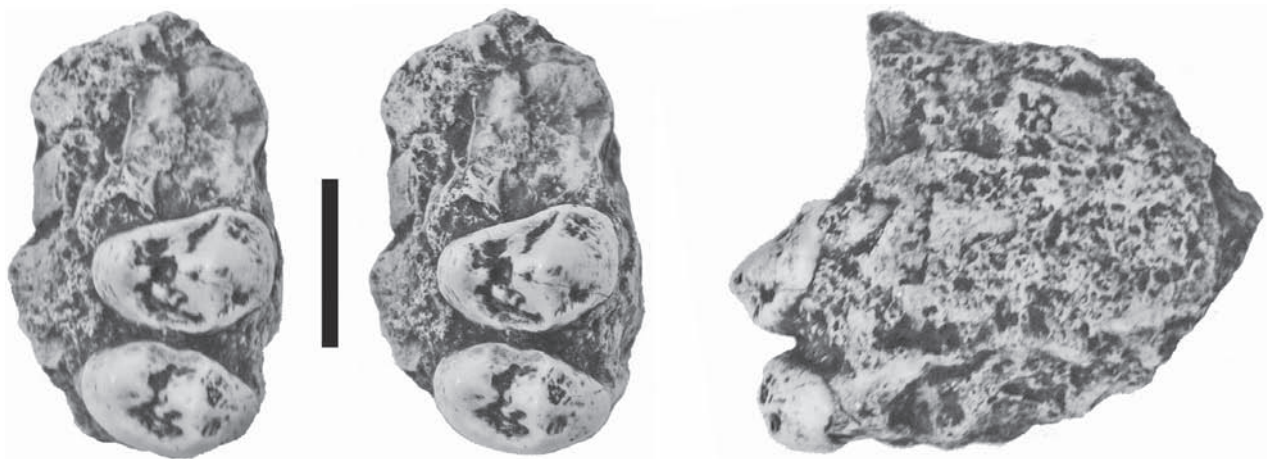


Fig. 12.—KNM CA 1855, cast of left maxilla with root of the canine and P3/-P4/ of *Ugandapithecus major*, from Chamtwara, Kenya (A - stereo occlusal and B - buccal views) (scale: 10 mm).

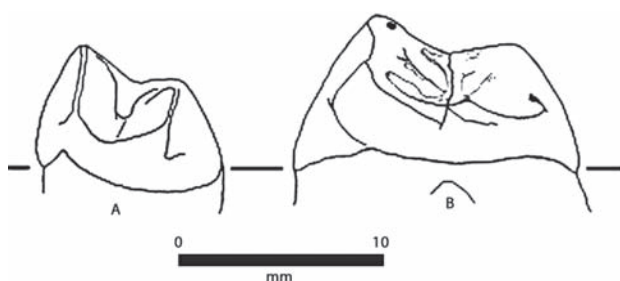


Fig. 13.—Distal views of right P4/s of A) M 14084, *Proconsul africanus* (reversed from holotype) from Koru and B) Nap V, UMP 69.01, *Ugandapithecus major* from Napak V, Uganda, showing greater buccal and lingual flare in *U. major* (teeth aligned with the buccal and lingual cervix at the same level). Note that the *U. major* tooth is worn, but even so the difference in flare from the situation in *P. africanus* is evident as is the continuation, in *Ugandapithecus major*, of the flare onto the lingual root (scale: 10 mm).

Upper P4/

The P4/s of *P. africanus* and *U. major* are almost as distinct from each other as the P3/s are (fig. 13). The difference between the degree of projection of the buccal and lingual cusps is less than in the P3/ of the two taxa, but it can nevertheless be observed in unworn teeth. The difference in the amount of overhang of the distal margin of the crown above the roots in the P3/ continues into the P4/, and even in very worn individuals of *U. major*, in which the distal margin has worn straight (eg Nap V, MUZM 146, MacLachy & Rossie, 2005b) evidence of the overhang remains. In *P. africanus*, the distal overhang is less than in *U. major*, and it becomes straight at a much more juvenile stage of wear, as for example in the young adult holotype of *P. africanus*.

The paracone and protocone of P4/s of *U. major* are closer together relative to total crown breadth than is the case in *P. africanus*, a feature that can still be observed in worn teeth due to the greater buccal flare of the paracone in *U. major*.

Upper first and second molars

Apart from size differences, it is also possible to distinguish upper first and second molars of *Ugandapithecus* and *P. africanus* from each other, even when they are moderately worn (fig. 14). The cusps of the molars in *U. major* (fig. 15) are more bulbous than those of *P. africanus*, as a result of which the occlusal basins are more confined in the former

than they are in the latter. This is reflected in the shape of the cusp surfaces bordering the occlusal basins. In *P. africanus*, the buccal surface of the protocone is concave, whereas in *Ugandapithecus*, the homologous surface is convex, sometimes with a low ridge leading into the centre of the basin.

Upper third molars

The upper third molar in the holotype of *P. africanus* is greatly foreshortened (fig. 1, 2, 3, 14), the metacone and hypocone being reduced to such an extent that they are barely differentiated from the lingual and distal cingulum.

In *Ugandapithecus* in contrast, the distal cusps of the upper third molar are not as greatly reduced, the metacone and hypocone being only slightly smaller than the paracone and protocone (fig. 14) and this results in a more triangular occlusal outline in *Proconsul* than the almost square outline in *Ugandapithecus*. This is especially visible in the Chamtwara maxillary teeth, but is also present in material from Napak, and also in a specimen from Koru (M 14331) described by Hopwood (1933a) (fig. 16B), which, although deeply worn, shows large hypocone and metacone areas.

Lower incisors

None of the large hominoid lower incisors from Koru, Songhor and Napak have been found *in situ* in mandibles, although in 2009, a symphysis was found at Napak V which contains the roots of the incisors and the right canine (fig. 35C). Large specimens from Nap XV (fig. 17, 20) and Koru (fig. 17), Kor 159'05 probably belong to *Ugandapithecus* (fig. 17A, 18A, 20A) while smaller specimens can be attributed to *P. africanus* (Bosler, 1981; Martin, 1981) or another species of hominoid. Apart from size, the main difference between the large and small lateral incisors, is that the specimens attributed to *Ugandapithecus* possess a concave lingual distal half (distal scoop) and the crown is expanded labio-lingually.

Lower canines

Lower canines of *Ugandapithecus* do not show a well developed distal heel (fig. 22, 23A-23B). In *P.*

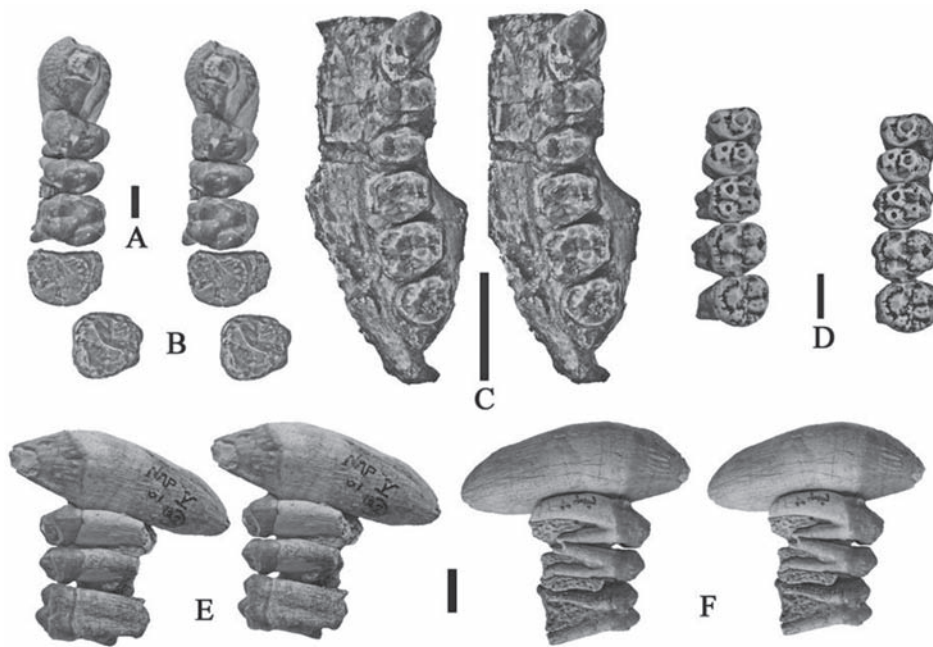


Fig. 14.—Comparison of palatal dentitions of right C1-/M2/ of *Ugandapithecus major* from Napak V, Uganda, A, E, F) stereo views, occlusal, lingual and buccal respectively; B) left M3/ possibly of the same individual; C) M 14084, holotype left maxilla of *Proconsul africanus*; D) cast of KNM CA 387-391, *Ugandapithecus* left upper cheek tooth row from Chamtwara. Stereo occlusal views of the specimens reduced to the same M1/-M3/ length in order to simplify comparisons (scale bars: 10 mm).

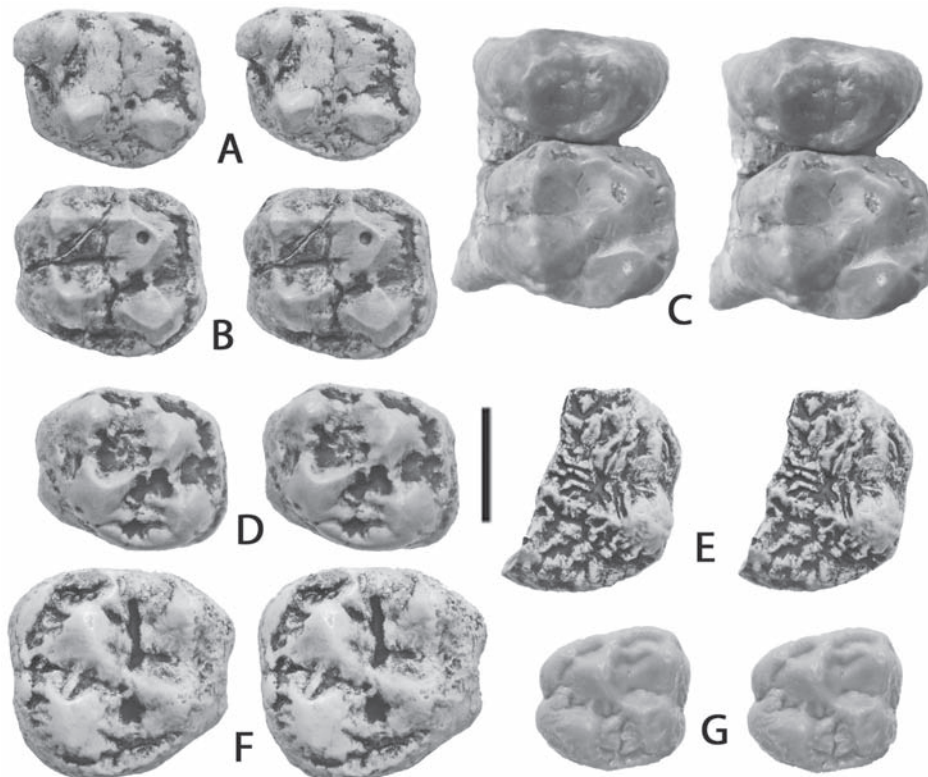


Fig. 15.—Stereo occlusal views of upper cheek teeth from Napak sites attributed to *Ugandapithecus* species. A) Nap I UMP 62.09, right M1/; B) Nap IV UMP 62.41, right M1/; C) Nap V UMP 69.01b, right P4/ + Nap V 1'03 right M1/; D) Nap V UMP 69.02, right M1/; E) Nap V, UMP 62.07, broken right M2/; F) Nap V UMP 62.08, left M3/; G) Nap I 28'01, left D4/ (scale bar: 10 mm).

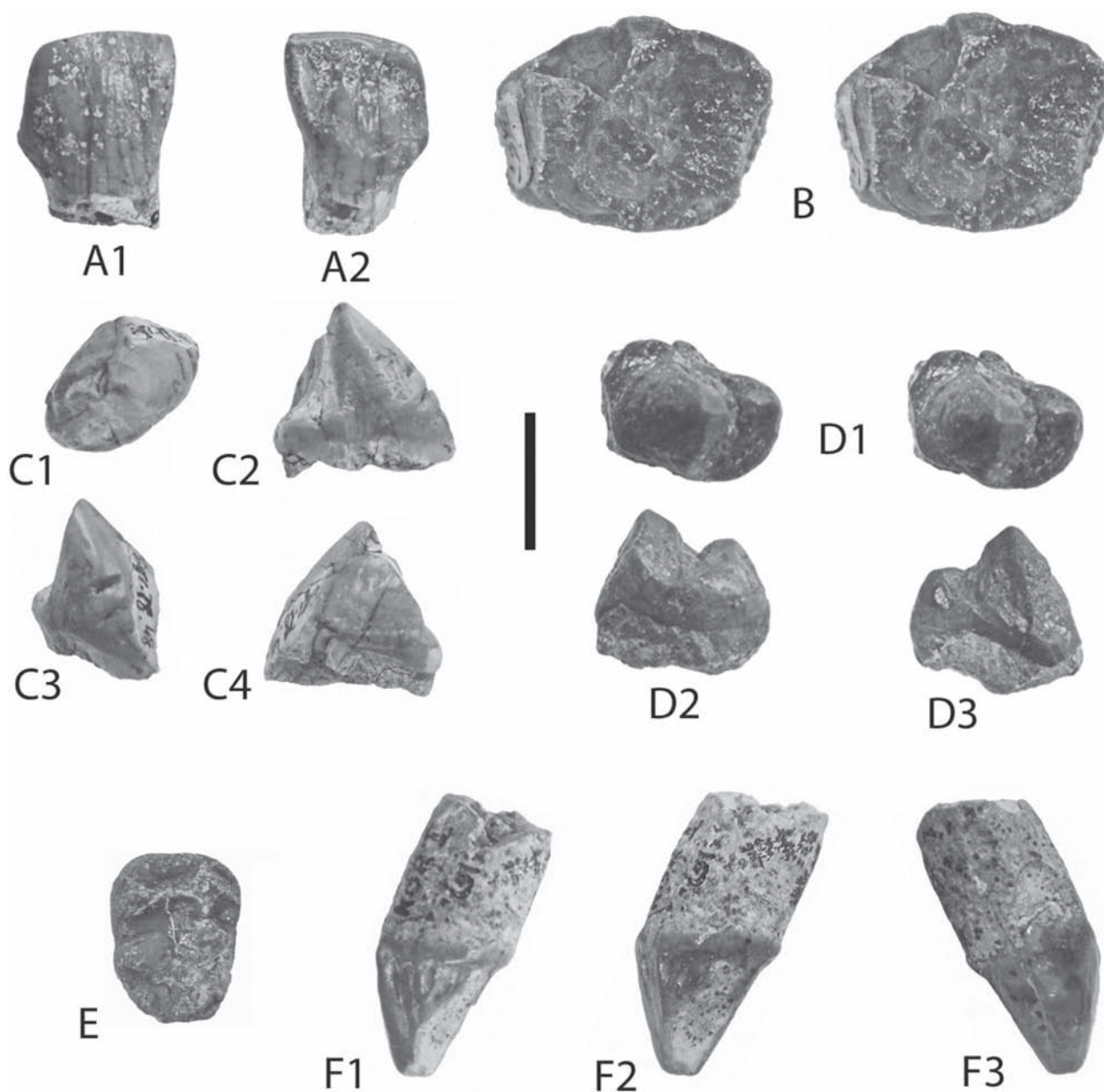


Fig. 16.—Historical collection of large hominoid teeth from Koru and Songhor, Kenya, housed in the Natural History Museum, London (all *Ugandapithecus major* except for F) which is *Proconsul africanus*). A) M 14297, left I1/ from Leakey's Red Bed, (A1 - labial and A2 - lingual views), B) M 14331, left M3/ from Koru, stereo occlusal view, C) M 44830, right p3/ from Songhor (C1 - occlusal, C2 - buccal, C3 - mesial and C4 - lingual views); D) M14331, right P3/ from Koru, (D1 - stereo occlusal view, D2 - distal view, D3 - mesial view); E) M 32237, right m3/ from Koru, occlusal view; F) M 44837, right C1/ from Koru, (F1 and F2 - lingual views, F3 - buccal view) (scale bar: 10 mm).

africanus, the apical wear facet developed on the upper canine indicates a different occlusal pattern from that developed in *Ugandapithecus*. As a result of this wear pattern, the lower p/3s of *P. africanus* do not experience excessive contact with the upper canine, whereas, those of *U. major*

the wear facet produced by the upper canine on the distal side of the lower canine is flat and vertical, with no tendency for hollowing or development of a concavity basally even in quite worn specimens, and the antero-buccal surface of the p/3 is often deeply worn.

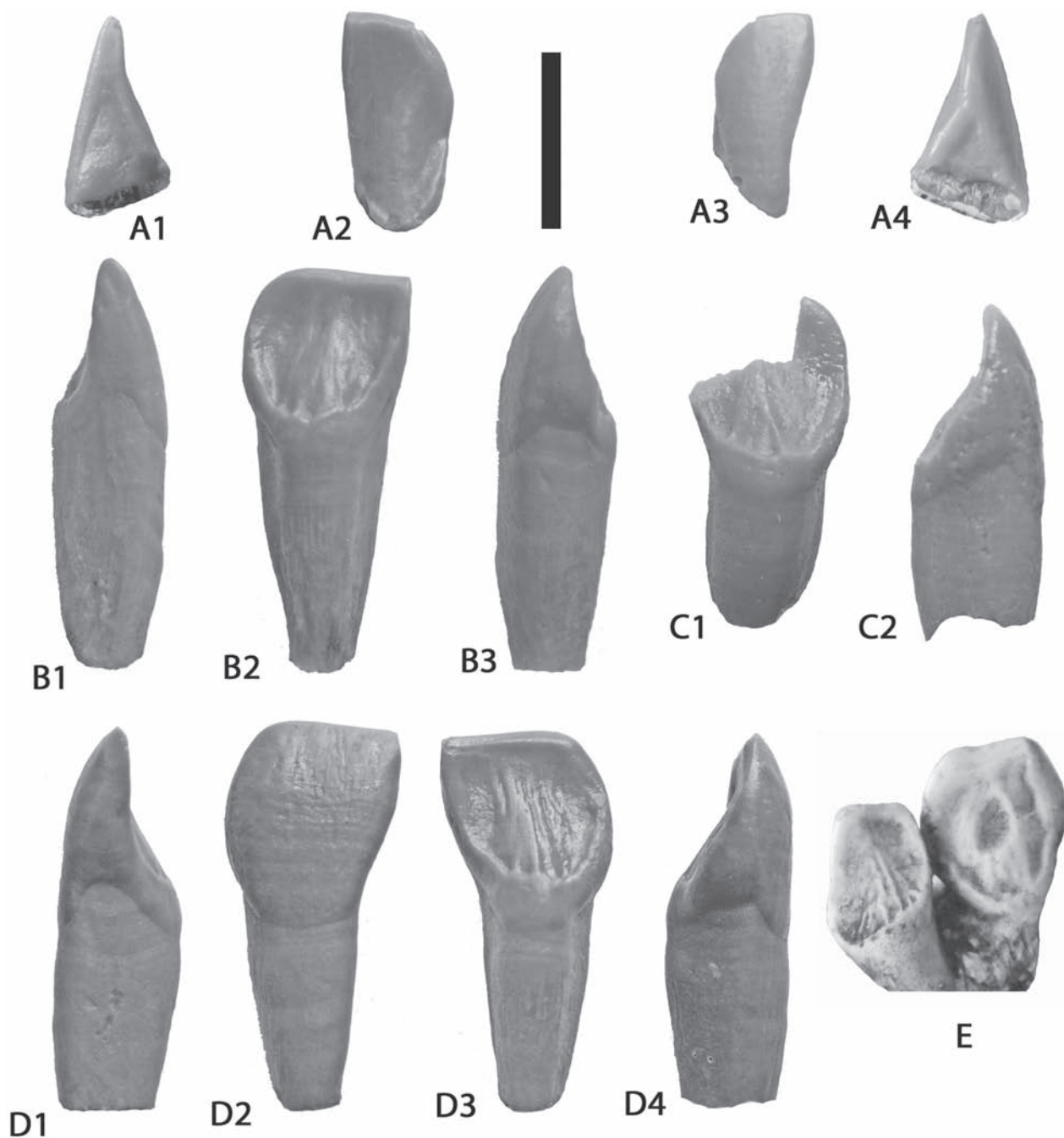


Fig. 17.—Casts of upper central and lateral incisors and a lower second incisor of *Ugandapithecus* species from Koru. A) Kor 159'05, right i/2 (note the distal scoop in the lateral lower incisor, which produces a distinct bend (almost a notch in this case) in the distal margin of the tooth) (A1 – mesial, A2 – lingual, A3 – labial, A4 – distal views); B) Kor 141'05, right I1/, (B1 - mesial, B2 - lingual and B3 - distal views); C) Kor 254'04, left I1/, (C1 - lingual and C2 - distal views); D) Kor 278'05, left I1/, (D1 - mesial, D2 - labial, D3 - lingual and D4 - distal views); E) KNM CA 1858, right I1-/I2/, lingual view (scale: 10 mm).

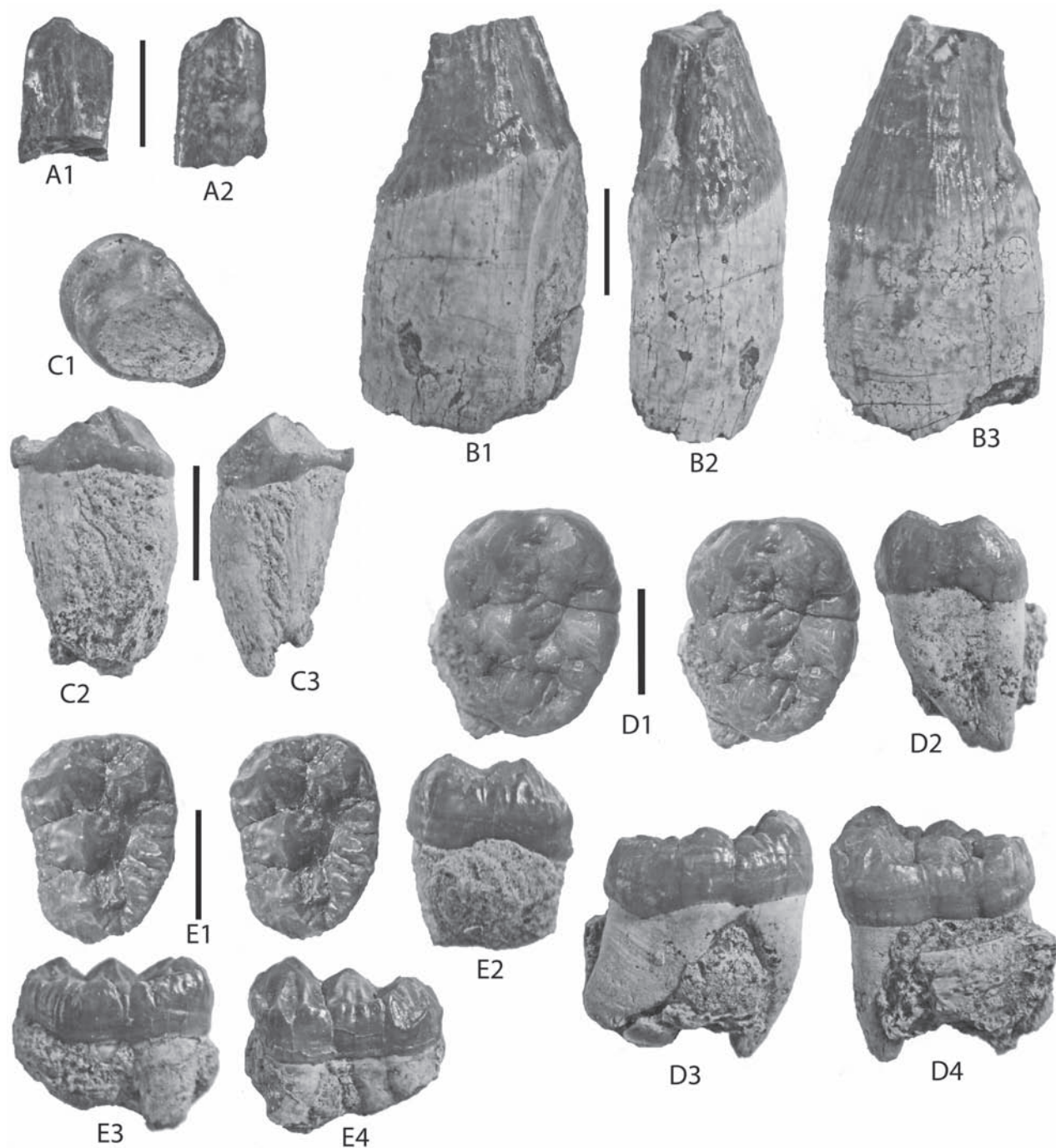


Fig. 18.—Isolated teeth of *Ugandapithecus major* from Napak XV, 2007 collection (see Fig. 19 for details of discovery points). A) Nap XV, 116'07, right I2/, (A1 - lingual and A2 - labial views); B) Nap XV, 62'07, left c/1, (B1 - lingual, B2 - distal and B3 - labial views); C) Nap XV, 61'07, left p/3, (C1 - occlusal, C2 - lingual and C3 - buccal views); D) Nap XV, 60'07, left m/3, (D1 - stereo occlusal, D2 - mesial, D3 - lingual and D4 - buccal views); E) Nap XV, 117'07, left m/3, (E1 - stereo occlusal, E2 - mesial, E3 - lingual and E4 - buccal views) (scales: 10 mm).

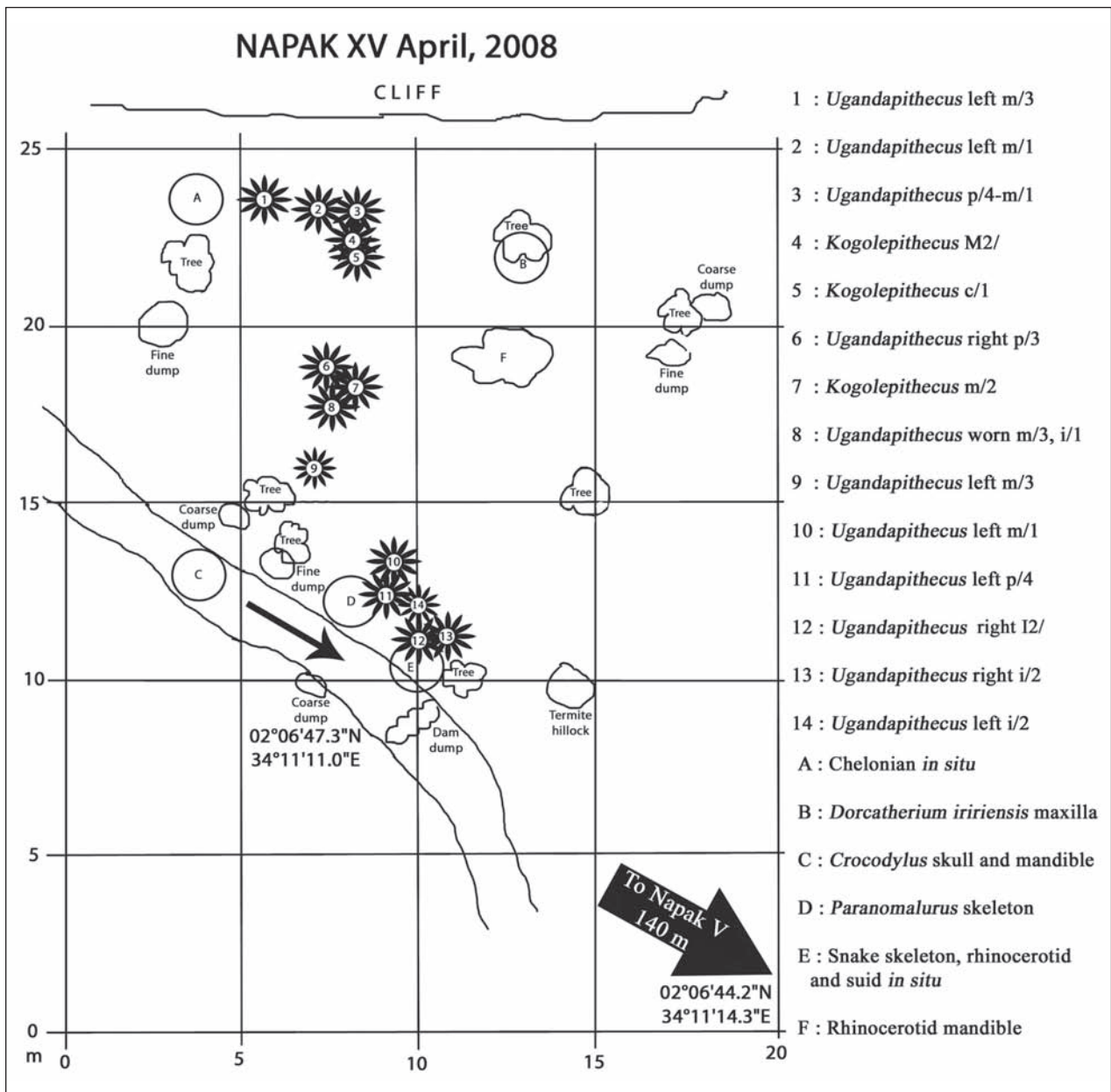


Fig. 19.—Sketch map of discovery points of *Ugandapithecus* and other fossil specimens at Nap XV, 2007 and 2008 field seasons.

Because of the form of the lingual cingulum, the mesial shoulder of the canine is positioned high in *Proconsul heseloni*, whereas it is lower in *Ugandapithecus*. In buccal view, in all available specimens of *Ugandapithecus*, the shoulder is at about 45-46% of the distance measured from the most basal part of the cervix on the labial aspect of the tooth to the apex of the crown, whereas in *Proconsul heseloni* it is about 54-55% above the cervix. A probable male individual of *Proconsul africanus* from Koru (Kor

65°04) shows a relatively higher mesial shoulder than occurs in *Ugandapithecus*. Furthermore, the latter tooth has a relatively higher crown, taking into account the wear which has removed the apex of the tooth, the relatively rectilinear distal ridge (fig. 23C, 24B), suggesting the absence of a blade-like apical morphology that typifies *Ugandapithecus*, and the position of the lingual cingulum relative to cervix.

Unworn lower canines attributed to *P. africanus* possess pointed apices whereas those of *U. major*

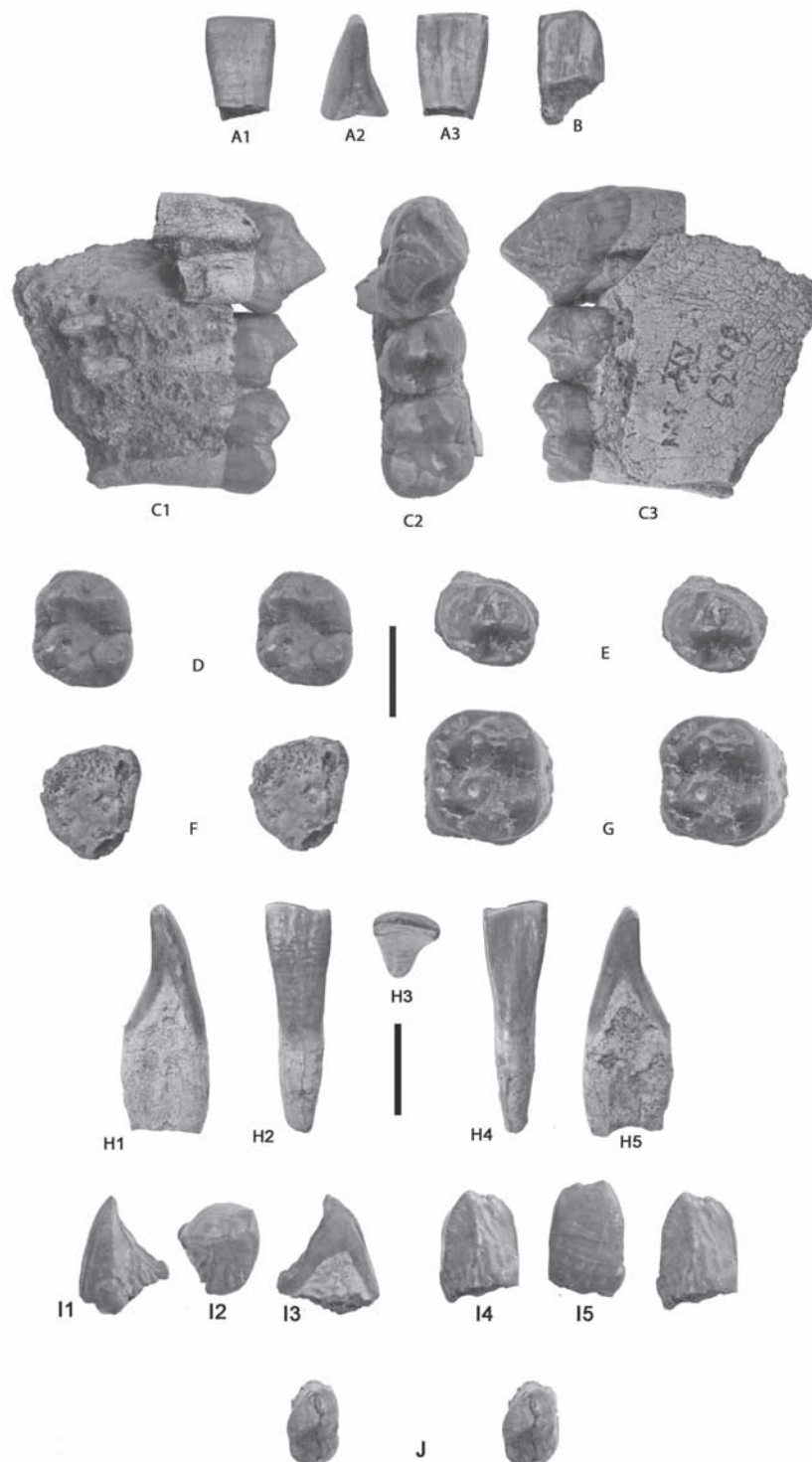


Fig. 20.—*Ugandapithecus major*, Napak V and Napak XV, April and August, 2008 collections. A) Nap XV 184'08, right i/1 (A1 - labial, A2 - mesial and A3 - lingual views); B) Nap XV, 35'08, apex of right i/2, (lingual view: see also Fig. 21C); C) Nap XV, 62'08, right mandible containing p/3-m/1 (C1 - lingual, C2 - occlusal and C3 - buccal views); D) Nap XV, 100'08, left m/1, (stereo occlusal view); E) Nap XV, 63'08, left p/4, (stereo occlusal view); F) Nap XV, 174'08, worn right m/3 (stereo occlusal view); G) Nap XV, 8'08, left m/2 (stereo occlusal view); H) Nap XV, 270'08, right i/1, (H1 - mesial, H2 - labial, H3 - occlusal, H4 - lingual, and H5 - distal views); I) Nap V, 140'08, right I2/, (I1 - distal, I2 - occlusal, I3 - mesial, I4 - stereo lingual, I5 - labial views); J) Nap XV, 348'08, right d/3, stereo occlusal view (scale bar: 10 mm).

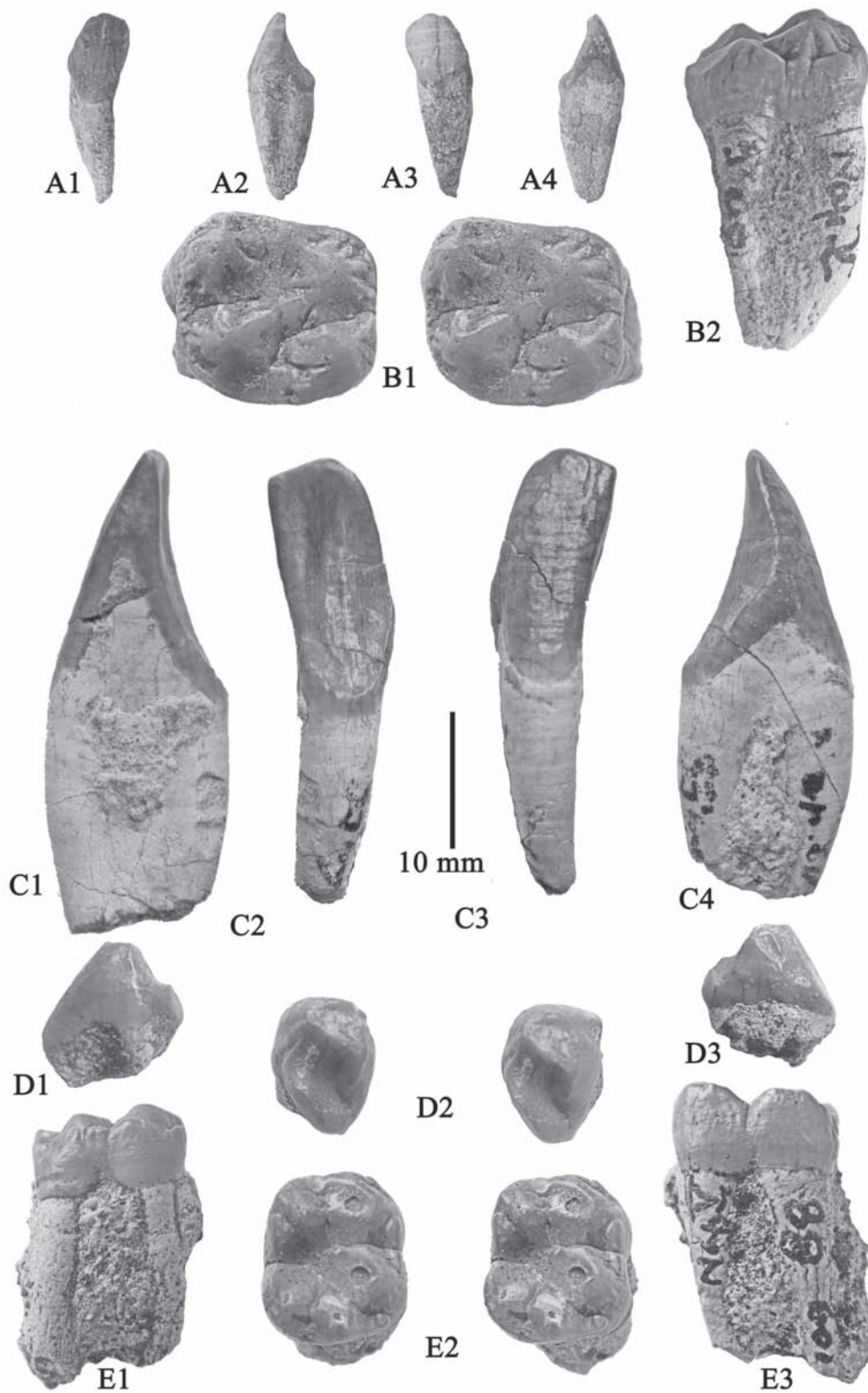


Fig. 21.—Isolated teeth of *Ugandapithecus major* from Napak, Uganda, March, 2009 field season. A) Nap I, 1'09, right lateral upper incisor, A1-A4) lingual, distal, labial and mesial views; B) Nap V 5'09, right M2/, B1) stereo occlusal, B2) lingual view; C) Nap XV 35'08 + 33'09, right i/2, C1-C4) mesial, lingual, labial and distal views; D) Nap V 95'09, left p/3, D1) buccal, D2) stereo occlusal, D3) lingual views; E) Nap V 88'09, right m/1, E1) buccal, E2) stereo occlusal, E3) lingual views.

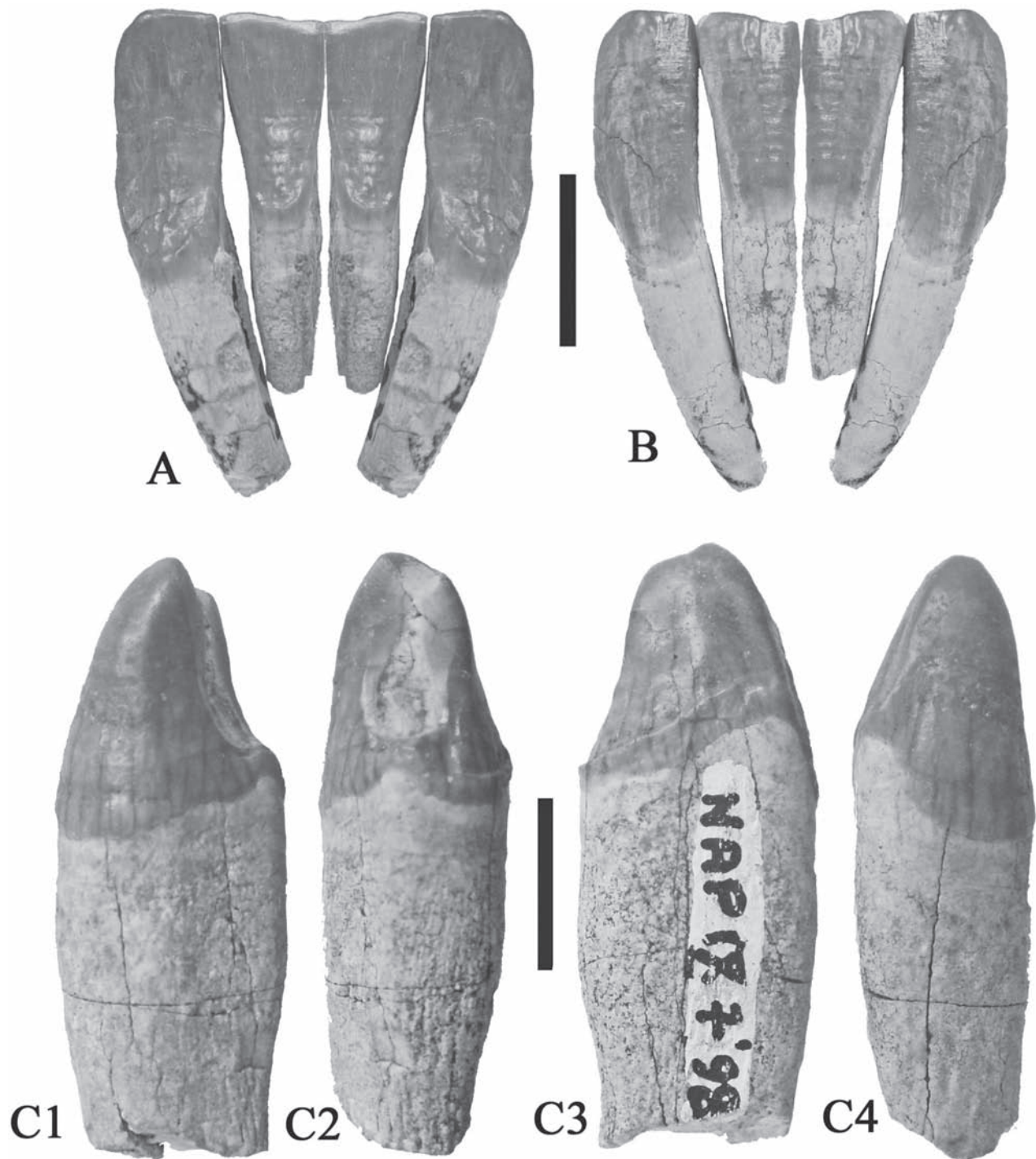


Fig. 22.—Anterior lower teeth of *Ugandapithecus major*, A-B Nap XV 270'08 (right i/1), Nap XV 35'08 + 33'09 (right i/2) with mirror images, (A – lingual, B – labial views); C) Nap IX 7'98, left lower canine (C1 – labial, C2 – distal, C3 – lingual and C4 – anterior views (scale: 10 mm).

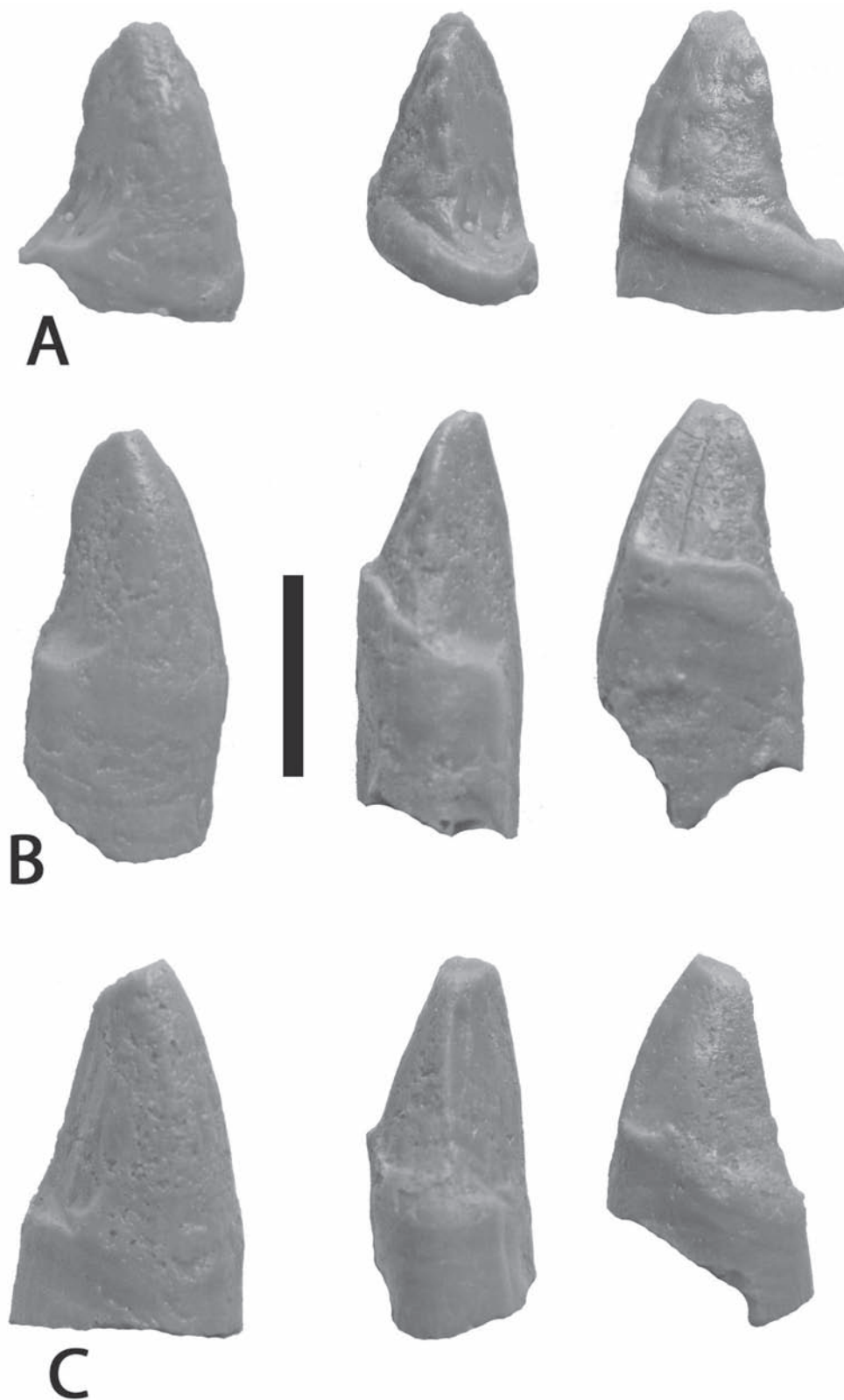


Fig. 23.—Casts of lower canines of *Ugandapithecus* species (A-B) and *Proconsul africanus* (C) from Koru, Kenya, A) Kor 2'04; B) Kor 251'04; C) Kor 65'04, from left to right, labial, distal and lingual views of (scale bar: 10 mm).

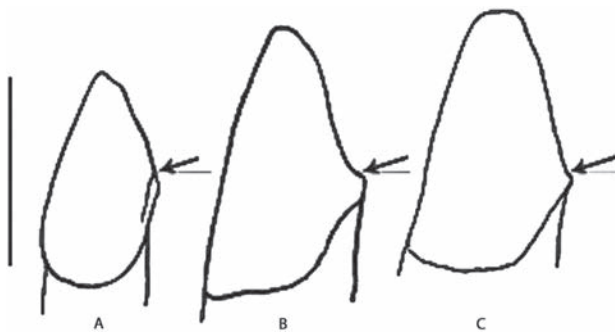


Fig. 24.—Buccal views of right lower canines to show position of mesial shoulder relative to the buccal portion of the cervix in A) KNM RU 7290, female individual of *Proconsul heseloni* from Rusinga, Kenya, B) Kor 65'04, from Koru probable male individual of *Proconsul africanus*, and C) Kor 251'04, female individual of *Ugandapithecus* from Koru. Arrows show the junction between the lingual cingulum and the mesial ridge of the crown (scale: 10 mm).

are shaped almost like a burin (so-called blade-like morphology in Senut *et al.*, 2000). The canine in the Songhor mandible, KNM SO 1112, although damaged anteriorly, shows a weak rise in the cingular outline, closer to the *Ugandapithecus* pattern than to the form in the mandible KNM RU 7290 a female individual attributed to *Proconsul heseloni*. As a result of this recurved lingual cervix, the mesial shoulder is higher in species of *Proconsul* than it is in *Ugandapithecus* (fig. 24). Both male (KNM SO 396) and female (KNM LG 452) canines of *Ugandapithecus* possess low mesial shoulders on the lower canines, whereas in both sexes of *Proconsul* species, the mesial shoulder is high (KNM RU 7290, female; KNM RU 1674, male; KNM RU 1947, male; Kor 65'04, male). The differences in shoulder height are therefore not likely to be due to sexual dimorphism. However, the samples are small, and because of the possibility of sexual and individual variation, we do not insist on these distinctions in our assessment of the taxonomy of *Ugandapithecus* and *Proconsul*, but merely point them out as a potential line of research once samples do become adequate.

Lower third premolars

The p/3 of *P. africanus* is still extremely poorly known (fig. 25, 26, 27). The p/3 in the mandible from Songhor, KNM SO 1112 (fig. 25), which for some time was attributed to *Rangwapithecus gordonii* by Andrews (1978) resembles that of *Ugandapithecus major*, but is considerably smaller (Bosler, 1981).

Lower fourth premolars

It is difficult to compare the lower fourth premolars of *U. major* and *P. africanus* as in the latter species this tooth is too poorly known (fig. 28, 29, 30).

Lower m/1 and m/2

Save for their dimensions, first and second lower molars of *Ugandapithecus* and *P. africanus* differ from each other in the form of the cusps, more bulbous in *Ugandapithecus* more angular in *P. africanus*. As a result, the occlusal basins are more restricted in molars of *Ugandapithecus* than they are in *Proconsul* (fig. 28, 29, 30).

Lower third molars

The lower third molars of *Ugandapithecus* are distally narrowed to such an extent that the disto-lingual cusp is reduced to a bead in the lingual cingulum, and the hypoconulid is small and located in a very lateral position, being in line with or even slightly buccal to the line made by the two anterior cusps on the buccal side (fig. 28, 29, 30, 32, 33). As a result of the reduction of the disto-lingual cusp and the very lateral position of the hypoconulid, in occlusal view the crown appears to be bent buccally in its distal half. In contrast, the lower third molars attributed to *P. africanus* are not as asymmetrical as those of *Ugandapithecus*, the hypoconulid is more centrally positioned, and the entoconid is not as reduced relative to the other cusps. In lower third molars from Koru attributed to *P. africanus*, in contrast, the hypoconulid is centrally positioned, and the disto-lingual cusp is not reduced (Hopwood, 1933a, b).

Metric analysis of *Ugandapithecus* and *Proconsul* teeth

Metric variation in *Ugandapithecus*

It has been known for a long time that fossils attributed to *Ugandapithecus major* were extremely variable in size. Specimens from Meswa Bridge are the smallest known (Andrews *et al.*, 1981; Bosler, 1981; Harrison & Andrews, 2009) having almost the same dimensions as *Proconsul africanus*, but

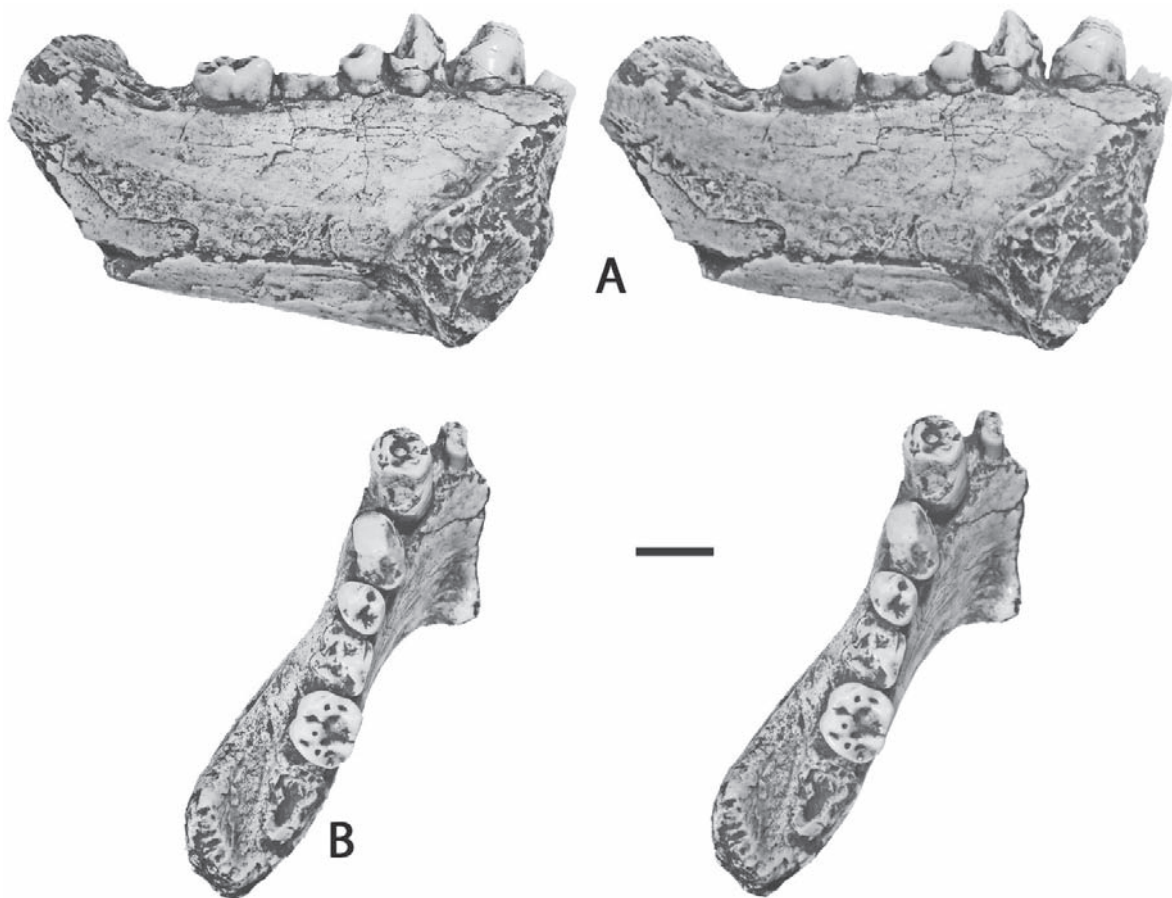


Fig. 25.—KNM SO 1112 from Songhor, Kenya, cast of left mandible of *Ugandapithecus meswae* containing the the root of the left lateral incisor, the stub of the canine, and complete p/3, p/4 and m/2, (A - stereo lingual, B - stereo occlusal views) (scale bar: 10 mm).



Fig. 26.—M. 14086 from Koru, Kenya, left mandible of a male individual of *Ugandapithecus legetetensis* sp. nov., containing the canine root, and p/3-m/2 (A - lateral, B - stereo occlusal and C - lingual views) (scale bar: 10 mm)

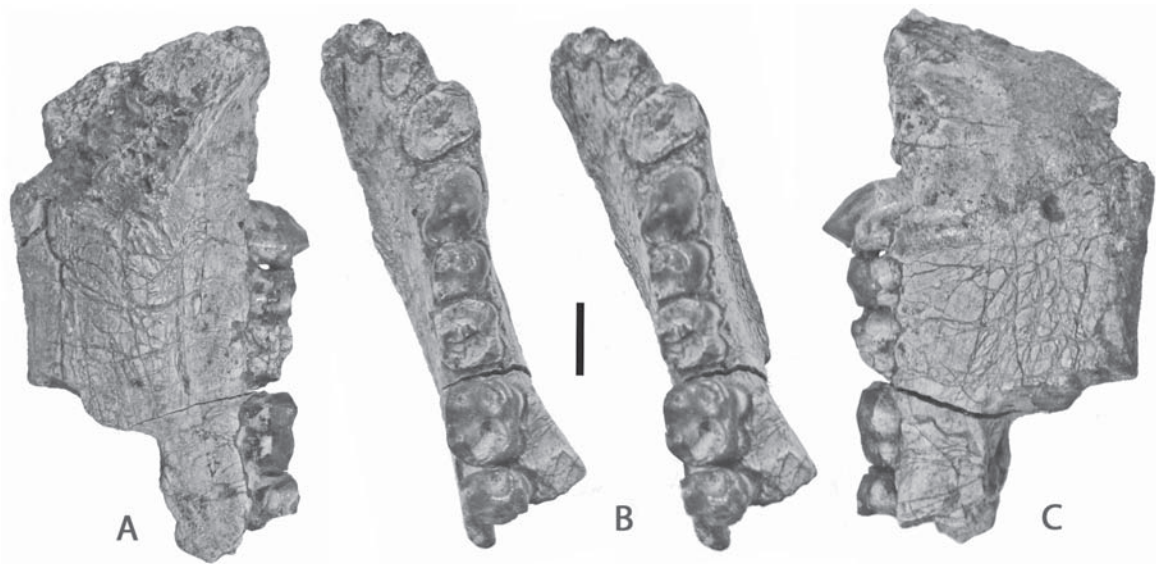


Fig. 27.—M 14086, right mandible of *Ugandapithecus legetetensis* sp. nov. from Koru containing roots of i/1-c/1, and p/3, p/4, m/1, m/2 and part of m/3 (A - lateral, B - stereo occlusal and C - lingual views) (scale bar: 10 mm).

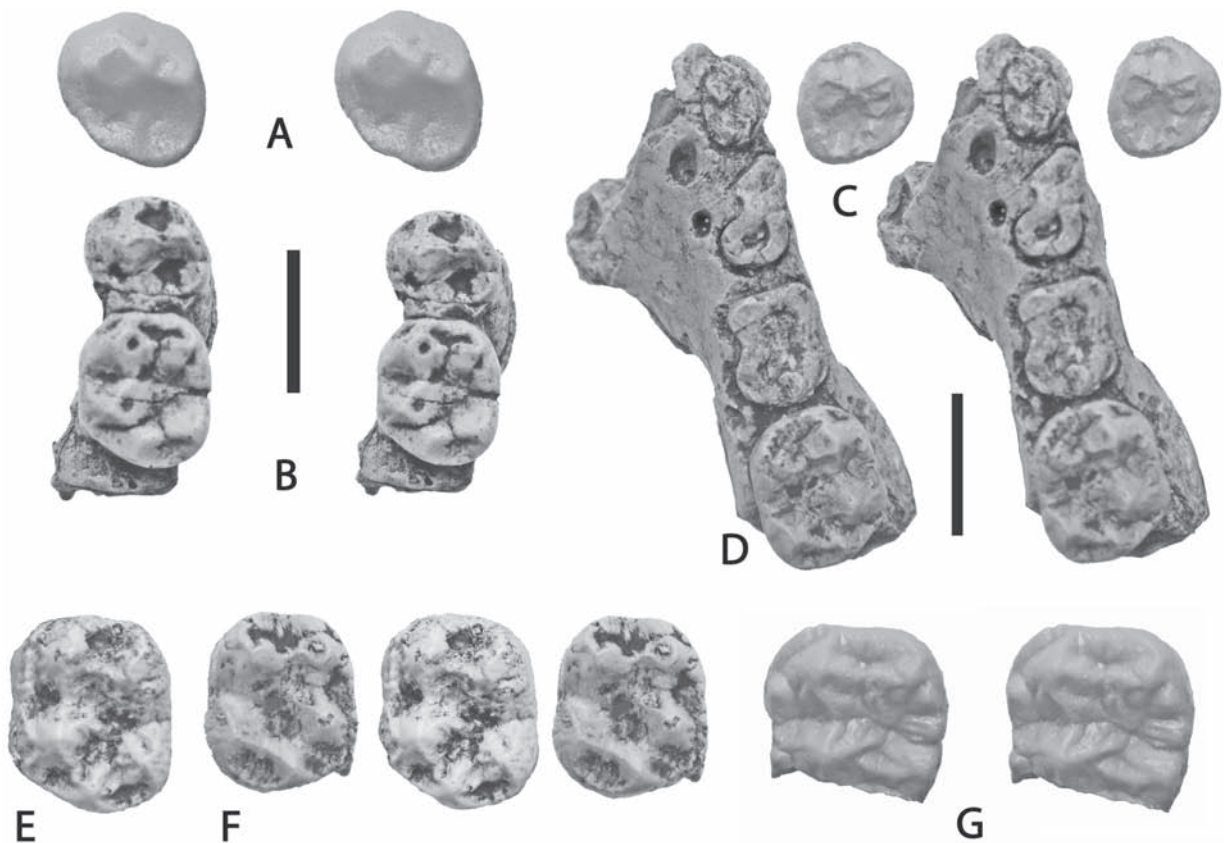


Fig. 28.—Stereo occlusal views of casts of *Ugandapithecus* species, A) Nap I, 2'99, left p/4; B) Nap I, UMP 62.16, left mandible fragment containing p/4 and m/1; C) Nap I, UMP 62.13, right p/4 extracted from crypt of juvenile mandible; D) Nap I, UMP 62.13, *Ugandapithecus major* right mandible with roots dc/1, d/3-d/4, and crown of m/1; E) Nap I, 62.15, left m/1; F) Nap I, 62.14, right m/1; G) Nap I, 49'00, broken left m/3 (scale: 10 mm).



Fig. 29.—M 16648, holotype right mandibular ramus of *Ugandapithecus major*, from Songhor, Kenya (A - lingual, B - stereo occlusal and C - buccal views) (scale: 10 mm).

divergent morphology (Martin, 1981; Harrison & Andrews, 2009) whereas some specimens from Songhor and Napak are huge, as is material from Moroto II and Kipsaraman previously attributed to the species but subsequently removed from it, either at the generic level (Gebo *et al.*, 1997) or specific level (Pickford *et al.*, 2003; Pickford & Kunimatsu, 2005). Traditionally, in order to account for this large range of metric variation, it has been proposed that *U. major* was exceptionally sexually dimorphic, with large males and small females (Pilbeam; 1969; Martin, 1981) but this proposal always had an ad hoc aura about it, because the proposed model of dimorphism invoked to explain the variation was unknown in any other fossil or extant primates (Bosler, 1981). The Moroto palate was for a while classified as *Proconsul major* (Pilbeam, 1969) but it was finally removed from the genus by Gebo *et al.* (1997) following work by Bosler (1981) and Martin (1981) which showed that it did not fit comfortably within this species (MacLatchy & Rossie, 2005a, 2005b; MacLatchy & Young, 2004; Young & MacLatchy, 2000, 2004). As it happens, the Moroto localities have yielded two taxa of large apes, *Afropithecus turkanensis* (the Moroto palate, for a while thought to be a separate genus and species *Morotopithecus bishopi*) and *Ugandapithecus* cf *gitongai* not only on the basis of dental remains (Pickford *et*

al., 1999), but also on postcranial evidence (Gomery *et al.*, 2002) (fig. 56).

During the 1980's there were four main obstacles to recognising credible subgroups of *Ugandapithecus major*. The first was the restricted nature of the available dental sample. Recent collections have gone a long way towards rectifying this deficiency, and we are now in a better position to carry out statistical analysis on the remains, with some hope of observing patterns that are biologically significant. The second was the taxonomic ambiance in which the fossils were interpreted. During the 1960's and 1970's there was a general tendency to lump fossil hominoid taxa together, initiated by Simons & Pilbeam in 1965 and largely diffused by both of these scientists (Simons *et al.*, 1978; Simons & Pilbeam, 1972; Pilbeam, 2001). For a while *Proconsul* was included within *Dryopithecus* as was the Indian genus *Sivapithecus*, while *Ramapithecus*, the female of *Sivapithecus*, was curiously kept in a different family, Hominidae. By the 1980's *Proconsul* had been reinstated as a valid genus, but it was considered to comprise two subgenera (*Proconsul* with three species and *Rangwapithecus* with two). The third hindrance to proper interpretation of the fossils was also due to influential authors such as Simons & Pilbeam (1965) who interpreted the fossils within a model of sexu-

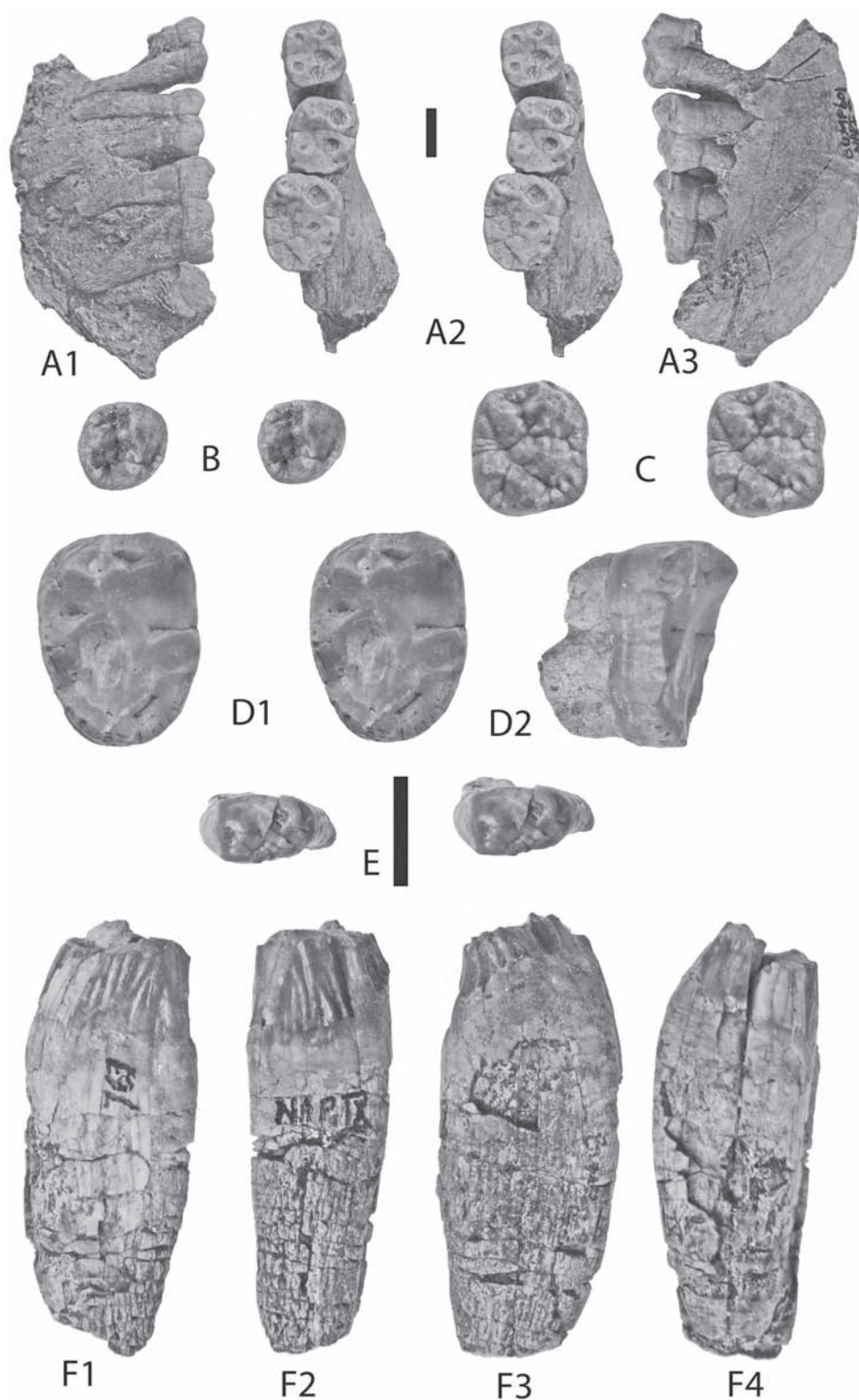


Fig. 30.—*Ugandapithecus major* from Napak, BUMP collection A) Nap I, BUMP 601 right mandible containing m/1-m/3, (A1 - lingual, A2 - stereo occlusal and A3 - buccal views); B) Nap CC, BUMP 889, right p/4, stereo occlusal view; C) Nap CC, BUMP 269, right m/1 stereo occlusal view; D) Nap I, BUMP 600, left m/3, (D1 - stereo occlusal and D2 - buccal views); E) Nap V, MUZM 146, right P4/, stereo occlusal view; F) Nap IX, BUMP 763, right upper canine erroneously reported to be from Napak I by MacLatchy and Rossie (2005b) (F1 - distal, F2 - mesial, F3 - lingual and F4 - labial views) (scale: 10 mm).

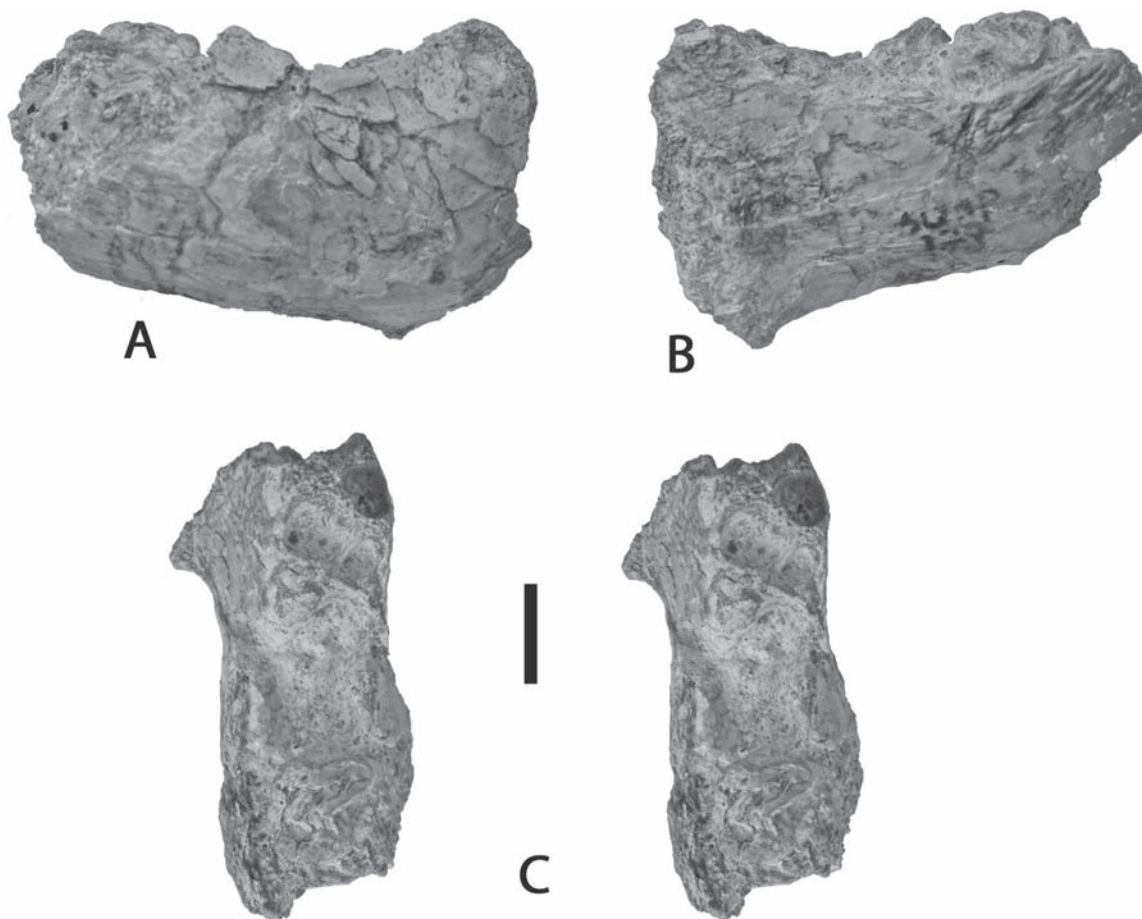


Fig. 31.—Nap CC, BUMP 127, right mandible lacking teeth, *Ugandapithecus major* (A - buccal, B - lingual and C - stereo view of alveolar surface) (NB, the catalogue number 173, written on the specimen is erroneous) (scale: 10 mm).

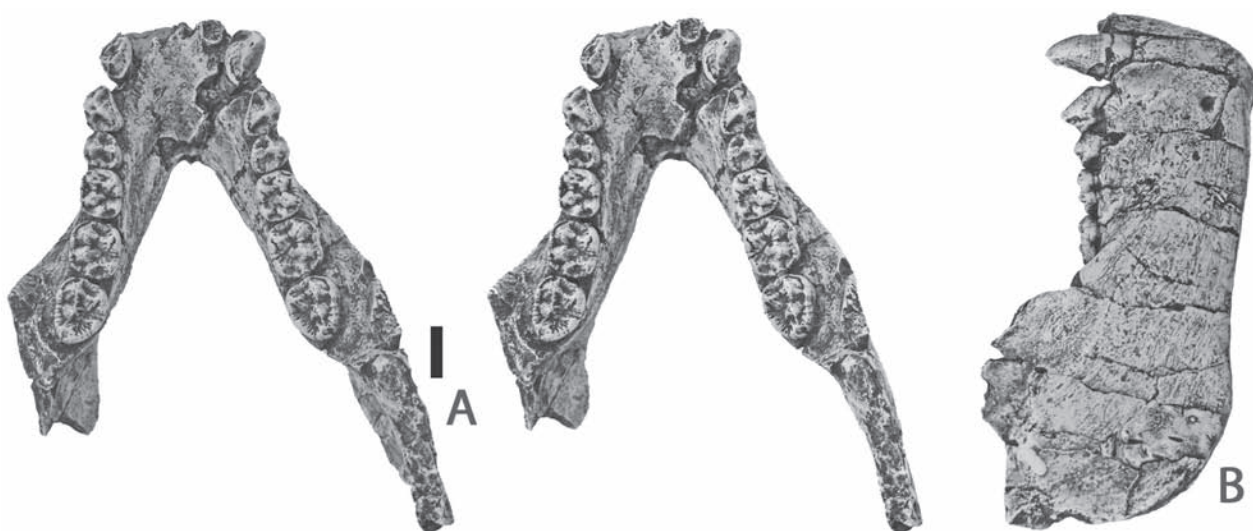


Fig. 32.—KNM LG 452, cast of holotype mandible of *Ugandapithecus legetetensis*, sp. nov., from the Legetet Formation, Koru, Kenya, attributed to a female of the species (A - stereo occlusal view, B - right lateral view) (scale bar: 10 mm).

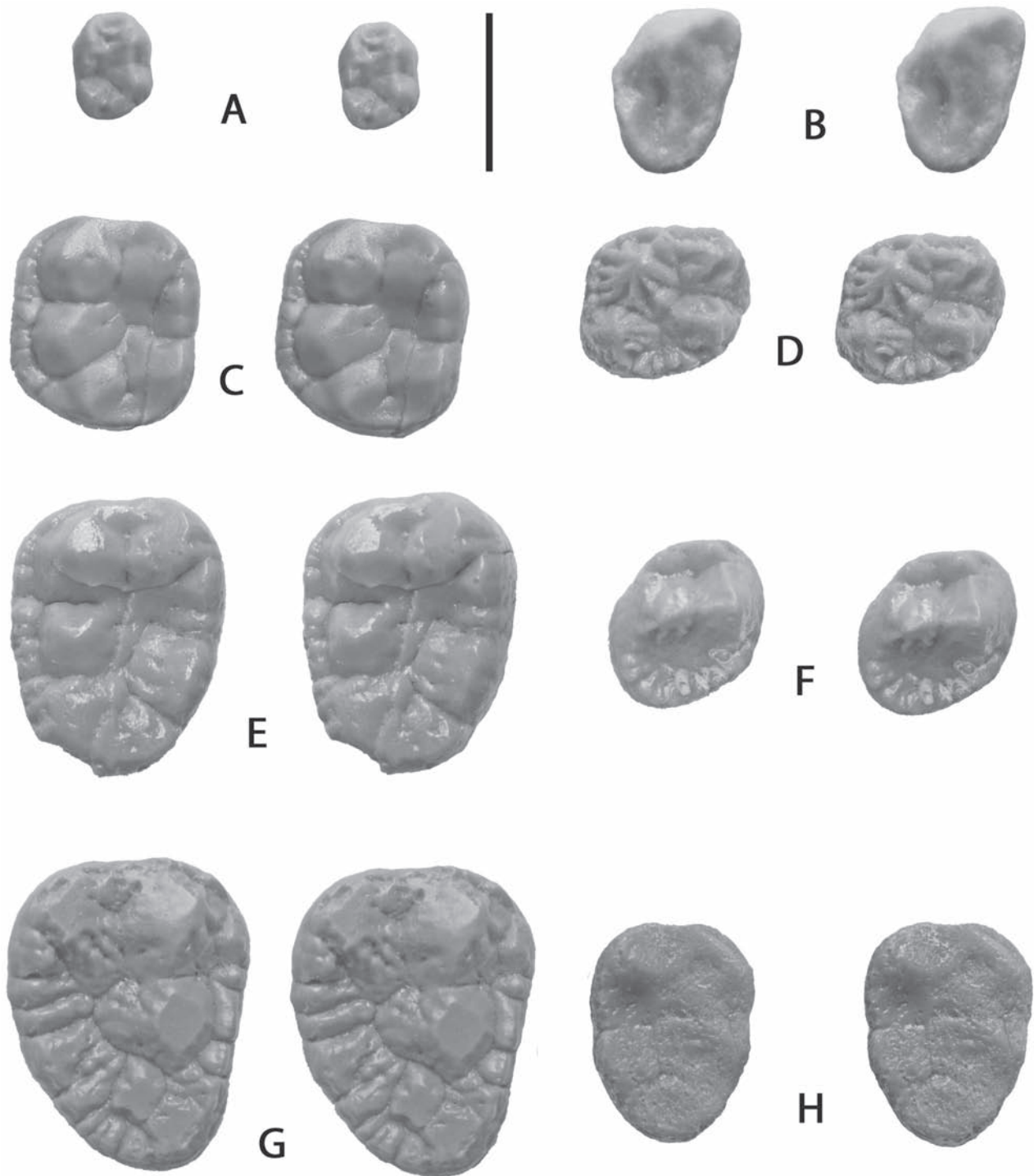


Fig. 33.—Stereo occlusal views casts of teeth of *Proconsul africanus* (A-B), *Ugandapithecus major* (C-G) and *Ugandapithecus leg-etetensis* sp. nov. (H) from Koru. A) Kor 158'05, right d/4; B) Kor 292'05, left p/3; C) Kor 252'04, left m/2; D) Kor 255'04, left M1; E) Kor 253'04, left m/3; F) Kor 280'05, right p/4; G) Kor 140'05, right m/3; H) Kor 90'04, right m/3 (Scale: 10 mm).



Fig. 34.—KNM SO 396, cast of mandible of *Ugandapithecus major* from Songhor, Kenya, attributed to a male of the species, with the occlusal surface of the cheek teeth oriented approximately horizontally, showing marked distal shallowing of ramal depth (scale bar: 10 mm).

al dimorphism that resulted in females (*Ramapithecus*) being classed as hominids, and the males of the same species (*Sivapithecus*) as apes. Fourthly, it appears that most authors were of the opinion that it would not be possible for two or more taxa of large hominoids to co-exist at any fossil site. This notion is still widespread, yet is no longer defensible. It is clear that several sites in Kenya (Kipsaraman, Fort Ternan, Songhor, Koru, Rusinga) and Uganda (Napak, Moroto) have yielded two or more large hominoid species, a point already published by Senut *et al.* (2000).

The mode of metric variation proposed for *Proconsul major* by Pilbeam (1969), Andrews *et al.* (1981) and Martin (1981) is not comparable to that seen in extant African apes (fig. 36), nor in any other known fossil hominoid, *Proconsul* included (Bosler, 1981; Pickford, 1986a; Cameron, 1991, Gingerich, 1977, Greenfield, 1972, 1977; Kelley 1986a, 1986b, 1995; Skaryd, 1971, Smith *et al.*, 2003; Uchida, 1996; Ungar *et al.*, 1996; Walker *et al.*, 1994, Zwell, 1972). This is because the cheek dentition in chimpanzees and gorillas is not very bimodal (fig. 37) unlike the proposed dimorphism in species of *Proconsul*. In extant apes, despite

large differences in body size between the sexes (Pickford, 1986a), there is extensive overlap in the range of metric variation of premolars and molars of males and females, but no overlap in canine dimensions (Pilbeam, 1969).

Because extant African apes possess extremely sexually bimodal canines (fig. 36), less bimodal premolars (fig. 37) and essentially unimodal first molars (fig. 38) and weakly bimodal third molars (fig. 39), Martin (1981) proposed that sex determination of individuals of unknown sex could be calculated from C1/M1 ratios. Extension of this concept to fossils led him and Walker *et al.* (1993) to propose the determination of the sex of fossils from Rusinga in which canines and first molars were associated. Thus a fossil lower jaw with a C1/M1 ratio of 0.79-0.97 was designated female, 0.98-1.19 as indeterminate, and 1.20-1.42 as male. For maxillae the female C1/M1 ratio is 0.90-1.12, indeterminate individuals range from 1.13-1.36, and males from 1.37-1.65. However, this approach is dependent upon the assumption that fossil hominoids would also have possessed minor bimodality of the first molars and extensive bimodality in the canines, as in extant apes. If a fossil species has sex-

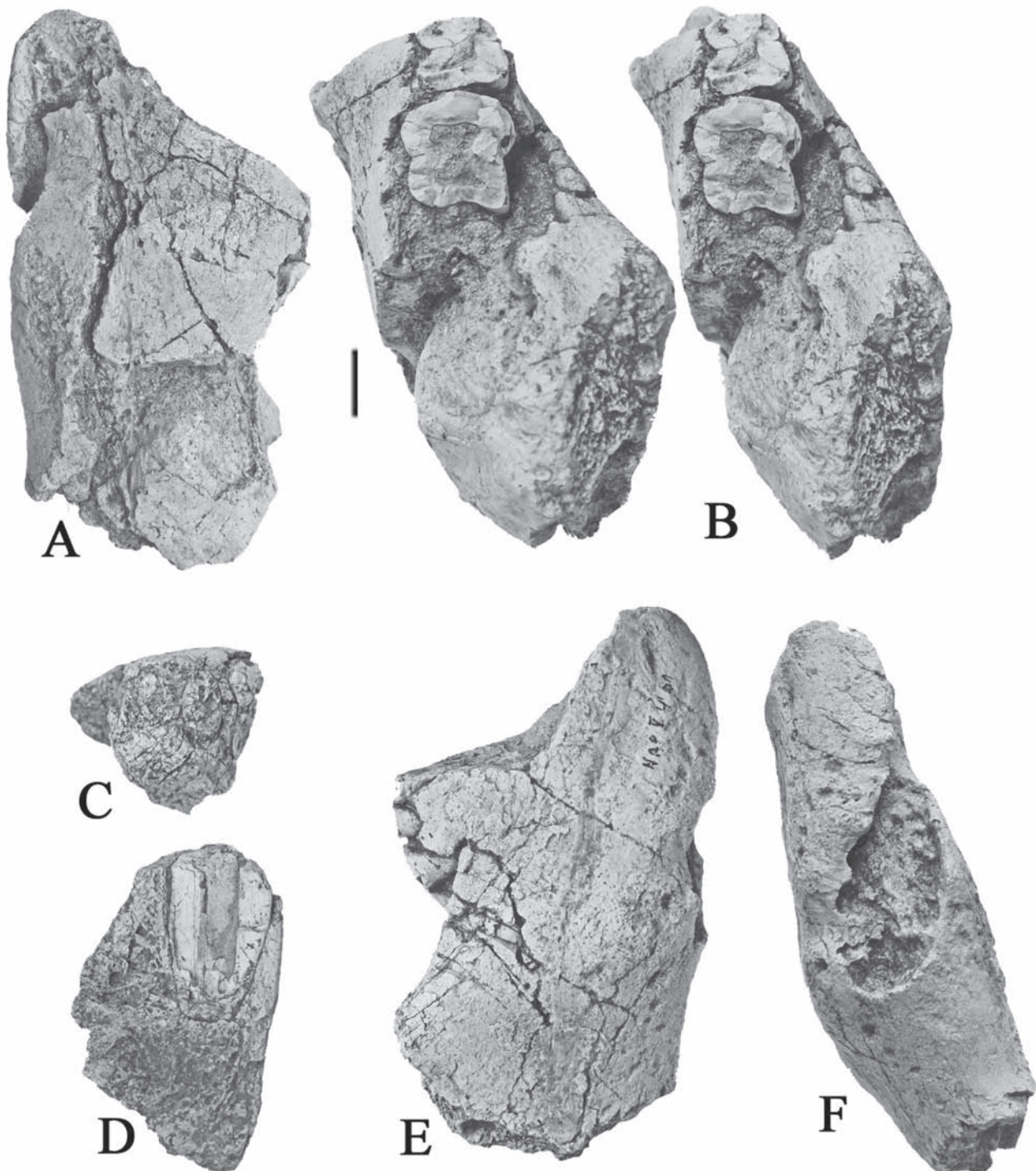


Fig. 35.—Nap V, 4'01, cast of pathologically altered right mandible and symphysis of *Ugandapithecus major*, with roots of the *i*/1-*i*/2, *c*/1, *m*/1 and *m*/2. (A - lingual, B - stereo occlusal, C - occlusal view of symphysis, D - posterior view of canine root, E - buccal and F - ventral views). The damage to the specimen (lesion in the ventral side, thickened secondary bone overlying normal bone) is consistent with the tropical disease yaws. Despite the pathology, the distal shallowing of the ramus is evident (scale: 10 mm).

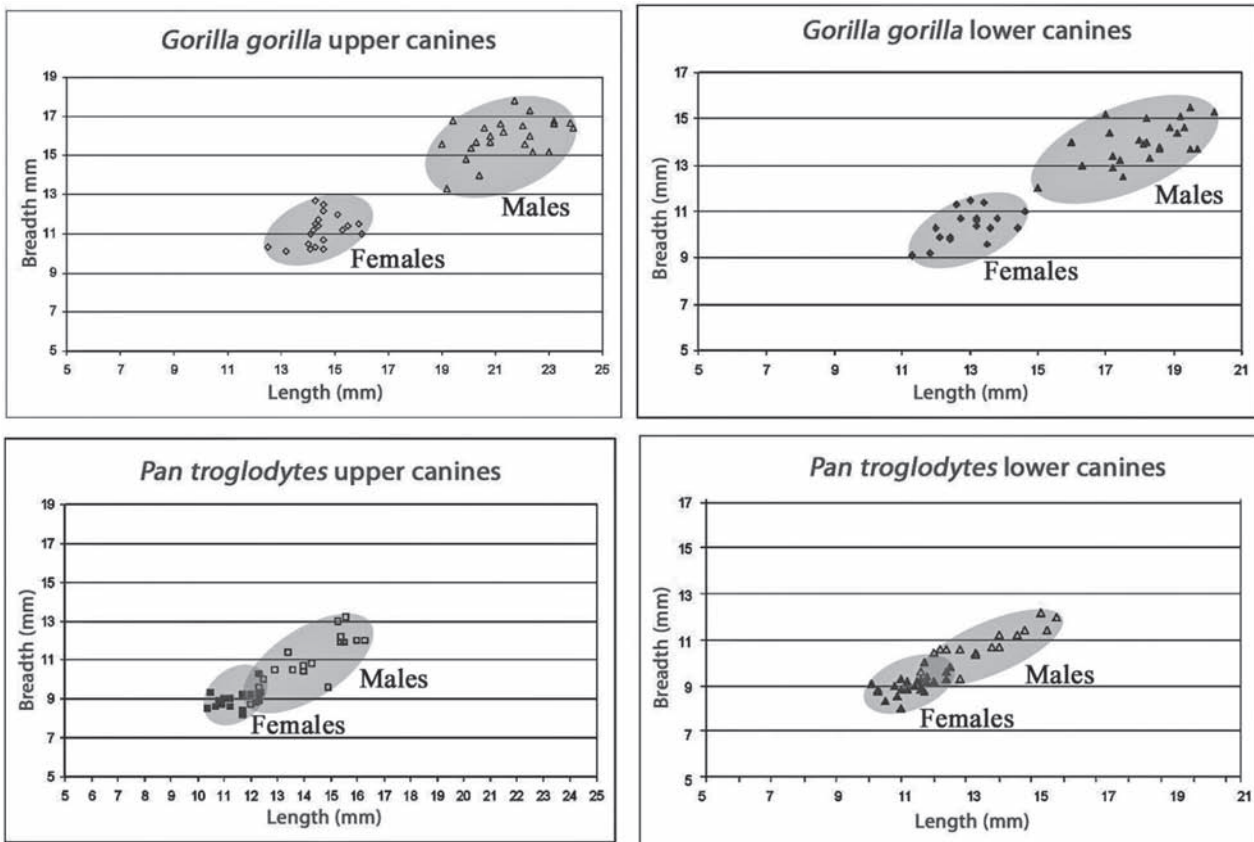


Fig. 36.—Canine bimodality in extant African Apes. Extant African apes possess a high degree of canine sexual bimodality, there being no overlap in the range of metric variation in male and female gorillas, and only a slight overlap in dimensions in male and female chimpanzees (data from Pilbeam, 1969, and authors' own measurements). (Symbols are explained in the diagram).

ually bimodal molars and canines, then the same ratio will not emerge from the measurements, and the approach would not be applicable to that species.

In their extensive analysis of the *Proconsul* remains from Rusinga Island, Walker *et al.* (1993) employed the C1/M1 ratio to determine the sex of several individuals in which these teeth were associated, and concluded that there were two species of *Proconsul* at Rusinga which differed in dimensions, a large species *Proconsul nyanzae* and a smaller one, *Proconsul heseloni*. However, some individuals such as the associated skull and mandible, KNM RU 7290, fell into the range of indeterminable specimens, but an index for the lower canine described by Kelley (1995) was used to determine the sex of this fossil as a female. Three other fossils from Rusinga proved enigmatic, or as the authors wrote, problematic (Walker *et al.*, 1993) including KNM RU 2088, KNM RU 1674 and KNM RU 16000. The enigmatic specimens which did not fall clearly

into one or other of these species were attributed as follows:- RU 2088 as a large male individual of *P. heseloni*, RU 1674 as a large male of *P. heseloni*, and RU 16000 as a small male of *P. nyanzae*, despite the fact that its canine is clearly too large to belong to *P. heseloni* and its molars too small to belong to *P. nyanzae*. The authors rejected the possibility that RU 16000 could represent a third species of *Proconsul* in the Rusinga deposits.

The attribution of specimens from Rusinga to two species of *Proconsul* by Walker *et al.* (1993) led to a bias in the sexual representation of each species as they themselves recognised. There appeared to be no females represented among the more complete specimens of *P. nyanzae*, and the two males in the material attributed to *P. heseloni* did not fit comfortably within the species. Bosler (1981) and Pickford (1986a) had already commented on this peculiarity in the interpretation of the Rusinga *Proconsul* assemblage. For these authors, *P. nyanzae* was rep-

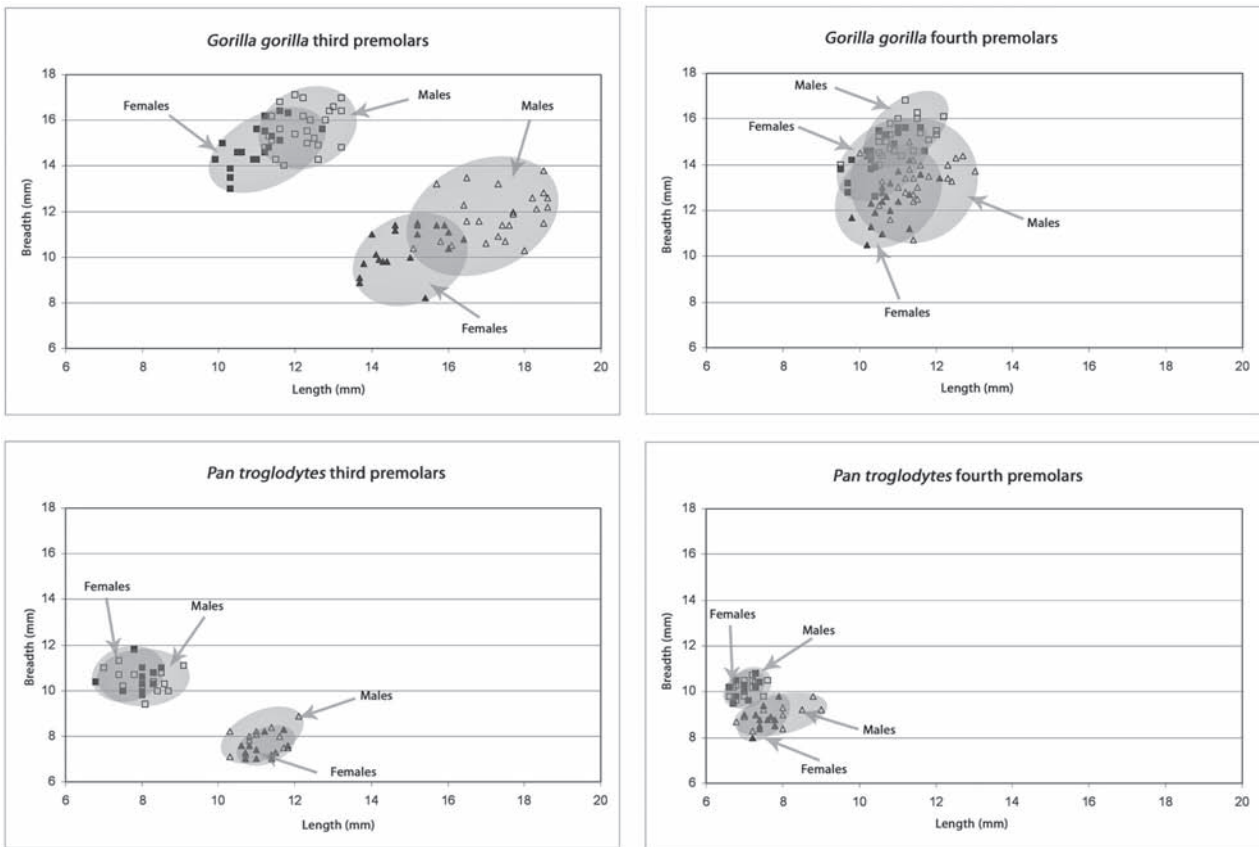


Fig. 37.—Length and breadth measurements of upper and lower premolars of males and females of extant African apes show extensive overlap in bivariate plots, meaning that they are not markedly sexually bimodal. Male gorillas tend to possess larger third premolars than females, but in both p/3 and P3/ about 30% of females plot into the range of variation of males. About 50% of male upper third premolars fall within the range of variation of females, whereas only a few lower third premolars do, indicating that the lower third premolar is a better indicator of maleness than the fourth premolars. In chimpanzees the metric overlap is so extensive that it is impossible to determine the sex of an isolated tooth with any degree of certainty (Data from Pilbeam, 1969 and authors' own measurements). (Symbols are explained in the diagram).

resented only by males, and *P. heseloni* exclusively by females except by the inclusion within the species of two enigmatic male specimens by Walker *et al.* (1993). If these individuals are attributed to *P. nyanzae* as small males (Bosler, 1981), then the sex bias becomes 100% for each species, a biologically unlikely scenario. We here propose a different sorting of the Rusinga *Proconsul* fossils, which results in a more equable proportion of males and females in the two species represented in the deposits (fig. 40, 41, 43, 45, 46, 47, 50, 52, 54).

In order to test whether the canine to molar size ratio is comparable in *Proconsul* and extant African apes we pay careful attention to variation in *Ugandapithecus*, a taxon related to *Proconsul*, in order to determine whether or not it shows the same pattern of C1/M1 variation as *Proconsul*.

Traditionally, *Ugandapithecus major*, which used to be classified as *Proconsul major*, has been considered to be a highly sexually dimorphic taxon with large males and small females (Pilbeam, 1969; Martin, 1981; Pickford, 1986a) with bimodal dental dimensions at every tooth position (fig. 45). In contrast the two Rusinga *Proconsul* species, each of which has been interpreted as having a considerable degree of dimorphism in body size (as calculated from the dimensions of the first molar or post-cranial bones for example) possessed essentially unimodal molars.

Martin (1981) attributed material from Koru, Songhor, Chamtwara, Legetet and Meswa Bridge in Kenya, and Napak and Moroto in Uganda, to *Proconsul major*, but noted that some of the material, in particular the Moroto and Meswa specimens, did

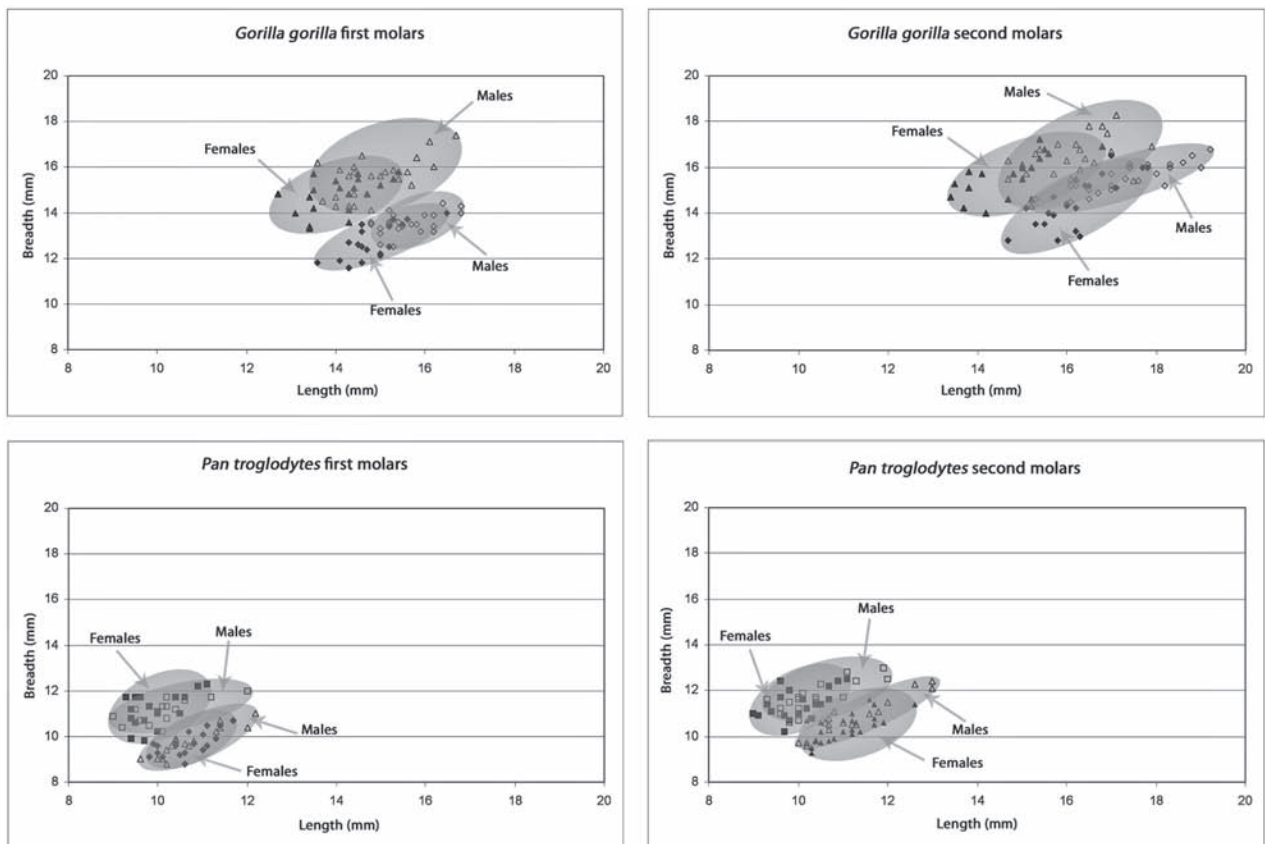


Fig. 38.—Upper and lower first and second molars of the two sexes of extant African apes show extensive overlap in their ranges of metric variation (Data from Pilbeam, 1969 and authors' own measurements). (Symbols are explained in the diagram).

not fit comfortably within a single species, either because their morphology was different (Moroto) or their dimensions were too divergent (Meswa). Since then, the Moroto fossils have been attributed to *Morotopithecus bishopi* by Gebo *et al.* (1997) which is a synonym of *Afropithecus turkanensis* (Leakey & Leakey, 1986; Leakey & Walker, 1997; Pickford *et al.*, 1999; Pickford, 2002a; Patel & Grossman, 2006), but the same locality has yielded other fossils which belong to *Ugandapithecus* (Pickford *et al.*, 2003), *U. gitongai*, first described from Kipsaraman, Kenya, from younger deposits (ca 14.5 Ma) than Moroto (17.5 Ma) and Napak (20–19 Ma). The Meswa material was recently revised and a new species *Proconsul meswae* created for it by Harrison & Andrews (2009). Harrison & Andrews (2009) showed that the Meswa material differs morphologically from similar-sized *Proconsul nyanzae*, but they opted to continue with its classification as *Proconsul* rather than as *Ugandapithecus*. However, we take the morphological differ-

ences noted by these authors to provide just the sort of evidence to indicate that the specimens belong instead to the genus *Ugandapithecus*. Their findings thus support our view that the genus *Ugandapithecus* differs from *Proconsul* at the generic level.

With the relatively small samples of *Ugandapithecus* fossils available to Martin (1981) and subsequent researchers (MacLatchy & Rossie, 2005b) it was not really possible to argue convincingly, either in support of a highly variable single species, or for the presence of two or more species in the erstwhile hypodigm of *Proconsul major*. Now that the authors have increased the samples of this large hominoid by 14 specimens from Koru and 22 from Napak (which contain a total of 54 teeth), the overall assemblage now available is comprehensive enough in some tooth positions to provide constraints on their interpretation.

Bivariate plots of the upper and lower teeth previously attributed to *Ugandapithecus major* are presented in figures 48, 49, 51, 53, 55. The plot for the

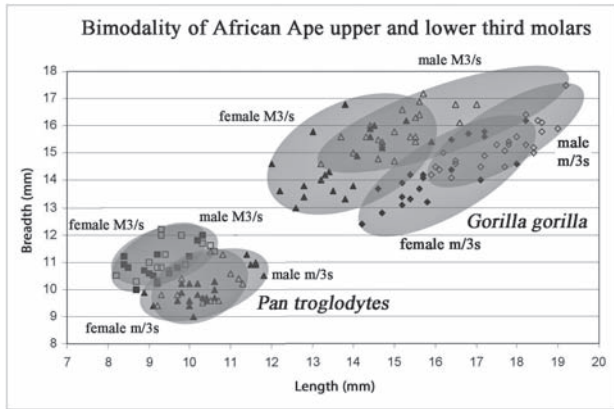


Fig. 39.—Third molars of extant African apes show extensive overlap in the range of metric variation of males and females. Gorillas have slightly greater sexual bimodality than chimpanzees, in which there is almost complete overlap between males and females (Data from Pilbeam, 1969, and authors' own measurements). (Symbols are explained in the diagram).

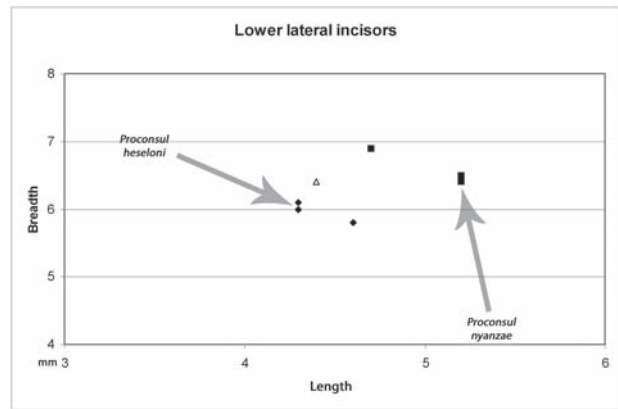
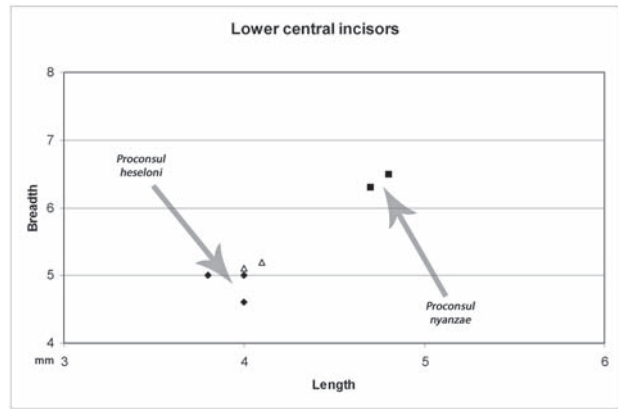


Fig. 41.—Revised sorting of lower incisors of *Proconsul* from Rusinga Island and associated deposits at Kisingiri, Kenya (open triangle – unattributed to species). (Symbols are explained in the diagram).

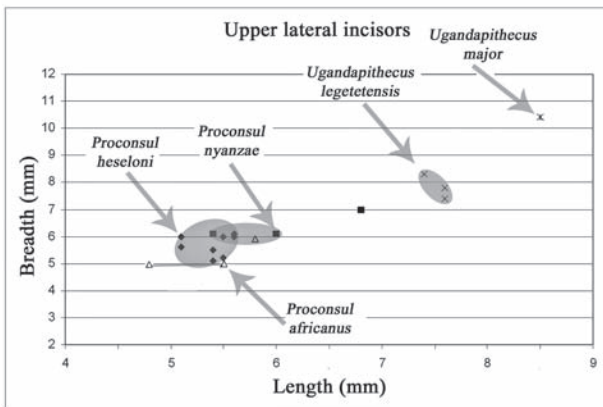
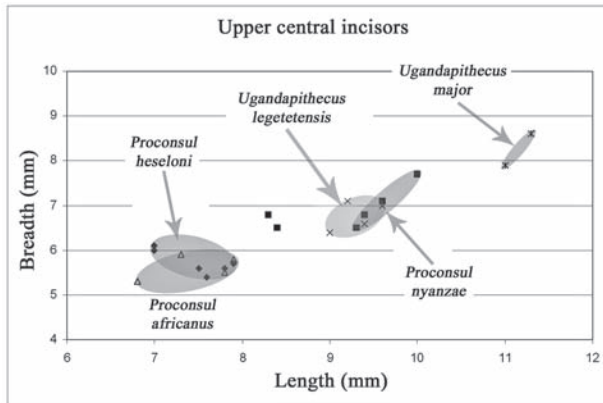


Fig. 40.—Revised sorting of upper incisors of *Proconsul* from Rusinga Island and associated deposits at Kisingiri, Kenya, as well as Songhor and Chamtwara and of *Ugandapithecus*. (Note the three outlying teeth (dark squares) identified as *Proconsul nyanzae*). Obviously worn teeth have been omitted (open triangle – *Proconsul africanus*??). (Symbols are explained in the diagram).

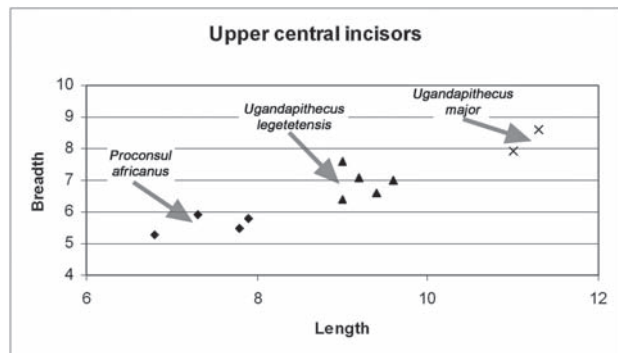


Fig. 42.—Upper incisors of *Ugandapithecus* species and *Proconsul africanus*. Among the incisors, only the upper central incisors are numerous enough to be analysed by this approach but see Figure 40 for I2/. The *Ugandapithecus* specimens cluster into two clearly separated groups, large *U. major* and smaller *U. legetetensis* sp. nov. (Symbols are explained in the diagram).

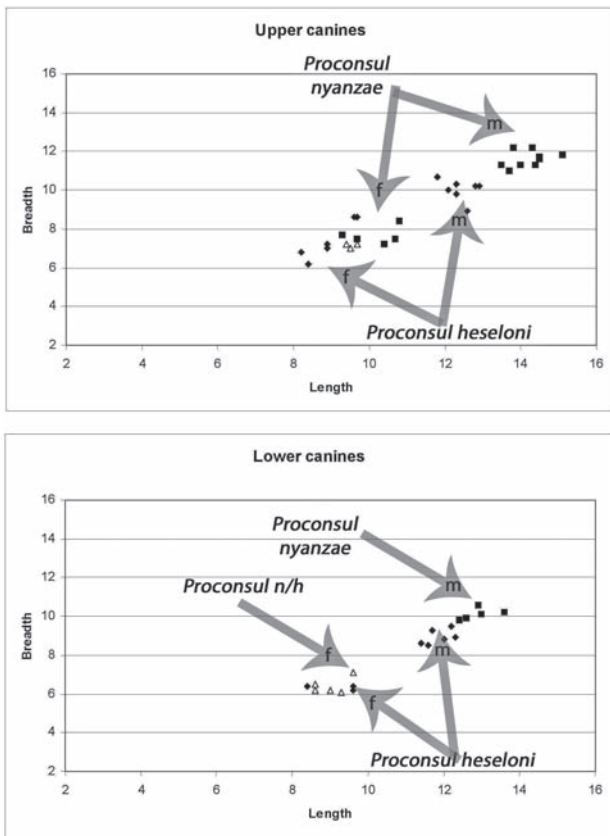


Fig. 43.—Bivariate scatter plots of upper and lower canines of *Proconsul* from Rusinga with revised sorting at the species level. Previous publications (Bosler, 1981; Walker *et al.*, 1993) had exactly the same sex determination as presented here, but all the male specimens with the exception of two were considered to belong to *Proconsul nyanzae* and all the female specimens were attributed to *Proconsul heseloni*. In this revised sorting, account is taken of the bimodal distribution of the male canines (grey arrows marked with an “m”), the cloud of large specimens being identified as *P. nyanzae* because it is in this cloud that the holotype occurs, and the cloud of smaller individuals as *P. heseloni*. The female canines (grey arrows marked with an “f”) are not so clearly bimodal, but have been identified for the most part on the basis of associated teeth. Those lower canines that could not be sorted on the basis of associated upper canines have been left unidentified (open triangles).

third molars reveal distinct clouds of points (fig. 55). The same pattern is observed with the first and second molars (fig. 51, 53), but because isolated intermediate molars are difficult to assign unequivocally to their meristic position (Bosler, 1981), in order to avoid circular reasoning we do not adopt this as solid evidence for the presence of two size groups for each tooth. For teeth *in situ* in mandibles and maxillae, however, there is no doubt that there are three clearly separable groups of first and second molars in *Ugandapithecus*, but the sample is small.

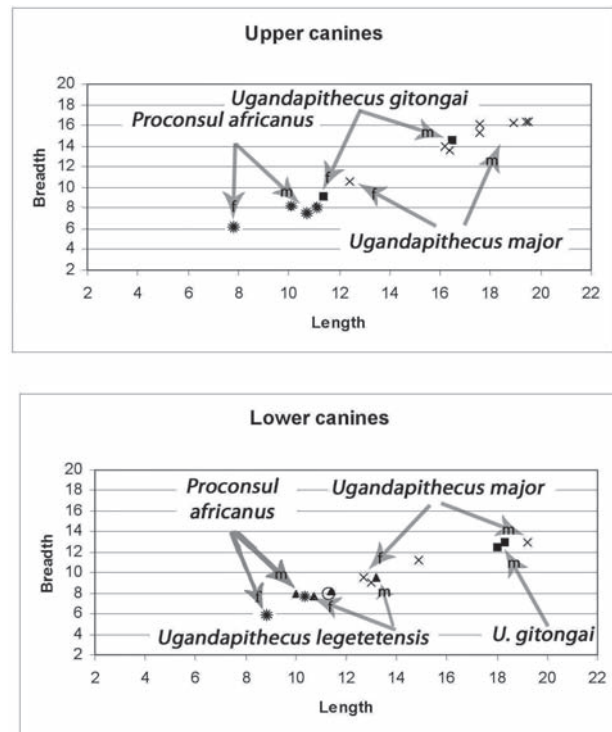


Fig. 44.—Identification of upper and lower canines of *Ugandapithecus* species and *Proconsul africanus*. Grey arrows identify the species to which the specimens belong, and “m” and “f” identify the sex of the individual specimens. Open circle is KNM SO 1112, interpreted as a male individual of *Ugandapithecus meswa*, which is almost identical in dimensions to the holotype of *Ugandapithecus legetetensis*, commonly accepted as a female individual; starbursts, *Proconsul africanus* (In lower frame stars identify Kor 65'04, interpreted as a male individual and KNM CA 2149, identified as a female); triangles are specimens attributed to *Ugandapithecus legetetensis*; crosses – *Ugandapithecus major*, squares – *U. gitongai*.

The same applies to the upper and lower premolars (fig. 48, 49), which show two entirely separate clouds of points for each tooth, but unlike the first and second molars, with these teeth the meristic position is not in doubt. The canines attributed to the species show two clear clouds of points, but there is a suggestion that each of the clouds of points is itself bimodal, hinting at the presence of two taxa in the sample rather than one. This is especially so for the lower canines, which are the most numerous.

Previous attribution of all *Ugandapithecus* specimens to a single sexually dimorphic species results in the unlikely situation that all teeth, including the molars, would be strongly bimodal, in which case sexual variation in *Ugandapithecus* would not have been like that expressed in extant African apes. If

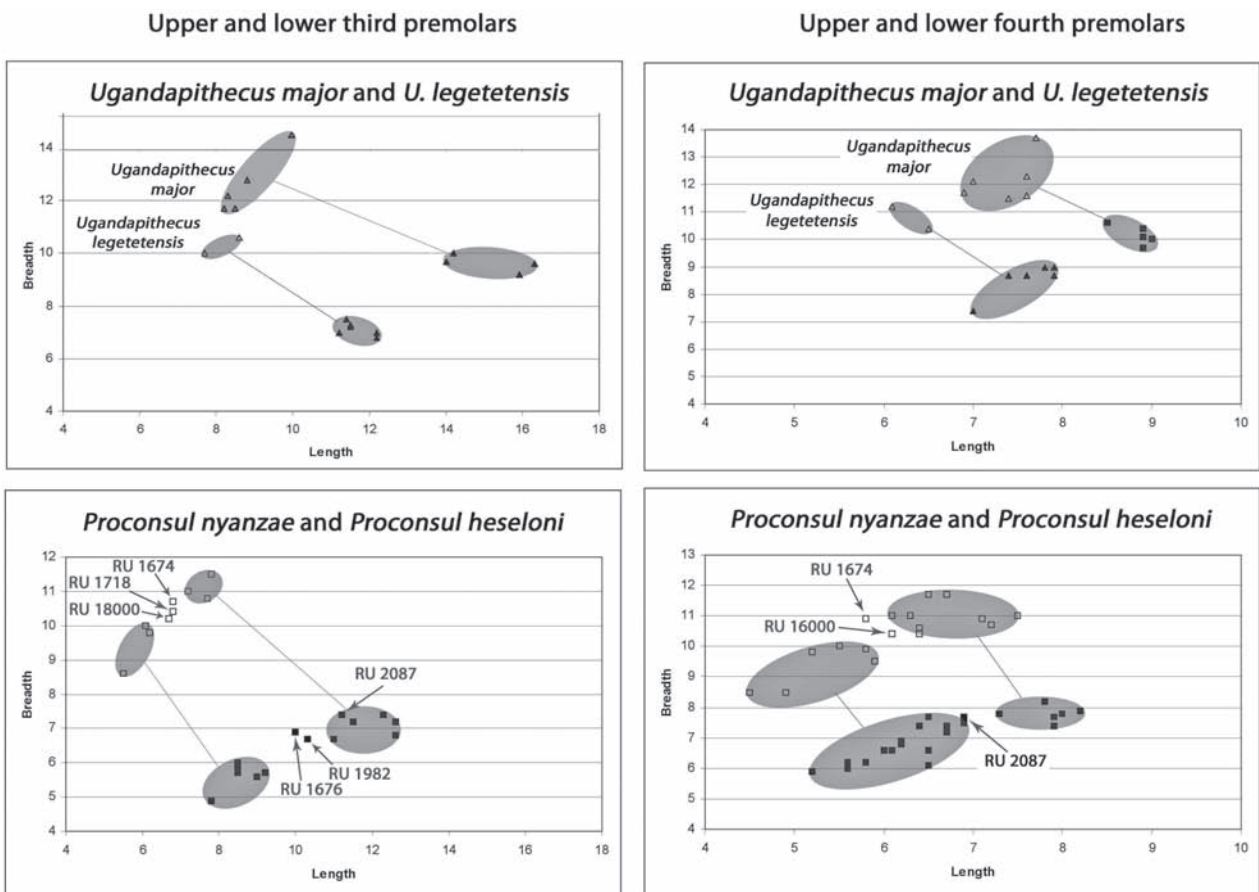


Fig. 45.—Bivariate scatter plots of premolars of *Ugandapithecus* and *Proconsul* from Rusinga. The scatter plots of upper and lower teeth are connected by lines. Enigmatic specimens from Rusinga are detailed by their catalogue numbers. Traditionally, the material of Rusinga *Proconsul* has been interpreted as belonging to two species whereas a similar mode of variation in *Ugandapithecus major* has previously been interpreted as representing two sexes of a single species. We conclude that if there are two species at Rusinga, then there must also be two species of *Ugandapithecus*.

this is so then the C1/M1 ratio of extant apes (Walker *et al.*, 1993) would not be applicable to the determination of sex in the Early Miocene fossils. However, if the sample contains two species, each with essentially unimodal molars, as proposed here, then it would conform in pattern to the extant African apes (fig. 43, 44).

Examination of the scatter plots of material of *Proconsul* from Rusinga reveals that bimodality of upper and lower canines is similar in pattern to that of *Ugandapithecus major*, and furthermore, that each of the scatters is itself bimodal (fig. 47, 48). The same applies to the premolars and molars (fig. 43, 45). Walker *et al.* (1993) argued for the presence of two species at Rusinga, in which case the *Ugandapithecus* material should be treated in the same way.

If, on the other hand, the *Ugandapithecus* fossils are interpreted as belonging to a single species (Pilbeam, 1969; Bosler, 1981; Martin, 1981), then it is difficult to evade the conclusion that all the Rusinga material should also be attributed to a single species, but this runs counter to the post-cranial evidence which indicates the presence of two taxa at Rusinga. This is particularly so when the morphology of the canines is taken into account. The canines of *Ugandapithecus* are now sufficiently abundant for a pattern to begin emerging. Out of 9 lower canines available, 7 are of female morphology and only two large specimens have characteristically male morphology. Out of 8 upper canines available, 7 are male and only one is female. If we interpret the scatter plots of *Ugandapithecus* teeth as providing evidence of two species in the sample, then this would give rise to

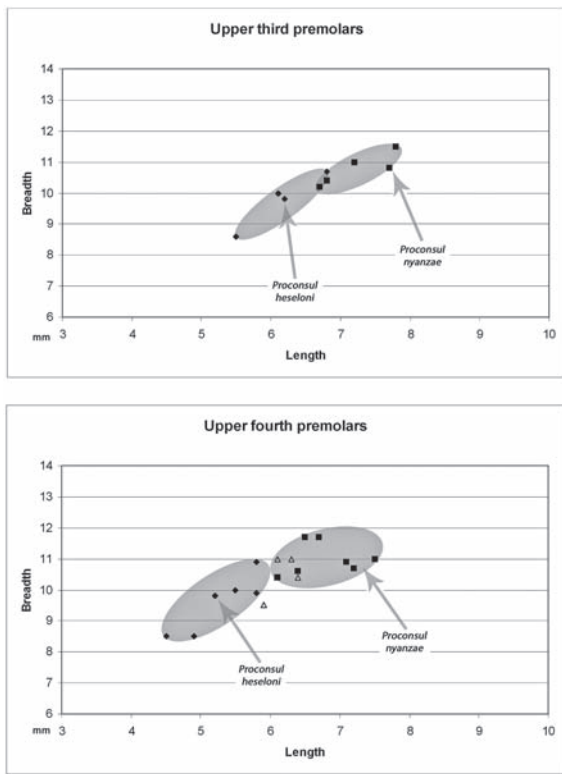


Fig. 46.—Revised sorting of upper premolars of Rusinga *Proconsul*. Taxonomic identifications are proposed on the basis of associated canine dimensions. Undetermined specimens are represented by open triangles.

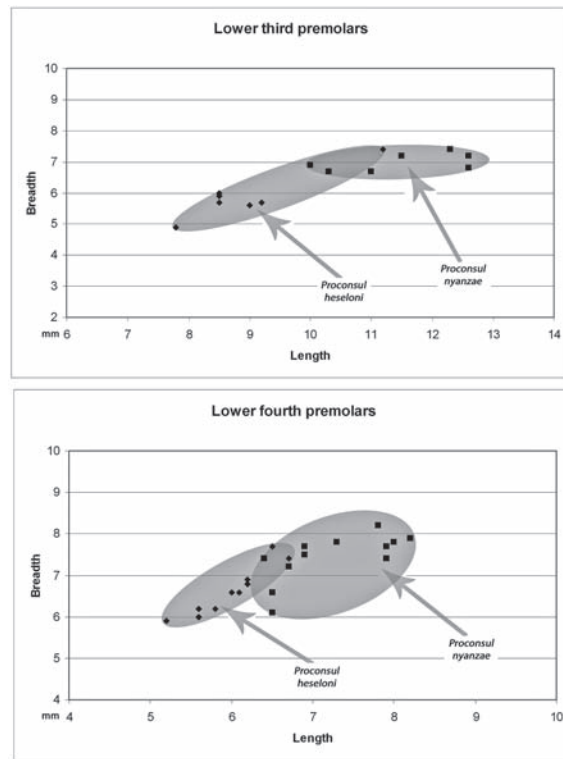


Fig. 47.—Bivariate scatter plots of lower premolars of *Proconsul* from Rusinga. Taxonomic identifications are based on the association of the teeth with canines. There is overlap between the scatter plots of *P. nyanzae* and *P. heseloni*.

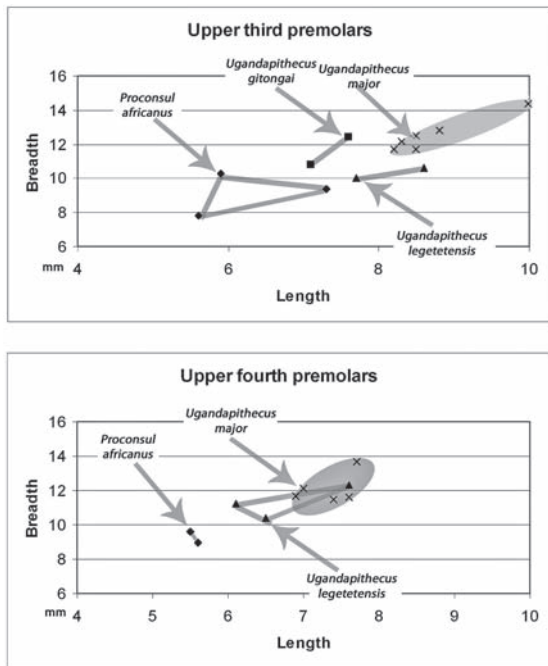


Fig. 48.—Bivariate scatter plots of upper premolars of *Ugandapithecus* species and *Proconsul africanus*.

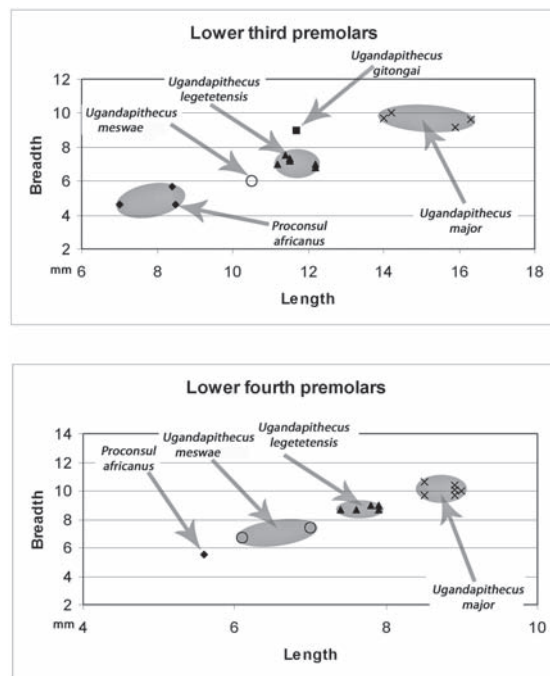


Fig. 49.—Bivariate plots of lower premolars of *Ugandapithecus* species and *Proconsul africanus*. There is clear separation of the teeth into separate groups.

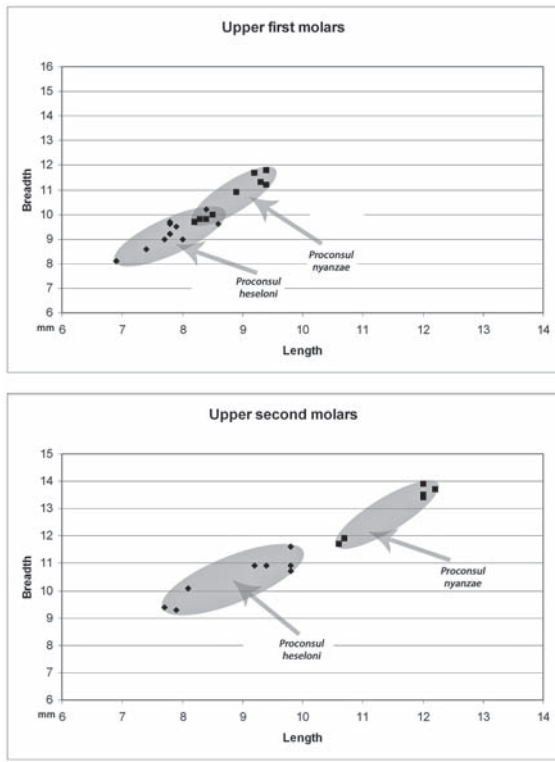


Fig. 50.—Revised sorting of upper first and second molars of *Proconsul* species from Rusinga and associated deposits, Kenya. Taxonomic sorting has been done on the basis of associated canines.

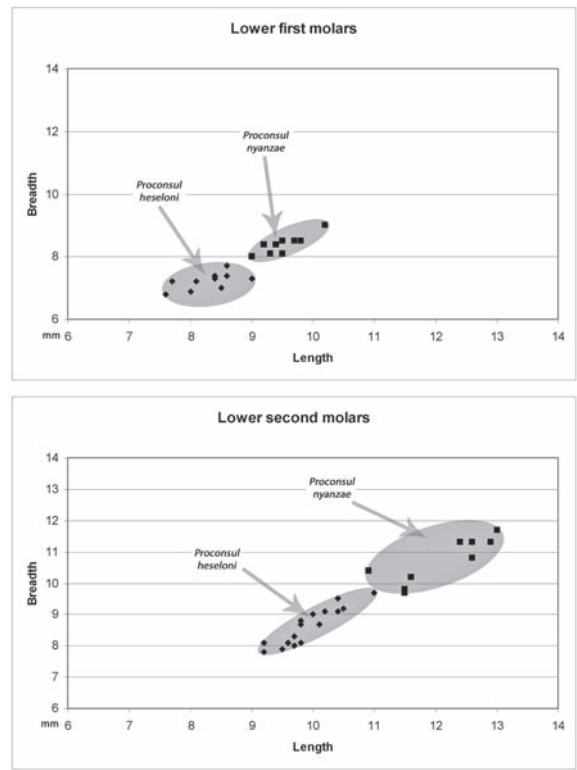


Fig. 52.—Bivariate scatter plots of lower first and second molars of *Proconsul* from Rusinga with revised taxonomic sorting.

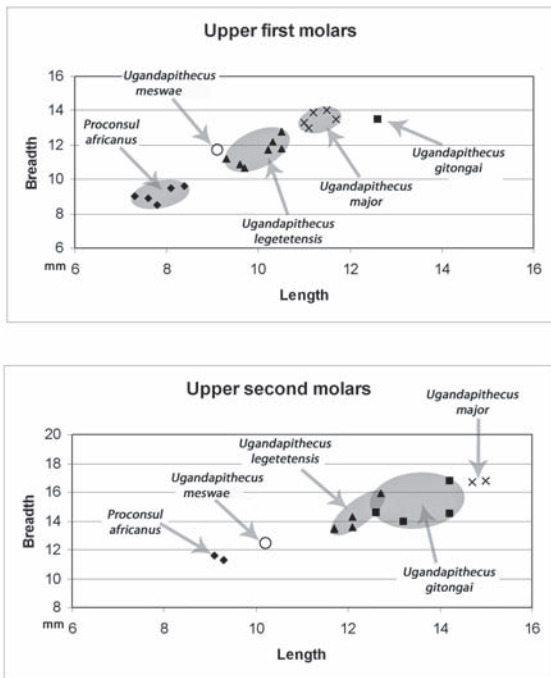


Fig. 51.—Bivariate scatter plots of upper molars of the various species of *Ugandapithecus*, and *Proconsul africanus* from Western Kenya (see Table 6).

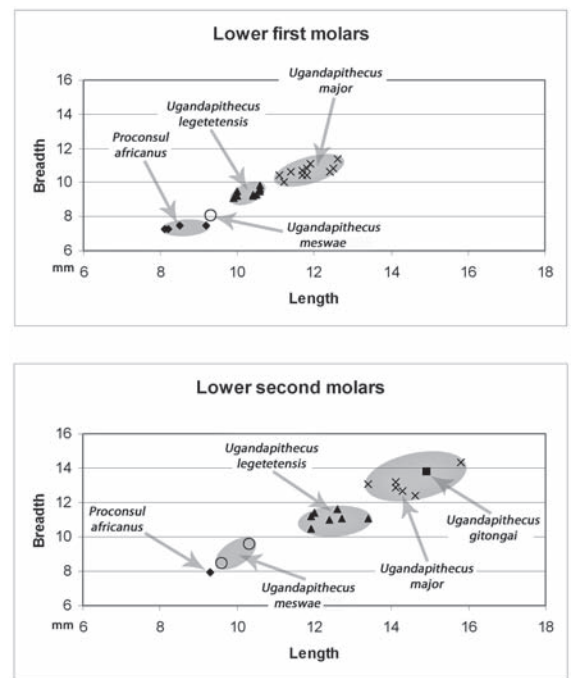


Fig. 53.—Bivariate plots of lower first and second molars of *Ugandapithecus* species and *Proconsul africanus* from Western Kenya (see Table 6).

the odd situation in which there would be only males in the large species, and only females in the smaller species, precisely the same bias that occurs at Rusinga under the two species concept and sorting of specimens of Walker *et al.* (1993).

A third possibility exists, which gains support from samples with sufficient teeth, in which each scatter plot is itself bimodal (fig. 50, 52 for example) indicating the presence of two species at both Rusinga and in the *Ugandapithecus* sample, each of which is bimodal (admittedly with some overlap in the scatter), but not in the ways previously calculated. Thus, the subset of smaller male canines attributed to *Proconsul nyanzae* belong to a second species, and the subset of smaller canines of *Ugandapithecus* belong to a species distinct from *U. major*. If this is so, then the representation of sexes would be more equable at Rusinga, with each species containing both males and females, and the same would apply to *Ugandapithecus*.

In our opinion, the most biologically plausible way of interpreting both the Rusinga *Proconsul* assemblage and the fossils attributed to *Ugandapithecus* should take into account the high probability that both sexes should be present in any taxon represented by a sufficient number of dento-gnathic specimens. With the Rusinga sample now numbering 253 teeth, it seems that it would be unnatural for there to be two species present, each of which is represented by only one sex (males for *P. nyanzae*; females for *P. heseloni*, unless two enigmatic male specimens are uncomfortably accepted within the latter species [Walker *et al.*, 1993]). It seems far more likely that there are two species present, each of which is represented by males and females, in which case past attribution of specimens to species needs re-assessment. In a previous interpretation of the Rusinga sample, Pickford (1986) tried to reconcile the data by lumping all the material into a single species (*P. nyanzae*) but it now seems more likely that there are indeed two species of *Proconsul* at the site.

When we consider the *Ugandapithecus* fossil assemblage it becomes even less likely that previous attribution of *Proconsul* specimens at Rusinga is correct. If we interpret the enlarged sample of *Ugandapithecus* teeth now available (198 specimens) (Table 7, 10) in the same way as Walker *et al.* (1993) did for the Rusinga *Proconsul* sample, then we would end up with two species of *Ugandapithecus*, each of which is represented by individuals of one sex only, males only for *U. major*, and females only for the smaller *Ugandapithecus legetetensis* sp. nov.

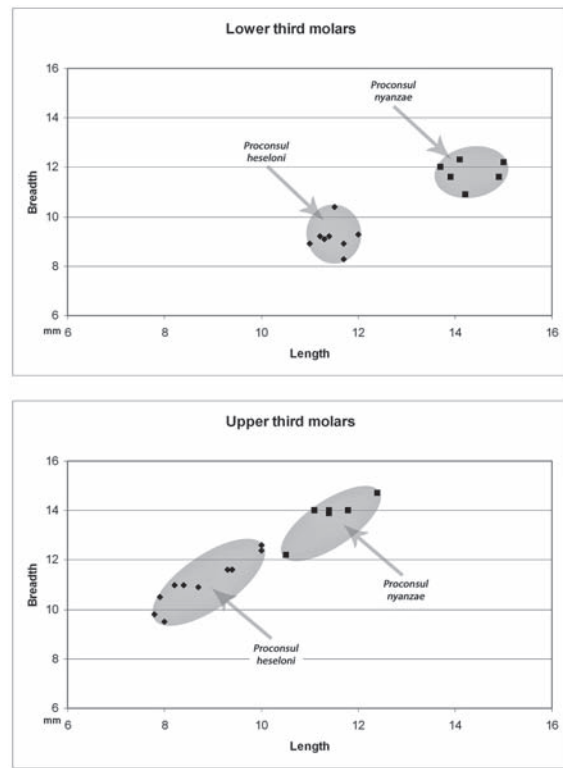


Fig. 54.—Bivariate plots of upper and lower third molars of *Proconsul* from Rusinga and associated deposits: revised taxonomic sorting.

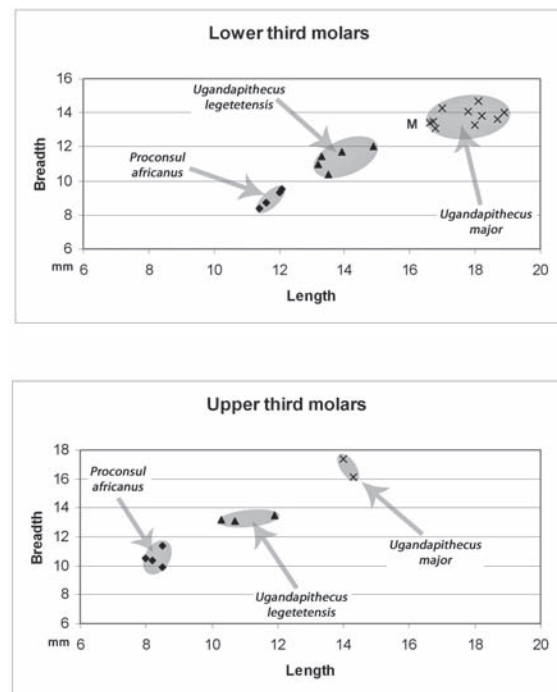


Fig. 55.—Bivariate plots of upper and lower third molars of *Ugandapithecus* and *Proconsul africanus*. M = Mor II, 10'08, left m/3 (see Fig. 56B) (for locality data see Tables 2, 3 and 6).

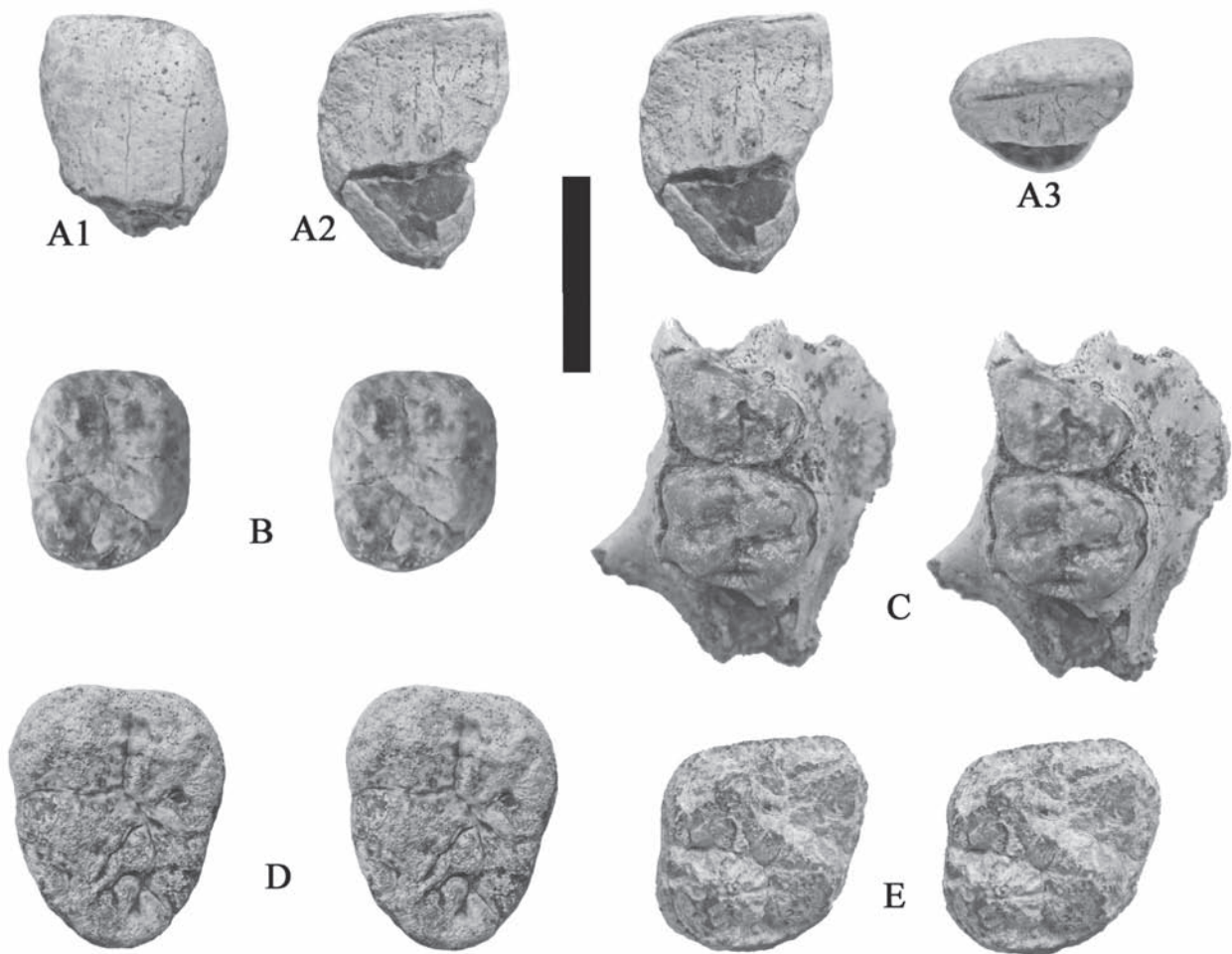


Fig. 56.—A) Mor II, 11'08, *Afropithecus turkanensis*, right I1/ (A1 - labial, A2 - stereo lingual and A3 - occlusal views); B) Mor II 1'08, *Afropithecus turkanensis*, right m/1, stereo occlusal view; C) Mor I 1'08, *Afropithecus turkanensis*, right maxilla containing D3/, D4/, stereo occlusal view; D) Mor II, 10'08, *Ugandapithecus cf. gitongai*, left m/3, stereo occlusal view; E) Mor II 2'98, left upper molar, *Ugandapithecus cf. gitongai*, stereo occlusal view. These specimens from Moroto I and Moroto II confirm the presence of two large bodied apes at the sites, a fact that was already demonstrated by Pickford *et al.*, (1999). This co-occurrence has implications for the identification of the Moroto large hominoid post-cranial remains (scale: 10 mm).

Instead, we prefer an interpretation that accepts the presence of two taxa at Rusinga as well as in the material hitherto attributed to *Ugandapithecus major*, but that sorts individual specimens in a different way from that carried out in previous studies, and resulting in the presence of males and females in each taxon present. However, because the two taxa in each assemblage (Rusinga *Proconsul* on the one hand and the combined *Ugandapithecus* sample on the other) there will inevitably be a few isolated specimens of first and second molars that are difficult to attribute with certainty to their correct species, mainly because their meristic position is unknown. Thus, although large male specimens at Rusinga are most likely to belong to *P. nyanzae*,

because the holotype is the largest specimen described, and small males are likely to belong to *P. heseloni*, because the holotype of the latter species, which lacks its canines, is small (Napier & Davies, 1959), it will be difficult to classify individuals intermediate in dimensions with certainty as they fall within the area of overlap between the species. Such intermediate fossils could thus belong to either species.

From this we draw the conclusion that there is a second species within the sample traditionally attributed to *Ugandapithecus major*. All the teeth of the new species are smaller than those of *U. major*. We select the most complete specimen available, KNM LG 452, as holotype, a mandible of a young

individual with the right canine, and all the premolars and molars on both sides in a relatively unworn condition. It was collected from the Maize Crib site at Koru, from which the holotype of *Proconsul africanus* was collected (Hopwood, 1933a, b). We agree with the separation of the Meswa sample from *Ugandapithecus major* and *Ugandapithecus legetetensis*, because it falls far outside the range of metric variation of both of these species. The Meswa species is almost the same size as *Proconsul africanus*, but its dentition is morphologically different from it as was documented by Andrews *et al.* (1981) and Harrison & Andrews (2009). In contrast, apart from one specimen, the Moroto specimens of *Ugandapithecus* are the size of *U. major* and *U. gitongai* (fig. 55, 56).

Systematic revision

Genus *Ugandapithecus* Senut, Pickford, Gommery & Kunimatsu, 2000

Type species: *Proconsul major* Le Gros Clark & Leakey, 1951

Diagnosis: Large hominoid, approximating the dimensions of large male chimpanzees and female gorillas, with sexually dimorphic canines, upper molars with prominent lingual cingula, M3/ not reduced distally, lower molars with buccal cingula, molar cusps bulbous, occlusal basins of molars confined, m/3 with reduced hypoconid very buccally positioned, lower molar roots elongated, upper and lower canines stubby with burin-like apices, upper canines with prominent distal ridge on roots, mesial margin of P3/ deeply concave in occlusal view, mandibular rami deep anteriorly, shallowing markedly towards the rear, symphyseal planum extensive, superior transverse torus prominent, no inferior transverse torus. Snout relatively short.

Differential diagnosis: *Ugandapithecus* differs from *Proconsul* and *Afropithecus* by a large quantity of dentognathic and postcranial characters. Mandibular ramus shallows markedly rearwards in *Ugandapithecus*, not so in *Proconsul*. Snout is short in *Ugandapithecus*, medium prognathic in *Proconsul* and elongated in *Afropithecus*. Upper central incisors of *Ugandapithecus* are broad and squat with a prominent lingual pillar and raised mesial and distal lingual ridges, slightly concave labial surface and a more extensive surface distal to the central pillar. In *Proconsul*, the upper central incisors are taller relative to mesio-distal diameter, the basal pillar is more strongly developed and the marginal ridges sharper. Upper lateral incisors of *Ugandapithecus* have no lingual cingulum, unlike *Afropithecus* and *Proconsul*, which do. Lingual expansion of I2/ crown is greater in *Ugandapithecus* than in *Proconsul* and *Afropithecus*. Upper canines of *Ugandapithecus* possess a burin-like apex and a prominent distal ridge on the root, unlike the pointed crown apex, and absence of ridge on the canine root in *Proconsul*. Upper canines of *Ugandapithecus* are more stubby, and the root more massive relative to the crown than in *Proconsul*, which have taller canines on more gracile roots. Upper premolars of *Ugandapithecus* have the buccal cusps more internally positioned than is the case in *Proconsul*, in which the post-

crista and precrista of the paracone are almost vertical. Mesial margin of P3/ in *Ugandapithecus* is concave (for accommodating the distal ridge on the root of the upper canine). In *Proconsul* the mesial margin of the P3/ is straighter. In *Ugandapithecus* the distal overhang of the crown of P4/ is greater and the buccal and lingual cusps are relatively closer together than they are in *Proconsul*. Upper molars possess more bulbous cusps than *Proconsul*. Upper third molars of *Ugandapithecus* are not abbreviated distally, unlike the foreshortened M3/s of *Proconsul* (reduced hypocone and metacone). Lower lateral incisors of *Ugandapithecus* possess a distal scoop, whereas those of *Proconsul* do not. Lower canines of *Ugandapithecus* do not show a well developed distal heel, unlike *Proconsul* which does. Mesial shoulder of lower canine is lower in *Ugandapithecus* than in *Proconsul*. Apex of lower canines blade-like (or burin-like) in *Ugandapithecus*, pointed in *Proconsul*. Lower molars of *Ugandapithecus* possess bulbous cusps, those of *Proconsul* have more pyramidal cusps. Lower third molars of *Ugandapithecus* narrow distally, the hypoconid is small and in a very lateral position, unlike the condition in *Proconsul* in which the hypoconid is more centrally positioned and not greatly reduced.

Radius head is posterolaterally flattened in *Ugandapithecus*, unlike *Proconsul*. Femur of *Ugandapithecus* is flattened between the base of the neck and the third trochanter, unlike *Afropithecus* and *Proconsul*. The intertrochanteric crest of the femur in *Ugandapithecus* reaches the base of the lesser trochanter, but it does not in *Afropithecus* or *Proconsul*. The tubercle for the crural is present in *Ugandapithecus* but absent in *Afropithecus* and *Proconsul*. The digital fossa of the femur in *Ugandapithecus* is almost circular, whereas in *Afropithecus* it is oval, as in cercopithecids. The lesser trochanter of the femur projects medially in *Ugandapithecus*, but is strongly posteriorly projecting in *Afropithecus* and *Proconsul*. The tibial malleolus of *Ugandapithecus* is thicker than it is in *Proconsul* and it has a wider anterior aspect of the talar facet. The lateral border of the talus extends further laterally in *Ugandapithecus* than in *Proconsul*.

Included species: *Ugandapithecus gitongai* Pickford & Kunimatsu, 2005, *Ugandapithecus legetetensis* sp. nov., *Ugandapithecus meswae* (Harrison & Andrews, 2009).

Species *Ugandapithecus major* (Le Gros Clark & Leakey, 1951)

Holotype: M 16648, right mandible containing p/4-m/3 (fig. 29).

Diagnosis: Large species of *Ugandapithecus*, p/3-m/3 length may exceed 65 mm (Andrews, 1978).

Differential diagnosis: *Ugandapithecus major* differs from *Ugandapithecus legetetensis* by its greater dimensions, from *Ugandapithecus gitongai* by its less “blocky” molar cusps and from *Ugandapithecus meswae* by its considerably greater dimensions.

Type locality: Songhor (Kenya).

Stratum typicum: Songhor Red Beds.

Age: Faunal Set P I, ca 20-19 Ma (Pickford, 1981, 1986b).

Distribution: Kenya (Legetet [Legetet Formation], Koru [unspecified formation], Brook’s Quarry [Legetet Formation], Chamtwara [Chamtwara Formation], Songhor [Songhor Red Beds]), Uganda (Napak I, IV, V, IX, XI, XV, CC [Napak Formation]).

Dental measurements and hypodigm: see table 2.

Table 2.—Dental specimen list with measurements and sex determination of fossils attributed to *Ugandapithecus major* Le Gros Clark & Leakey, 1951

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>KNM SO 396</i>	14.9	11.3	c/1	Songhor	Male
KNM SO 404	13.0	9.0	c/1	Songhor	Female
Nap IX 7'98	12.7	9.5	c/1 left	Napak IX	Female
Nap XV 62'07	19.2	13.0	c/1 left	Napak XV	Male
Nap V 179'09	15.3	—	c/1 right	Napak V	
KNM SO 585	19.5	16.4	C1/	Songhor	Male
Nap IX BUMP 763	17.6	15.3	C1/	Napak IX	Male
Mor II UMP 62.12	17.6	16.1	C1/	Moroto II	Male
Nap I UMP 62.05	18.9	16.3	C1/ left	Napak I	Male
Nap I UMP 62.03	16.4	13.6	C1/ right	Napak I	Male
<i>Nap V UMP 62.04</i>	19.4	16.4	C1/ right	Napak V	Male
<i>KNM CA 1855</i>	12.4	10.6	C1/ root	Chamtware	
Nap XV 394'08	8.3	6.0	d/3 right	Napak XV	
<i>KNM SO 541</i>	7.0	5.0	dc/1	Songhor	
Nap V 1'99	8.6	7.5	dC1/ left	Napak V	
Nap UMP 66.20	7.2	6.8	dC1/ right	Napak IV	
<i>KNM SO 541</i>	9.0	7.4	dp/4	Songhor	
Nap I 28'01	8.9	10.0	dP4/ left	Napak I	
KNM CA 1886	6.1	6.1	i/1	Chamtware	
KNM LG 629	6.0	5.6	i/1	Legetet	
KNM SO 475	5.6	4.8	i/1	Songhor	
KNM SO 555	5.9	5.2	i/1	Songhor	
Kor 283'05	—	7.8	i/1 left	Chamtware	
Nap XV 270'08	7.0	9.6	i/1 right	Napak XV	
Nap V 50'06	—	7.0	i/1 right	Napak V	
Nap XV 184'08	7.4	7.0e	i/1 right	Napak XV	
Nap XV 35'08 + Nap XV 33'09	8.0	12.5	i/2 right	Napak XV	
M 14297	11.0	7.9	I1/	Songhor	
Nap I 181'02	11.3	8.6	I1/ right	Napak I	
Nap V 169'08	9.0++	7.6	I1/ right	Napak V	
Nap V 140'08	8.5	10.4	I2/ right	Napak V	
Nap XV 116'07	7.5+	—	I2/ right	Napak XV	
Nap I 1'09	8.6	10.7	I2/ right	Napak I	
KNM CA 2229	11.4	10.6	m/1	Chamtware	
KNM LG 1472	12.4	10.6	m/1	Legetet	
<i>KNM SO 396</i>	11.7	10.7	m/1	Songhor	
KNM SO 470	11.1	10.4	m/1	Songhor	
KNM SO 472	11.8	10.8	m/1	Songhor	
<i>KNM SO 541</i>	11.2	10.0	m/1	Songhor	
KNM SO 915	11.2	10.0	m/1	Songhor	
KNM SO 917	12.5	10.8	m/1	Songhor	
<i>M 16648</i>	11.7	10.4	m/1	Songhor	Male
Nap XV 100'08	12.4	11.5	m/1 left	Napak XV	
Nap CC BUMP 269	11.9	11.1	m/1 right	Napak CC	
<i>Nap I BUMP 601</i>	12.6	11.4	m/1 right	Napak I	
Nap I UMP 62.14	11.8	10.4	m/1 right	Napak I	
<i>Nap XV 62'08</i>	12.3	11.4	m/1 right	Napak XV	
Nap V 88'09	12.6	11.2	m/1 right	Napak V	
KNM CA 1298	14.1	13.2	m/2	Chamtware	
KNM LG 47	14.1	12.9	m/2	Legetet	
<i>KNM SO 396</i>	13.4	13.1	m/2	Songhor	
KNM SO 415	15.8	14.3	m/2	Songhor	
<i>M 16648</i>	14.6	12.4	m/2	Songhor	Male
Nap XV 8'08	12.9	11.5	m/2 left	Napak XV	
<i>Nap I BUMP 601</i>	14.3	12.7	m/2 right	Napak I	
<i>KNM SO 396</i>	17.0	14.3	m/3	Songhor	
KNM SO 920	16.8	13.1	m/3	Songhor	

Data from Bosler, 1981; Martin, 1981; MacLachy & Rossie, 2005b, and the authors' own measurements. Specimens in italic characters represent individuals with associated teeth.

Table 2.—Dental specimen list with measurements and sex determination of fossils attributed to *Ugandapithecus major* Le Gros Clark & Leakey, 1951 (continuation)

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>M 16648</i>	18.0	13.3	m/3	Songhor	Male
M 32237	16.6	13.4	m/3	Songhor	
Nap I 49'00	—	13.5	m/3	Napak I	Male
Nap I BUMP 600	18.2	13.8	m/3 left	Napak I	
Nap XV 117'07	18.7	13.6	m/3 left	Napak XV	Male
Nap XV 60'07	18.9	14.0	m/3 left	Napak XV	
Kor 140'05	18.1	14.7	m/3 right	Chamtwarra	Male
<i>Nap I BUMP 601</i>	17.8	14.1	m/3 right	Napak I	
Nap V UMP 62.07	11.2	13.9	M1/ left	Napak V	Male
Nap I UMP 62.09	11.1	13.0	M1/ right	Napak I	
Nap IV UMP 66.41	11.7	13.5	M1/ right	Napak IV	Male
<i>Nap V I'03</i>	11.5	14.0	M1/ right	Napak V	
Nap V UMP 69.02	11.0	13.3	M1/ right	Napak V	Male
KNM SO 485	14.7	16.7	M2/	Songhor	
Nap V 5'09	13.0	14.7	M2/ right	Napak V	Male
Nap V UMP 62.08	15.0	16.8	M3/ left	Napak V	
KNM CA 1780	14.3	16.1	M3/	Chamtwarra	Male
M 14331 B	14.0	17.4	M3/	Songhor	
KNM SO 465	16.3	9.6	p/3	Songhor	Male
KNM SO 466	15.9	9.2	p/3	Songhor	
Nap XV 61'07	14.0	9.7	p/3 left	Napak XV	Male
M 44830	14.2	10.0	p/3 right	Songhor	
<i>Nap XV 62'08</i>	16.3	10.6	p/3 right	Napak XV	Male
<i>KNM SO 396</i>	8.9	10.1	p/4	Songhor	
KNM SO 416	8.9	10.4	p/4	Songhor	Male
<i>M 16648</i>	8.9	9.7	p/4	Songhor	
Nap V UMP 62.06	8.5	9.7	p/4	Napak V	Male
Nap I 2'99	8.5	10.6	p/4 left	Napak I	
Nap XV 63'08	9.3	11.6	p/4 left	Napak XV	Male
Kor 280'05	9.0	10.0	p/4 right	Brook's Quarry	
<i>Nap XV 62'08</i>	9.0	10.0	p/4 right	Napak XV	Male
<i>KNM CA 1855</i>	8.3	12.2	P3/	Chamtwarra	
<i>KNM CA 387</i>	8.5	12.5	P3/	Chamtwarra	Male
<i>KNM SO 529 A</i>	8.5	11.7	P3/	Songhor	
<i>KNM SO 529 B</i>	8.2	11.7	P3/	Songhor	Male
M 14331 A	8.8	12.8	P3/	Songhor	
<i>Nap V 220'09</i>	10.0	14.5	P3/ right	Napak V	Male
<i>KNM CA 1855</i>	6.9	11.7	P4/	Chamtwarra	
KNM SO 441	7.4	11.5	P4/	Songhor	Male
<i>KNM SO 529</i>	7.6	11.6	P4/	Songhor	
Nap V MUZM 146	7.0	12.1	P4/ right	Napak V	Male
<i>Nap V UMP 69.01</i>	7.7	13.7	P4/ right	Napak V	

Data from Bosler, 1981; Martin, 1981; MacLatchy & Rossie, 2005b, and the authors' own measurements. Specimens in italic characters represent individuals with associated teeth.

Species *Ugandapithecus legetetensis* nov.

Holotype: KNM LG 452, mandible containing complete right canine, left canine stub and all post-canine cheek teeth on both sides (fig. 32).

Diagnosis: Medium-sized species of *Ugandapithecus*, ca 17% smaller than *Ugandapithecus major*; lower molar row ca 35 mm long, p/3-m/3 length ca 54 mm.

Differential diagnosis: *Ugandapithecus legetetensis* differs from *Ugandapithecus major* and *Ugandapithecus gitongai* by

its smaller dimensions and from *Ugandapithecus meswae* by its greater dimensions.

Type locality: Maize Crib, Koru (Kenya).

Stratum typicum: Legetet Formation.

Age: Faunal Set P I, ca 20-19 Ma (Pickford, 1981, 1986b).

Distribution: Kenya (Juma's Red Bed [Koru Formation], Legetet [Legetet Formation], Koru [unspecified formation], Chamtwara [Chamtwarra Formation], Songhor [Songhor Red Beds]), Uganda (Napak [Napak Formation]).

Dental measurements and hypodigm: see table 3.

Table 3.—Dental specimen list with measurements and sex determination of fossils attributed to *Ugandapithecus legetetensis* sp. nov.

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>KNM LG 452</i>	11.4	8.2	c/1	Legetet	Female
<i>M 14086</i>	13.2	9.6	c/1	Koru	Male
Kor 2'04	10.7	7.7	c/1 right	Legetet	Female
Kor 251'04	10.0	8.0	c/1 right	Juma's Red Bed	Female
KNM SO 584	16.2	14.0	C1/	Songhor	Female
<i>KNM SO 542</i>	7.8	6.1	dC1/	Songhor	
<i>KNM SO 542</i>	6.9	7.5	dP3/	Songhor	
<i>KNM SO 542</i>	8.7	9.4	dP4/	Songhor	
Kor 159'05	5.7	6.6	i/2 right	Chamtware	
Nap XV 33'09	12.5	7.0	i/2 right	Napak XV	
KNM CA 1300	9.2	7.1	I1/	Chamtware	
Kor 254'04	9.0	6.4	I1/ left	Juma's Red Bed	
Kor 278'05	9.4	6.6	I1/ left	Legetet	
Kor 141'05	9.6	7.0	I1/ right	Chamtware	
KNM CA 1387	7.6	7.8	I2/	Chamtware	
KNM CA 1858	7.4	8.3	I2/	Chamtware	
KNM SO 554	7.6	7.4	I2/	Songhor	
Nap I 1'09	8.6	10.7	I2/ right	Napak I	
KNM CA 1856	10.6	9.5	m/1	Chamtware	
KNM CA 394	10.6	9.6	m/1	Chamtware	
KNM SO 1113	10.6	9.8	m/1	Songhor	
Mor II UMP 62.12	10.4	9.3	m/1	Moroto II	
Nap I UMP 62.13	10.0	9.5	m/1	Napak I	
<i>KNM LG 452</i>	10.4	9.2	m/1 left	Legetet	Female
<i>M 14086</i>	9.9	9.1	m/1 left	Koru	Male
Nap I UMP 62.16	10.5	9.3	m/1 left	Napak I	
<i>KNM LG 452</i>	10.0	9.2	m/1 right	Legetet	Female
KNM CA 395	12.7	11.1	m/2	Chamtware	
KNM SO 914	13.4	11.1	m/2	Songhor	
<i>M 14086</i>	11.9	10.5	m/2	Koru	Male
<i>KNM LG 452</i>	11.9	11.2	m/2 left	Legetet	Female
Kor 252'04	12.6	11.6	m/2 left	Juma's Red Bed	
Nap UMP 62.15	12.4	11.0	m/2 left	Napak I	
<i>KNM LG 452</i>	12.0	11.4	m/2 right	Legetet	Female
KNM CA 393	13.9	11.7	m/3	Chamtware	
<i>KNM LG 452</i>	13.2	11.0	m/3 left	Legetet	Female
Kor 253'04	14.9	12.0	m/3 left	Juma's Red Bed	
Nap XV 174'08	12.4	11.3	m/3 right	Napak XV	
<i>KNM LG 452</i>	13.3	11.4	m/3 right	Legetet	Female
Kor 90'04	13.5	10.4	m/3 right	Legetet	
<i>KNM CA 390</i>	10.3	12.2	M1/	Chamtware	
KNM CA 568	10.5	11.8	M1/	Chamtware	
<i>KNM SO 418</i>	9.3	11.2	M1/	Songhor	
<i>KNM SO 542</i>	10.5	12.8	M1/	Songhor	
KNM SO 934	10.2	11.7	M1/	Songhor	
KNM SO 939	9.6	10.9	M1/	Songhor	
Kor 255'04	9.7	10.7	M1/ left	Juma's Red Bed	
<i>KNM CA 388</i>	12.1	13.6	M2/	Chamtware	
<i>KNM CA 392</i>	12.1	13.6	M2/	Chamtware	
KNM LG 924	11.7	13.5	M2/	Legetet	
KNM SO 381	12.1	14.3	M2/	Songhor	
KNM SO 382	12.7	15.9	M2/	Songhor	
KNM CA 1299	10.7	13.1	M3/	Chamtware	
<i>KNM CA 389</i>	11.9	13.5	M3/	Chamtware	
KNM CA 397	10.3	13.2	M3/	Chamtware	
KNM CA 2251	11.5	7.3	p/3	Chamtware	
KNM SO 1114	11.4	7.5	p/3	Songhor	

Data from Bosler, 1981; Martin, 1981; MacLachy & Rossie, 2005b, and the authors own measurements. Specimens in italic characters represent associated teeth.

Table 3.—Dental specimen list with measurements and sex determination of fossils attributed to *Ugandapithecus legetetensis* sp. nov. (continuation)

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>KNM LG 452</i>	11.2	7.0	p/3 left	Legetet	Female
<i>M 14086</i>	12.2	7.0	p/3 left	Koru	Male
<i>KNM LG 452</i>	11.5	7.2	p/3 right	Legetet	Female
<i>M 14086</i>	12.2	6.8	p/3 right	Koru	Male
Nap V 95'09	12.5	7.4	p/3 left	Napak V	Male
<i>KNM LG 452</i>	7.4	8.7	p/4	Legetet	Female
<i>M 14086</i>	7.6	8.7	p/4	Koru	Male
Nap IV UMP 66.02	7.8	9.0	p/4	Napak V	
Nap I UMP 62.16	7.9	9.0	p/4 left	Napak I	
Nap CC BUMP 889	7.9	8.7	p/4 right	Napak CC	
<i>KNM SO 418</i>	8.6	10.6	P3/	Songhor	
<i>KNM SO 527</i>	7.7	10.0	P3/	Songhor	
<i>KNM CA 391</i>	7.6	12.3	P4/	Chamtwara	
<i>KNM SO 418</i>	6.1	11.2	P4/	Songhor	
<i>KNM SO 527</i>	6.5	10.4	P4/	Songhor	

Data from Bosler, 1981; Martin, 1981; MacLatchy & Rossie, 2005b, and the authors own measurements. Specimens in italic characters represent associated teeth.

Species *Ugandapithecus gitongai* Pickford & Kanimatsu, 2005

Holotype: Bar 737'02 and Bar 210'02, left M1/ and M2/ respectively, representing a single individual (on the basis of concordant interstitial contact facets).

Diagnosis: Large species of *Ugandapithecus*, plotting within the upper part and beyond the range of metric variation of *Ugandapithecus major* and with higher cusp relief and more blocky cusps than occur in the latter species; lingual cingulum in upper molars extremely broad, having the tendency to form an accessory cusplet at the mesio-lingual corner of the crown and to extend onto the mesial half of the hypocone, protocone more buccally positioned than in *U. major*; buccal cingulum present in upper molars, even if sometimes weak; trigon basin of upper molars deeper and more voluminous than in *U. major*; enamel more coarsely wrinkled and thus fewer wrinkles on occlusal surface than in *U. major*; distal fovea of upper molars deeper than in *U. major*; M1/ slightly larger than in *U. major*; m/3 with metaconid subdivided into two cusplets, separated from the entoconid by an additional small cusplet; accessory cusplet between entoconid and hypoconid; hypoconulid has tendency to form accessory cusplets lingually and mesially; cingulum on buccal and distal aspects of hypoconulid; mesial fovea reduced in bucco-lingual breadth (from Pickford & Kanimatsu, 2005).

Differential diagnosis: *Ugandapithecus gitongai* differs from *Ugandapithecus legetetensis* and from *Ugandapithecus meswae* by its greater dimensions and from *U. major* by the tendency for the cheek teeth to develop large accessory tubercles on the cingula.

Type locality: Kipsaraman (Kenya).

Stratum typicum: Muruyur Formation.

Age: Faunal Set P IIIb, ca 14.5 Ma (Pickford, 1981, 1986b).

Distribution: Kenya (Kipsaraman, Buluk), Uganda (Moroto II).

Measurements and dental hypodigm: see table 4.

Species *Ugandapithecus meswae* (Harrison & Andrews, 2009)

Holotype: KNM ME 11, left maxilla containing complete deciduous dentition and fully erupted M1/ and other teeth in their crypts.

Paratypes: KNM ME 1, mandible containing left dc/1, dp/3-dp/4, and right dp/3-dp/4 and permanent teeth in their crypts; KNM ME 2, frontal bone of a juvenile individual; KNM ME 3, m/1; KNM ME 4, right M1/; KNM ME 5, right m/2; KNM ME 6, di/2; KNM ME 7, i/1; KNM ME 8, dc/1; KNM ME 9, right maxilla with dP3/-dP4/ and germ of P3/; KNM ME 10, right dp/4; KNM ME 19, left M2/.

Referred specimens: KNM SO 1112 from Songhor, Kenya, left mandible containing the stub of c/1, p/3-p/4 and m/2.

Diagnosis: See Harrison & Andrews, 2009. Small species of the genus *Ugandapithecus* ca 17% smaller than *U. legetetensis*, 30% smaller than *U. major*, 33% smaller than the restricted sample of *U. gitongai*.

Differential diagnosis: *Ugandapithecus meswae* differs from other species of the genus by its smaller dimensions. It differs from similar sized *Proconsul africanus* and *Proconsul nyanzae* by the possession of bulbous molar cusps, and thus by its more restricted occlusal basins, and its tendency to produce tubercles from the cingula on the molars.

Type Locality: Meswa Bridge (Kenya).

Stratum typicum: Koru Formation.

Age: Faunal Set P 0, ca 21 Ma (Pickford, 1981, 1986b).

Distribution: Kenya (Meswa Bridge, Koru Formation) Songhor (Songhor Red Beds, Faunal Set P I).

Measurements: see table 5 for dental measurements.

Discussion: Andrews *et al.* (1981) were reticent to name a new species for the Meswa Bridge fossils, because they believed at the time that the material belonged to the genus *Proconsul* and they preferred to wait for the recovery of adult

Table 4.—Dental specimens of *Ugandapithecus gitongai* from Kipsaraman, Kenya and material that could belong to the species from Moroto, Uganda, and Buluk, Kenya, together with measurements of the teeth

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>KNM WS 11599</i>	18.3	13.0	c/1	Buluk	
Mor II	18.0	12.5	c/1	Moroto II	Male
<i>KNM WS 11599</i>	16.5	14.6	C1/	Buluk	
Mor IIa	11.4	9.1	C1/	Moroto II	Female
Bar 282'02	8.0	8.0	dC1/	Kipsaraman	
KNM TH 18690	14.9	13.8	m/2	Kipsaraman	
Bar 213'02	16.4	12.5	m/3	Kipsaraman	
Bar 215'02	12.6	13.5	M1/	Kipsaraman	
<i>Bar 737'02</i>	12.1	14.3	M1/	Kipsaraman	
<i>Bar 210'02</i>	14.2	16.8	M2/	Kipsaraman	
Bar 35'02	13.2	14++	M2/	Kipsaraman	
<i>KNM WS 11599</i>	12.6	14.6	M2/	Buluk	
Mor IIb 2'98	14.2	14.5	M2/	Moroto II	
Mor II	11.7	9.0	p/3	Moroto II	
<i>KNM WS 11599</i>	7.6	12.4	P3/	Buluk	
Mor II 14'01	7.1	10.8	P3/	Moroto II	
Mor II 10'08	16.1	13.4	m/3	Moroto II	

TH measurement from Hill *et al.*, 1991; other measurements from Pickford & Kunimatsu, 2005, and Pickford *et al.*, 2003.

++ = Part of the tooth is broken, the real breadth would be appreciably greater than this figure.

The two specimens in italic characters from Baringo, even though they have distinct register numbers, represent a single individual, the holotype.

Table 5.—Dental specimens *Ugandapithecus meswae* from Meswa Bridge, Kenya, together with measurements of the teeth

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
<i>KNM SO 1112</i>	11.3	8.0	c/1	Songhor	Male
<i>KNM ME 1</i>	8.0	6.6	dc/1	Meswa Bridge	
KNM ME 8	7.2	5.2	dc/1	Meswa Bridge	
<i>KNM ME 11</i>	6.6	6.2	dC1/	Meswa Bridge	
<i>KNM ME 9</i>	6.6	5.8	dC1/	Meswa Bridge	
KNM ME 6	4.0	4.4	di/2	Meswa Bridge	
<i>KNM ME 11</i>	6.4	4.7	dI1/	Meswa Bridge	
<i>KNM ME 11</i>	4.4	3.6	dI2/	Meswa Bridge	
<i>KNM ME 1</i>	8.1	5.4	dp/3	Meswa Bridge	
<i>KNM ME 1</i>	8.6	7.0	dp/4	Meswa Bridge	
KNM ME 10	8.9	7.1	dp/4	Meswa Bridge	
<i>KNM ME 11</i>	6.7	8.6	dP3/	Meswa Bridge	
<i>KNM ME 9</i>	6.2	7.3	dP3/	Meswa Bridge	
<i>KNM ME 4</i>	9.1	11.7	M1/	Meswa Bridge	
<i>KNM ME 11</i>	8.2	10.6	dP4/	Meswa Bridge	
<i>KNM ME 9</i>	7.3	8.7	dP4/	Meswa Bridge	
KNM ME 7	5.5	4.1	i/1	Meswa Bridge	
KNM ME 3	9.3	8.1	m/1	Meswa Bridge	
KNM ME 5	10.3	9.6	m/2	Meswa Bridge	
<i>KNM SO 1112</i>	9.6	8.5	m/2	Songhor	
<i>KNM ME 11</i>	9.1	11.7	M1/	Meswa Bridge	
<i>KNM ME 19</i>	10.2	12.5	M2/	Meswa Bridge	
<i>KNM SO 1112</i>	10.5	6.0	p/3	Songhor	
<i>KNM SO 377</i>	8.5	4.6	p/3	Songhor	
KNM KO 98	7.0	7.4	p/4	Koru	
<i>KNM SO 1112</i>	6.1	6.7	p/4	Songhor	
<i>KNM SO 377</i>	5.6	5.5	p/4	Songhor	
<i>KNM ME 25</i>	8.4	9.6	p/4	Meswa Bridge	

Additional specimens from Songhor and Koru attributed to this taxon are added for comparative purposes.

Data from Andrews *et al.*, 1981, Bosler, 1981; Martin, 1981; Harrison & Andrews, 2009; and the authors' own measurements. Associated teeth are in italic characters.

Table 6.—Dental hypodigm with measurements of *Proconsul africanus*

Catalogue number	Length (mm)	Breadth (mm)	Tooth	Locality	Sex
KNM CA 2149	8.8	5.8	<i>c/1</i>	Chamtware	
KNM SO 521	10.7	7.4	<i>C1/</i>	Songhor	
Kor 284'05	7.8	6.2	<i>C1/ left</i>	Chamtware	
Kor 65'04	10.3	7.8	<i>c/1 right</i>	Legetet	Male
<i>M 14084</i>	11.1	8.2	<i>CI/ left</i>	Koru	Male
M 44837	10.1	8.2	<i>CI/ right</i>	Koru	
Kor 158'05	6.1	5.0	<i>dp/4 right</i>	Chamtware	
KNM SO 428	4.3	4.8	<i>i/1</i>	Songhor	
KNM SO 473	3.9	4.4	<i>i/1</i>	Songhor	
KNM LG 1481	5.6	5.7	<i>i/2</i>	Legetet	
KNM LG 52	4.6	5.2	<i>i/2</i>	Legetet	
KNM SO 551	7.8	5.5	<i>I1/</i>	Songhor	
KNM SO 552	6.8	5.3	<i>I1/</i>	Songhor	
KNM CA 1801	7.3	5.9	<i>I1/</i>	Chamtware	
KNM SO 553	7.9	5.8	<i>I1/</i>	Songhor	
KNM CA 1779	5.5	5.0	<i>I2/</i>	Chamtware	
KNM SO 549	4.8	4.9	<i>I2/</i>	Songhor	
Kor 303'05	—	4.8	<i>I2/ right</i>	Chamtware	
KNM CA 1771	8.1	7.3	<i>m/1</i>	Chamtware	
KNM CA 1773	8.5	7.5	<i>m/1</i>	Chamtware	
KNM SO 486	9.2	7.5	<i>m/1</i>	Songhor	
KNM SO 903	8.2	7.3	<i>m/1</i>	Songhor	
KNM LG 1389	12.0	9.3	<i>m/3</i>	Legetet	
KNM SO 921	11.6	8.7	<i>m/3</i>	Songhor	
M 14087	12.1	9.5	<i>m/3</i>	Koru	
KNM CA 1872	8.4	9.6	<i>M1/</i>	Chamtware	
KNM CA 1893	7.6	8.9	<i>M1/</i>	Chamtware	
KNM KQ 1	7.3	9.0	<i>M1/</i>	Koru	
KNM LG 902	7.8	8.5	<i>M1/</i>	Legetet	
<i>M 14084</i>	8.1	9.5	<i>M1/</i>	Koru	Male
KNM SO 946	9.1	11.6	<i>M2/</i>	Songhor	
<i>M 14084</i>	9.3	11.3	<i>M2/</i>	Koru	Male
KNM CA 2250	8.5	9.9	<i>M3/</i>	Chamtware	
KNM KO 95A	8.2	10.4	<i>M3/</i>	Koru	
KNM SO 442	8.5	11.4	<i>M3/</i>	Songhor	
<i>M 14084</i>	8.0	10.5	<i>M3/</i>	Koru	Male
Kor 292'05	7.0	4.6	<i>p/3 left</i>	Chamtware	
KNM CA 1887	5.9	10.3	<i>P3/</i>	Chamtware	
KNM SO 596	5.6	7.8	<i>P3/</i>	Songhor	
<i>M 14084</i>	7.3	9.4	<i>P3/</i>	Koru	Male
KNM SO 524	5.5	9.6	<i>P4/</i>	Songhor	
<i>M 14084</i>	5.6	9.0	<i>P4/</i>	Koru	Male

Associated teeth are in italic characters.

specimens before naming a new species. However, after the present paper had been submitted for publication - it included a proposal to erect a new species for the Meswa Bridge material - Harrison & Andrews (2009) published a paper based on the original fossils and a few unpublished specimens. We thus modify our presentation to take account of the new species name, although we consider that the evidence marshalled by Harrison & Andrews (2009) in support of the distinctiveness of the fossils from similar sized *Proconsul nyanzae* at the species level, provides excellent support for the distinctiveness of the fossils at the generic level. Their evidence thus supports our contention that *Ugandapithecus* is a great ape distinct from *Proconsul* at the generic level.

In terms of dimensions the Meswa fossils are close to *Proconsul nyanzae*, but they differ from that species by their morphology, especially the more flared cusps in the molars. Furthermore, Andrews *et al.* (1981) included the Songhor mandible, KNM SO 1112, in *Proconsul africanus*, and the combination of factors made them cautious about naming a new taxon. Since the creation of *Ugandapithecus*, and the realisation that the Meswa Bridge fossils belong to this genus and not to *Proconsul*, the reasons for not creating a new species falls away. The addition of the Songhor mandible to the species *U. meswae* provides supporting evidence of the existence of a small species of *Ugandapithecus* in East African Early Miocene deposits, being best known from deposits older than 19 Ma.

Table 7.—Distribution of dental specimens of *Ugandapithecus* and *Proconsul africanus* by locality

Locality / Taxon	Faunal Set	<i>U. major</i>	<i>U. cf gitongai</i>	<i>U. legetetensis</i>	<i>U. meswae</i>	<i>P. africanus</i>	TOTAL
Moroto I, II,	III	1		1	0	0	19
Buluk,	III						
Kipsaraman	IV		17				
Napak (I, IV, V, IX, XV, CC)	I	41	0	6	0	0	47
Songhor	I	35	0	18	6	14	73
Chamtwara	I	10	0	18	0	13	41
Legetet	I	4	0	14	0	5	23
Koru (JRB, MC)	I	0	0	11	1	10	22
Meswa	0	0	0	0	21	0	21
TOTAL		91	17	68	28	42	246

Note the preponderance of large specimens of *Ugandapithecus* in the youngest levels, medium sized specimens in the intermediate levels and small specimens in the oldest levels. *U. cf gitongai* is the combined total from Moroto I, II, Buluk and Kipsaraman. JRB = Juma's Red Bed; MC = Maize Crib.

Discussion

Geochronology of East African hominoid-bearing localities

In order to understand evolutionary trends in any group of organisms, a sense of the order in which the species lived is essential and knowledge of their absolute ages is a bonus. The East African stratigraphic succession is well dated on account of the abundance of volcanic deposits associated with the fossiliferous sediments. Since the 1960's hundreds of age determinations have been carried out in East Africa on deposits ranging in age from 25 Ma to Recent, resulting in a well calibrated succession of deposits and their contained faunas.

The hominoid specimens discussed in this paper are all of Early and Middle Miocene age, ranging from ca 21.5 Ma to ca 14.5 Ma. The main fossiliferous localities have been grouped into faunal sets (FS) (Pickford (1981, 1986b) each of which spans about 2 million years. The preliminary results of Pickford (1986b) have been updated as new age determinations and new palaeontological field work has been done. One result of this work is that sites such as Napak, which used to be considered to represent a short period of time with little faunal change through the sequence, is now known to span a longer period of time, with a lower Songhor-like faunal assemblage (19-20 Ma), and a later assemblage that shares some taxa with Rusinga (17.8 Ma). Pickford (2002b) showed that in the lower unit the only tragulid species was *Dorcatherium songhorensis*, whereas the upper unit contained *Dorcatherium parvum*, *Dorcatherium piggoti* and *Dorcatherium iriense*, the

latter species being smaller than the large Rusinga tragulid *Dorcatherium chappuisi*. From this, the author concluded that the lower part of the Napak succession was the same age as Songhor, whereas the upper part was somewhat younger, but not as young as Rusinga. An age of ca 19.5-19 Ma for the lower part of the succession and of 19-18.5 Ma for the upper part would fit with the faunal evidence.

Likewise, the Meswa-Koru-Legetet-Chamtwara stratigraphic succession spans an appreciable period of time. Meswa was recognised early on to be older than Koru, which is why it was arranged into Faunal Set P 0. Koru, Legetet and Chamtwara were all arranged in FS I, along with Songhor, yet it is likely that some of the faunal differences documented between sites are due to age differences, with Songhor being the youngest of the FS I sites, and Koru the oldest.

Taking into account these adjustments to the ages of the localities, it is clear that with few exceptions, the oldest levels yield the smallest specimens of *Ugandapithecus* (*U. meswae*), the intermediate levels yield medium sized specimens (*U. legetetensis*), whilst the youngest levels yield the largest specimens (*U. major*) (Table 7). There are a few exceptions, including the mandible KNM SO 1112 from Songhor, and a tooth from Napak XV attributed to *U. legetetensis* which occurs side by side with *U. major*.

Evolutionary trends in Ugandapithecus

The Meswa Bridge fossils previously attributed to *Proconsul major* (Andrews *et al.*, 1981), are the

smallest specimens assigned to the genus *Ugandapithecus* as *U. meswae*. Other fossils from the Koru Formation are of a larger species, *Ugandapithecus legetetensis* sp. nov., which extends upwards in time into the Legetet and Chamtwara Formations. The next largest species is *Ugandapithecus major*, well represented at Songhor and Napak. The largest species of the genus is *Ugandapithecus gitongai* defined at Kipsaraman, Kenya (ca 14.5 Ma) but possibly also present at the older site of Moroto, Uganda (ca 17.5 Ma). In some tooth dimensions it overlaps with large individuals of *Ugandapithecus major*, but the morphology of the teeth of the two species is different, as described by Pickford & Kuniatsu (2005). It thus appears that the various species of *Ugandapithecus* represent evolutionary lineages that got larger and larger with the passage of geological time while it underwent relatively modest changes in dental morphology. Figure 57 provides a résumé of the evidence concerning evolution in *Ugandapithecus* over time. Age determinations of the various localities which have yielded *Ugandapithecus* are summarised in Pickford (1981, 1983, 1986b, 1986c, 1998) and Pickford *et al.* (1986).

The youngest known representative of the genus, *Ugandapithecus gitongai*, is possibly the ancestral group from which one or other of the Late Miocene East African genera *Samburupithecus*, *Chororapithecus* and *Nakalipithecus* and the gorilliform from the Tugen Hills might have evolved, but the latter genera are poorly known (Ishida & Pickford, 1997; Suwa *et al.*, 2007; Kuniatsu *et al.*, 2007; Pickford & Senut, 2004), and any relationship, if valid, would be difficult to demonstrate on the basis of currently available fossil samples. Superficially, out of these three Late Miocene great apes recently described from East Africa, on the basis of its lower molar morphology, *Chororapithecus* appears to be closer to *Ugandapithecus* than *Nakalipithecus* does, whereas *Samburupithecus* seems to be closer to *Ugandapithecus* from the point of view of the morphology of its upper molars.

Post-cranial skeleton of *Ugandapithecus* species

Gommery *et al.* (1998, 2002) and Rafferty *et al.* (1995a, 1995b) described the available post-cranial remains of *Ugandapithecus*, notably from

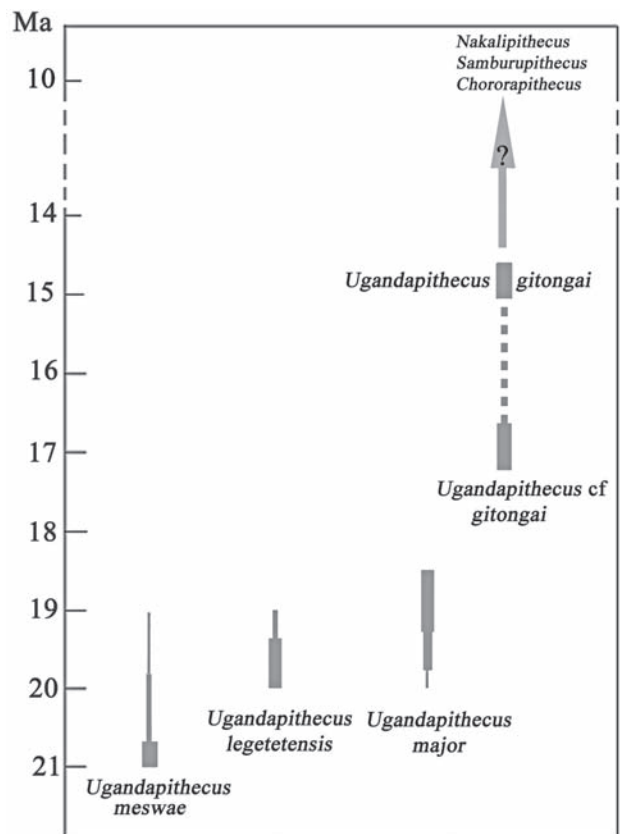


Fig. 57.—Stratigraphic ranges of species of *Ugandapithecus*. The thickness of the vertical lines represents relative abundance of the species at various levels on the basis of dental counts. Note that the large species is commonest in the youngest levels, the smaller in the oldest, suggesting the presence of a lineage that got larger and larger with the passage of geological time.

Napak, Uganda, and concluded that in some features they are morphologically closer to extant African apes than *Proconsul* and *Afropithecus* are. Recently, MacLatchy (2009) provided information about the distal humerus and proximal radius of *U. major* from Napak. Despite the fact that the post-cranial skeleton of *Ugandapithecus* is still poorly known, it is clear that it differs fundamentally from skeletal remains attributed to *Proconsul nyanzae* and *Proconsul heseloni* of which many specimens are known (Rose, 1983, 1994a, 1994b, 1996; Senut, 1986, 1987; Walker, 1997; Ward, 1998). It is not necessary to expand on what Gommery *et al.* (2002) already published. We agree with MacLatchy (2009) that *U. major* probably had a locomotor repertoire that differed fundamentally from those of the various *Proconsul* species.

Table 8.—Specimens listed in the hypodigms of *Proconsul heseloni* and *Proconsul nyanzae* by Walker *et al.* (1993) together with their comments on the identifications (in brackets)

Specimen N.º	Taxon	Sex determination
KNM RU 1706	<i>Proconsul heseloni</i>	None
KNM RU 7290	<i>Proconsul heseloni</i>	Female
KNM RU 2036	<i>Proconsul heseloni</i> (holotype)	Female
KNM RU 2088	<i>Proconsul heseloni</i>	Male
KNM RU 1674	<i>Proconsul heseloni</i>	Male
KNM RU 2087	<i>Proconsul heseloni</i>	Male
KNM RU 1705	<i>Proconsul heseloni</i>	Female
KNM RU 1769	<i>Proconsul heseloni</i>	Female
KNM MW 160	<i>Proconsul heseloni</i>	Female
KNM RU 16000	<i>Proconsul nyanzae</i> (possibly)	Male
M 16647	<i>Proconsul nyanzae</i> (holotype)	Male

Reassessment of *Proconsul* fossils from Rusinga and related deposits in Western Kenya

We here present a revised sorting of *Proconsul* fossils from Rusinga Island and other deposits in the Kisingiri complex of sites. We agree that there are two species in the deposits (Walker *et al.*, 1993) but we assign the fossils differently from these authors, which results in a more equable presence of males and females in the two taxa, Walker *et al.* (1993) themselves commented on the bias that their sorting of specimens produced, which resulted in the biologically unlikely scenario that *P. nyanzae* was represented only by males, and *P. heseloni* only by females, unless two or three male specimens were shoe-horned into it as a result increasing its range of metric variation. These authors did not provide detailed hypodigms for the two taxa, but did specify to which taxon a few of the more complete specimens belonged (Table 8).

We consider that the new sorting of fossils is closer to reflecting the composition of the two species, even though there remains a small handful of specimens that could represent either taxon. Indeed, for some isolated molars, a change in the meristic position would resolve the uncertainty, as would adjustment of measurements to take into account interstitial wear which can reduce the mesio-distal length of a tooth by up to 10%, but we provisionally retain the identifications that such teeth have been given in the literature. The quantity of doubtfully attributed specimens is minor in comparison with the overall total of specimens available from Rusinga, so it does not provide a serious obstacle to acceptance of the new sorting. Since many of the specimens from Rusinga

are relatively complete mandibles and maxillae with associated teeth, there is a good basis for knowing which teeth go with which other teeth, unlike the *Ugandapithecus* sample which consists predominantly of isolated teeth and only a few mandibles and maxillae.

Table 9 provides a list of the identified fossils and the sex determination where it is known or for post-canine teeth where it can be inferred from association with sexable canines.

Walker *et al.* (1993) provided diagnoses of *P. africanus* and *P. heseloni*. The part of the diagnosis of *P. africanus* dealing with the mandible was based on the Songhor mandible, KNM SO 1112, which is here transferred to *Ugandapithecus meswae*. The major differences between mandibular morphology and lower dentition of *P. africanus* and *P. heseloni* noted by Walker *et al.* (1995) are therefore not valid for distinguishing these two species from each other. Whether the remaining characters in the two diagnoses sustain the specific separation of *P. africanus* from *P. heseloni* needs to be restudied. Bosler (1981) for example, considered that much of the the Rusinga *Proconsul* material belonged to *P. africanus*.

Conclusions

Re-examination of dentognathic remains attributed to *Proconsul africanus*, Hopwood, 1933a, and *Proconsul major* Le Gros Clark & Leakey, 1951, reveals a suite of morphological and metric differences in the teeth, maxillae and mandibles that leads us to conclude that the two species cannot realistically be retained in a single genus (Table 10), a result already anticipated by Senut *et al.* (2000)

Table 9.—Detailed attribution of *Proconsul* specimens from the Kisingiri complex of localities arranged by tooth type

Catalogue number	Mesio-distal length (mm)	Bucco-lingual breadth (mm)	Taxon	Tooth	Locality	Sex determination
<i>KNM RU 2036</i>	8.4	6.4	<i>Proconsul heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 7290</i>	9.6	6.2	<i>Proconsul heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 7290</i>	9.6	6.4	<i>Proconsul heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 1674 A</i>	11.4	8.6	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>KNM RU 1791</i>	11.7	9.3	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>KNM RU 2087</i>	11.6	8.5	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>KNM RU 2087</i>	12.0	8.8	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>M 32236 Ru</i>	12.2	9.5	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>KNM RU 2048</i>	12.3	8.9	<i>Proconsul heseloni</i>	c/1	Rusinga	Male
<i>KNM RU 1676 A</i>	12.6	9.9	<i>Proconsul nyanzae</i>	c/1	Rusinga	Male
<i>KNM RU 1847</i>	12.9	10.6	<i>Proconsul nyanzae</i>	c/1	Rusinga	Male
<i>KNM RU 1889</i>	13.0	10.1	<i>Proconsul nyanzae</i>	c/1	Rusinga	Male
<i>KNM RU 1926</i>	12.4	9.8	<i>Proconsul nyanzae</i>	c/1	Rusinga	Male
<i>KNM RU 1982 C</i>	13.6	10.2	<i>Proconsul nyanzae</i>	c/1	Rusinga	Male
<i>KNM MW 160</i>	9.0	6.2	<i>Proconsul nyanzae/heseloni</i>	c/1	Mfwangano	Female
<i>KNM MW 45</i>	9.6	7.1	<i>Proconsul nyanzae/heseloni</i>	c/1	Mfwangano	Female
<i>KNM RU 1769 B</i>	8.6	6.5	<i>Proconsul nyanzae/heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 1769 D</i>	8.6	6.2	<i>Proconsul nyanzae/heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 1914</i>	9.3	6.1	<i>Proconsul nyanzae/heseloni</i>	c/1	Rusinga	Female
<i>KNM RU 1687</i>	11.8	10.7	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 1688</i>	8.2	6.8	<i>Proconsul heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 1707</i>	8.9	7.0	<i>Proconsul heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 1815 A</i>	12.1	10.0	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 1815 B</i>	12.3	9.8	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 1845</i>	12.8	10.2	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 1891</i>	8.9	7.2	<i>Proconsul heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 1971</i>	12.3	10.3	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 2041</i>	8.4	6.2	<i>Proconsul heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 2088 B</i>	12.6	8.9	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 4424</i>	12.9	10.2	<i>Proconsul heseloni</i>	C1/	Rusinga	Male
<i>KNM RU 7290</i>	9.7	8.6	<i>Proconsul heseloni</i>	C1/ left	Rusinga	Female
<i>KNM RU 7290</i>	9.6	8.6	<i>Proconsul heseloni</i>	C1/ right	Rusinga	Female
<i>KNM RU 16000</i>	14.5	11.7	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1677 B</i>	14.0	11.3	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1677 E</i>	13.7	11	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1684</i>	14.4	11.3	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1686</i>	10.4	7.2	<i>Proconsul nyanzae</i>	C1/	Rusinga	Female
<i>KNM RU 1722</i>	10.8	8.4	<i>Proconsul nyanzae</i>	C1/	Rusinga	Female
<i>KNM RU 1723</i>	10.7	7.5	<i>Proconsul nyanzae</i>	C1/	Rusinga	Female
<i>KNM RU 1763</i>	13.5	11.3	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1813</i>	14.5	11.6	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1871</i>	9.3	7.7	<i>Proconsul nyanzae</i>	C1/	Rusinga	Female
<i>KNM RU 1942</i>	9.7	7.5	<i>Proconsul nyanzae</i>	C1/	Rusinga	Female
<i>KNM RU 1960 A</i>	14.3	12.2	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1960 B</i>	13.8	12.2	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>M 16647</i>	15.1	11.8	<i>Proconsul nyanzae</i>	C1/	Rusinga	Male
<i>KNM RU 1769 A</i>	9.4	7.2	<i>Proconsul nyanzae/heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 1769 C</i>	9.7	7.2	<i>Proconsul nyanzae/heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 2049</i>	9.5	7.0	<i>Proconsul nyanzae/heseloni</i>	C1/	Rusinga	Female
<i>KNM RU 2036</i>	4.0	4.6	<i>Proconsul heseloni</i>	i/1	Rusinga	Female
<i>KNM RU 7290</i>	3.8	5.0	<i>Proconsul heseloni</i>	i/1 left	Rusinga	Female
<i>KNM RU 7290</i>	4.0	5.0	<i>Proconsul heseloni</i>	i/1 right	Rusinga	Female
<i>KNM RU 1947</i>	4.8	6.5	<i>Proconsul nyanzae</i>	i/1 left	Rusinga	Male
<i>KNM RU 1947</i>	4.7	6.3	<i>Proconsul nyanzae</i>	i/1 right	Rusinga	Male
<i>KNM RU 1769 I</i>	4.1	5.2	<i>Proconsul nyanzae/heseloni</i>	i/1	Rusinga	Female

Specimens in italic letters belong to an association of teeth and therefore their meristic positions are known with confidence. Specimens in normal script are isolated teeth, and thus for some positions such as first and second molars there may be doubt about the meristic position.

Table 9.—Detailed attribution of *Proconsul* specimens from the Kisingiri complex of localities arranged by tooth type (continuation)

Catalogue number	Mesio-distal length (mm)	Bucco-lingual breadth (mm)	Taxon	Tooth	Locality	Sex determination
<i>KNM RU 1769 J</i>	4.0	5.1	<i>Proconsul nyanzae/heselsoni</i>	i/1	Rusinga	Female
<i>KNM RU 2036</i>	4.6	5.8	<i>Proconsul heselsoni</i>	i/2 right	Rusinga	Female
<i>KNM RU 7290</i>	4.3	6.0	<i>Proconsul heselsoni</i>	i/2 left	Rusinga	Female
<i>KNM RU 7290</i>	4.3	6.1	<i>Proconsul heselsoni</i>	i/2 right	Rusinga	Female
<i>KNM RU 1730</i>	4.7	6.9	<i>Proconsul nyanzae</i>	i/2	Rusinga	
<i>KNM RU 1947</i>	5.2	6.4	<i>Proconsul nyanzae</i>	i/2 left	Rusinga	Male
<i>KNM RU 1947</i>	5.2	6.5	<i>Proconsul nyanzae</i>	i/2 right	Rusinga	Male
<i>KNM RU 1769 H</i>	4.4	6.4	<i>Proconsul nyanzae/heselsoni</i>	i/2	Rusinga	Female
<i>KNM RU 7290</i>	7.0	6.1	<i>Proconsul heselsoni</i>	I1/ left	Rusinga	Female
<i>KNM RU 7290</i>	7.0	6.0	<i>Proconsul heselsoni</i>	I1/ right	Rusinga	Female
<i>KNM RU 1933</i>	7.5	5.6	<i>Proconsul heselsoni</i>	I1/	Rusinga	
<i>KNM MW 562</i>	7.6	5.4	<i>Proconsul heselsoni</i>	I1/	Mfwangano	
<i>KNM RU 1979</i>	7.8	5.6	<i>Proconsul heselsoni</i>	I1/	Rusinga	
<i>KNM RU 1769 E</i>	7.9	5.7	<i>Proconsul heselsoni</i>	I1/	Rusinga	Female
<i>KNM RU 1685</i>	8.3	6.8	<i>Proconsul nyanzae</i>	I1/	Rusinga	
<i>KNM RU 1712</i>	8.4	6.5	<i>Proconsul nyanzae</i>	I1/	Rusinga	
<i>KNM RU 1975</i>	9.3	6.5	<i>Proconsul nyanzae</i>	I1/	Rusinga	
<i>KNM RU 1677 D</i>	9.4	6.8	<i>Proconsul nyanzae</i>	I1/	Rusinga	Male
<i>KNM RU 1677 C</i>	9.6	7.1	<i>Proconsul nyanzae</i>	I1/	Rusinga	Male
<i>KNM RU 1681</i>	10.0	7.7	<i>Proconsul nyanzae</i>	I1/	Rusinga	
<i>KNM RU 5571</i>	5.1	4.1	<i>Proconsul heselsoni</i>	I2/	Rusinga	
<i>KNM RU 2036</i>	5.4	5.1	<i>Proconsul heselsoni</i>	I2/ right	Rusinga	Female
<i>KNM RU 2036</i>	5.5	5.2	<i>Proconsul heselsoni</i>	I2/ left	Rusinga	Female
<i>KNM MW 57</i>	5.4	5.5	<i>Proconsul heselsoni</i>	I2/	Mfwangano	
<i>KNM MW 47</i>	5.1	5.6	<i>Proconsul heselsoni</i>	I2/	Mfwangano	
<i>KNM RU 7290</i>	5.1	6.0	<i>Proconsul heselsoni</i>	I2/ left	Rusinga	Female
<i>KNM RU 7290</i>	5.5	6.0	<i>Proconsul heselsoni</i>	I2/ right	Rusinga	Female
<i>KNM RU 1674 C</i>	5.6	6.0	<i>Proconsul heselsoni</i>	I2/	Rusinga	Male
<i>KNM RU 1674 D</i>	5.6	6.1	<i>Proconsul heselsoni</i>	I2/	Rusinga	Male
<i>KNM RU 1998</i>	5.4	6.1	<i>Proconsul nyanzae</i>	I2/	Rusinga	
<i>KNM RU 2035</i>	6.0	6.1	<i>Proconsul nyanzae</i>	I2/	Rusinga	
<i>KNM RU 1690</i>	6.8	7.0	<i>Proconsul nyanzae</i>	I2/	Rusinga	
<i>KNM RU 1769 G</i>	5.8	5.9	<i>Proconsul nyanzae/heselsoni</i>	I2/	Rusinga	Female
<i>KNM RU 1824</i>	7.6	6.8	<i>Proconsul heselsoni</i>	m/1	Rusinga	
<i>KNM RU 5871</i>	8.0	6.9	<i>Proconsul heselsoni</i>	m/1	Rusinga	
<i>KNM RU 1768</i>	8.5	7.0	<i>Proconsul heselsoni</i>	m/1	Rusinga	
<i>KNM RU 1706</i>	7.7	7.2	<i>Proconsul heselsoni</i>	m/1	Rusinga	
<i>KNM RU 1955</i>	8.1	7.2	<i>Proconsul heselsoni</i>	m/1	Rusinga	
<i>KNM RU 1674</i>	9.0	7.3	<i>Proconsul heselsoni</i>	m/1	Rusinga	Male
<i>KNM RU 7290</i>	8.4	7.3	<i>Proconsul heselsoni</i>	m/1 right	Rusinga	Female
<i>KNM RU 2036</i>	8.6	7.4	<i>Proconsul heselsoni</i>	m/1 left	Rusinga	Female
<i>KNM RU 2036</i>	8.4	7.4	<i>Proconsul heselsoni</i>	m/1 right	Rusinga	Female
<i>KNM RU 7290</i>	8.4	7.4	<i>Proconsul heselsoni</i>	m/1 left	Rusinga	Female
<i>KNM RU 2087</i>	8.6	7.7	<i>Proconsul heselsoni</i>	m/1 right	Rusinga	Male
<i>KNM RU 1678</i>	9.0	8.0	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1711</i>	9.3	8.1	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1789</i>	9.5	8.1	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1947</i>	9.4	8.4	<i>Proconsul nyanzae</i>	m/1 left	Rusinga	Male
<i>KNM RU 1947</i>	9.2	8.4	<i>Proconsul nyanzae</i>	m/1 right	Rusinga	Male
<i>KNM RU 1676 D</i>	9.7	8.5	<i>Proconsul nyanzae</i>	m/1	Rusinga	Male
<i>KNM RU 1679</i>	9.8	8.5	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1780</i>	9.5	8.5	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 2000</i>	9.5	8.5	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1927</i>	10.2	9.0	<i>Proconsul nyanzae</i>	m/1	Rusinga	
<i>KNM RU 1818</i>	9.2	7.8	<i>Proconsul heselsoni</i>	m/2	Rusinga	

Specimens in italic letters belong to an association of teeth and therefore their meristic positions are known with confidence. Specimens in normal script are isolated teeth, and thus for some positions such as first and second molars there may be doubt about the meristic position.

Table 9.—Detailed attribution of *Proconsul* specimens from the Kisingiri complex of localities arranged by tooth type (continuation)

Catalogue number	Mesio-distal length (mm)	Bucco-lingual breadth (mm)	Taxon	Tooth	Locality	Sex determination
KNM RU 1945	9.5	7.9	<i>Proconsul heseloni</i>	m/2	Rusinga	
KNM RU 1959	9.7	8.0	<i>Proconsul heseloni</i>	m/2	Rusinga	
<i>KNM RU 2036</i>	9.8	8.1	<i>Proconsul heseloni</i>	m/2 left	Rusinga	Female
<i>KNM RU 2036</i>	9.6	8.1	<i>Proconsul heseloni</i>	m/2 right	Rusinga	Female
<i>KNM RU 5871</i>	9.2	8.1	<i>Proconsul heseloni</i>	m/2	Rusinga	
<i>KNM RU 1706</i>	9.7	8.3	<i>Proconsul heseloni</i>	m/2	Rusinga	
KNM RU 1823	9.8	8.7	<i>Proconsul heseloni</i>	m/2	Rusinga	
<i>KNM RU 1824</i>	10.1	8.7	<i>Proconsul heseloni</i>	m/2	Rusinga	
<i>KNM RU 7290</i>	9.8	8.8	<i>Proconsul heseloni</i>	m/2 left	Rusinga	Female
<i>KNM RU 7290</i>	10.0	9.0	<i>Proconsul heseloni</i>	m/2 right	Rusinga	Female
<i>KNM RU 1674</i>	10.2	9.1	<i>Proconsul heseloni</i>	m/2 left	Rusinga	Male
KNM RU 2032	10.4	9.1	<i>Proconsul heseloni</i>	m/2	Rusinga	
<i>KNM RU 1674</i>	10.5	9.2	<i>Proconsul heseloni</i>	m/2 right	Rusinga	Male
<i>KNM RU 2087</i>	10.4	9.5	<i>Proconsul heseloni</i>	m/2 right	Rusinga	Male
<i>KNM RU 2087</i>	11.0	9.7	<i>Proconsul heseloni</i>	m/2 left	Rusinga	Male
<i>KNM RU 1678</i>	11.5	9.7	<i>Proconsul nyanzae</i>	m/2	Rusinga	
<i>KNM RU 1710</i>	11.5	9.8	<i>Proconsul nyanzae</i>	m/2	Rusinga	
<i>KNM RU 1947</i>	11.6	10.2	<i>Proconsul nyanzae</i>	m/2	Rusinga	Male
KNM RU 1694	10.9	10.4	<i>Proconsul nyanzae</i>	m/2	Rusinga	
KNM RU 1695	12.6	10.8	<i>Proconsul nyanzae</i>	m/2	Rusinga	
<i>KNM RU 1676E</i>	12.9	11.3	<i>Proconsul nyanzae</i>	m/2	Rusinga	Male
KNM RU 1734	12.6	11.3	<i>Proconsul nyanzae</i>	m/2	Rusinga	
<i>KNM RU 1982</i>	12.4	11.3	<i>Proconsul nyanzae</i>	m/2	Rusinga	Male
<i>KNM RU 1982 I</i>	13.0	11.7	<i>Proconsul nyanzae</i>	m/2	Rusinga	Male
KNM RU 1820	11.0	8.9	<i>Proconsul heseloni</i>	m/3	Rusinga	
<i>KNM RU 7290</i>	11.2	9.2	<i>Proconsul heseloni</i>	m/3 right	Rusinga	Female
<i>KNM RU 7290</i>	11.3	9.1	<i>Proconsul heseloni</i>	m/3 left	Rusinga	Female
<i>KNM RU 1674</i>	11.4	9.2	<i>Proconsul heseloni</i>	m/3 right	Rusinga	Male
<i>KNM RU 2087</i>	11.5	10.4	<i>Proconsul heseloni</i>	m/3	Rusinga	Male
<i>KNM RU 1706</i>	11.7	8.3	<i>Proconsul heseloni</i>	m/3	Rusinga	
KNM RU 1931	11.7	8.9	<i>Proconsul heseloni</i>	m/3	Rusinga	
<i>KNM RU 1674</i>	12.0	9.3	<i>Proconsul heseloni</i>	m/3 left	Rusinga	Male
KNM RU 1735	13.7	12	<i>Proconsul nyanzae</i>	m/3	Rusinga	
<i>KNM RU 1947</i>	13.9	11.6	<i>Proconsul nyanzae</i>	m/3 left	Rusinga	Male
<i>KNM RU 1676 F</i>	14.1	12.3	<i>Proconsul nyanzae</i>	m/3	Rusinga	Male
KNM RU 1923	14.2	10.9	<i>Proconsul nyanzae</i>	m/3	Rusinga	
KNM RU 1764	14.9	11.6	<i>Proconsul nyanzae</i>	m/3	Rusinga	
<i>KNM RU 1982 J</i>	15.0	12.2	<i>Proconsul nyanzae</i>	m/3	Rusinga	Male
<i>KNM RU 1674 B</i>	8.4	10.2	<i>Proconsul heseloni</i>	M1/	Rusinga	Male
KNM RU 1795	8.0	9.0	<i>Proconsul heseloni</i>	M1/	Rusinga	
<i>KNM RU 1904</i>	7.4	8.6	<i>Proconsul heseloni</i>	M1/	Rusinga	
KNM RU 1936	7.7	9.0	<i>Proconsul heseloni</i>	M1/	Rusinga	
KNM RU 1954	7.8	9.2	<i>Proconsul heseloni</i>	M1/	Rusinga	
<i>KNM RU 1973</i>	6.9	8.1	<i>Proconsul heseloni</i>	M1/	Rusinga	
<i>KNM RU 2036</i>	7.8	9.7	<i>Proconsul heseloni</i>	M1/	Rusinga	Female
<i>KNM RU 2088</i>	8.6	9.6	<i>Proconsul heseloni</i>	M1/	Rusinga	Male
<i>KNM RU 7290</i>	7.8	9.6	<i>Proconsul heseloni</i>	M1/	Rusinga	Female
<i>KNM RU 7290</i>	7.9	9.5	<i>Proconsul heseloni</i>	M1/	Rusinga	Female
KNM MW 161	8.2	9.7	<i>Proconsul nyanzae</i>	M1/	Mfwangano	
<i>KNM RU 16000</i>	8.5	10.0	<i>Proconsul nyanzae</i>	M1/	Rusinga	Male
<i>KNM RU 1677 A</i>	9.3	11.3	<i>Proconsul nyanzae</i>	M1/	Rusinga	Male
<i>KNM RU 1677 B</i>	9.4	11.2	<i>Proconsul nyanzae</i>	M1/	Rusinga	Male
KNM RU 1741	8.4	9.8	<i>Proconsul nyanzae</i>	M1/	Rusinga	
KNM RU 1742	8.3	9.8	<i>Proconsul nyanzae</i>	M1/	Rusinga	
KNM RU 1747	8.9	10.9	<i>Proconsul nyanzae</i>	M1/	Rusinga	

Specimens in italic letters belong to an association of teeth and therefore their meristic positions are known with confidence. Specimens in normal script are isolated teeth, and thus for some positions such as first and second molars there may be doubt about the meristic position.

Table 9.—Detailed attribution of *Proconsul* specimens from the Kisingiri complex of localities arranged by tooth type (continuation)

Catalogue number	Mesio-distal length (mm)	Bucco-lingual breadth (mm)	Taxon	Tooth	Locality	Sex determination
<i>M 16647</i>	9.2	11.7	<i>Proconsul nyanzae</i>	M1/	Rusinga	Male
<i>M 16647</i>	9.4	11.8	<i>Proconsul nyanzae</i>	M1/	Rusinga	Male
<i>KNM RU 1904</i>	7.7	9.4	<i>Proconsul heseloni</i>	M2/	Rusinga	
<i>KNM RU 1973</i>	7.9	9.3	<i>Proconsul heseloni</i>	M2/	Rusinga	
<i>KNM RU 2036</i>	8.1	10.1	<i>Proconsul heseloni</i>	M2/	Rusinga	Female
<i>KNM RU 7290</i>	9.2	10.9	<i>Proconsul heseloni</i>	M2/	Rusinga	Female
<i>KNM RU 7290</i>	9.4	10.9	<i>Proconsul heseloni</i>	M2/	Rusinga	Female
<i>KNM RU 1674 B</i>	9.8	11.6	<i>Proconsul heseloni</i>	M2/	Rusinga	Male
<i>KNM RU 2088 A</i>	9.8	10.7	<i>Proconsul heseloni</i>	M2/	Rusinga	Male
<i>KNM RU 2088 E</i>	9.8	10.9	<i>Proconsul heseloni</i>	M2/	Rusinga	Male
<i>KNM RU 16000</i>	10.6	11.7	<i>Proconsul nyanzae</i>	M2/	Rusinga	Male
<i>KNM RU 1803</i>	10.7	11.9	<i>Proconsul nyanzae</i>	M2/	Rusinga	
<i>KNM RU 1677 A</i>	12.0	13.5	<i>Proconsul nyanzae</i>	M2/	Rusinga	Male
<i>KNM RU 1677 I</i>	12.0	13.9	<i>Proconsul nyanzae</i>	M2/	Rusinga	Male
<i>M 16647</i>	12.0	13.4	<i>Proconsul nyanzae</i>	M2/	Rusinga	Male
<i>M 16647</i>	12.2	13.7	<i>Proconsul nyanzae</i>	M2/	Rusinga	Male
<i>KNM RU 1671</i>	7.8	9.8	<i>Proconsul heseloni</i>	M3/	Rusinga	
<i>KNM RU 1920</i>	7.9	10.5	<i>Proconsul heseloni</i>	M3/	Rusinga	
<i>KNM RU 1672</i>	8.0	9.5	<i>Proconsul heseloni</i>	M3/	Rusinga	
<i>KNM RU 7290</i>	8.2	11.0	<i>Proconsul heseloni</i>	M3/	Rusinga	Female
<i>KNM RU 7290</i>	8.4	11.0	<i>Proconsul heseloni</i>	M3/	Rusinga	Female
<i>KNM RU 1922</i>	8.7	10.9	<i>Proconsul heseloni</i>	M3/	Rusinga	
<i>KNM RU 2088 A</i>	9.3	11.6	<i>Proconsul heseloni</i>	M3/	Rusinga	Male
<i>KNM RU 2088 F</i>	9.4	11.6	<i>Proconsul heseloni</i>	M3/	Rusinga	Male
<i>KNM RU 1674 B</i>	10.0	12.6	<i>Proconsul heseloni</i>	M3/	Rusinga	Male
<i>KNM RU 1910</i>	10.0	12.4	<i>Proconsul heseloni</i>	M3/	Rusinga	
<i>KNM RU 16000</i>	10.5	12.2	<i>Proconsul nyanzae</i>	M3/	Rusinga	Male
<i>M 16647</i>	11.1	14.0	<i>Proconsul nyanzae</i>	M3/	Rusinga	Male
<i>KNM RU 1677 H</i>	11.4	13.9	<i>Proconsul nyanzae</i>	M3/	Rusinga	Male
<i>M 16647</i>	11.4	14.0	<i>Proconsul nyanzae</i>	M3/	Rusinga	Male
<i>KNM RU 1677 A</i>	11.8	14.0	<i>Proconsul nyanzae</i>	M3/	Rusinga	Male
<i>KNM RU 1697</i>	12.4	14.7	<i>Proconsul nyanzae</i>	M3/	Rusinga	
<i>KNM RU 1955</i>	7.8	4.9	<i>Proconsul heseloni</i>	p/3	Rusinga	
<i>KNM RU 2008</i>	9.0	5.6	<i>Proconsul heseloni</i>	p/3	Rusinga	
<i>KNM RU 2087</i>	11.2	7.4	<i>Proconsul heseloni</i>	p/3	Rusinga	Male
<i>KNM RU 2036</i>	8.5	5.9	<i>Proconsul heseloni</i>	p/3 left	Rusinga	Female
<i>KNM RU 7290</i>	8.5	5.7	<i>Proconsul heseloni</i>	p/3 left	Rusinga	Female
<i>KNM RU 2036</i>	8.5	6.0	<i>Proconsul heseloni</i>	p/3 right	Rusinga	Female
<i>KNM RU 7290</i>	9.2	5.7	<i>Proconsul heseloni</i>	p/3 right	Rusinga	Female
<i>KNM RU 1676 B</i>	10.0	6.9	<i>Proconsul nyanzae</i>	p/3	Rusinga	Male
<i>KNM RU 1782 A</i>	11.0	6.7	<i>Proconsul nyanzae</i>	p/3	Rusinga	
<i>KNM RU 1924</i>	12.6	6.8	<i>Proconsul nyanzae</i>	p/3	Rusinga	
<i>KNM RU 1982 F</i>	10.3	6.7	<i>Proconsul nyanzae</i>	p/3	Rusinga	Male
<i>M 32235</i>	11.5	7.2	<i>Proconsul nyanzae</i>	p/3	Rusinga	
<i>KNM RU 1947</i>	12.3	7.4	<i>Proconsul nyanzae</i>	p/3 left	Rusinga	Male
<i>KNM RU 1947</i>	12.6	7.2	<i>Proconsul nyanzae</i>	p/3 right	Rusinga	Male
<i>KNM MW 56</i>	6.0	6.6	<i>Proconsul heseloni</i>	p/4	Mfwangano	
<i>KNM RU 1674</i>	6.5	7.7	<i>Proconsul heseloni</i>	p/4	Rusinga	Male
<i>KNM RU 1868</i>	6.1	6.6	<i>Proconsul heseloni</i>	p/4	Rusinga	
<i>KNM RU 1955</i>	5.6	6.2	<i>Proconsul heseloni</i>	p/4	Rusinga	
<i>KNM RU 2036</i>	5.6	6.0	<i>Proconsul heseloni</i>	p/4	Rusinga	Female
<i>KNM RU 2036</i>	5.8	6.2	<i>Proconsul heseloni</i>	p/4	Rusinga	Female
<i>KNM RU 2044</i>	5.6	6.0	<i>Proconsul heseloni</i>	p/4	Rusinga	
<i>KNM RU 2087</i>	6.7	7.4	<i>Proconsul heseloni</i>	p/4	Rusinga	Male
<i>KNM RU 5871</i>	5.2	5.9	<i>Proconsul heseloni</i>	p/4	Rusinga	

Specimens in italic letters belong to an association of teeth and therefore their meristic positions are known with confidence. Specimens in normal script are isolated teeth, and thus for some positions such as first and second molars there may be doubt about the meristic position.

Table 9.—Detailed attribution of *Proconsul* specimens from the Kisingiri complex of localities arranged by tooth type (continuation)

Catalogue number	Mesio-distal length (mm)	Bucco-lingual breadth (mm)	Taxon	Tooth	Locality	Sex determination
<i>KNM RU 7290</i>	6.2	6.9	<i>Proconsul heseloni</i>	p/4	Rusinga	Female
<i>KNM RU 7290</i>	6.2	6.8	<i>Proconsul heseloni</i>	p/4	Rusinga	Female
KNM MW 55	6.9	7.7	<i>Proconsul nyanzae</i>	p/4	Mfwangano	
<i>KNM RU 1676c</i>	8.0	7.8	<i>Proconsul nyanzae</i>	p/4	Rusinga	Male
<i>KNM RU 1678</i>	6.7	7.2	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1679</i>	7.3	7.8	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1706</i>	6.5	6.1	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1710</i>	7.9	7.4	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1710</i>	7.9	7.4	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1711</i>	6.9	7.5	<i>Proconsul nyanzae</i>	p/4	Rusinga	
KNM RU 1716	8.2	7.9	<i>Proconsul nyanzae</i>	p/4	Rusinga	
KNM RU 1731	7.9	7.7	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1780</i>	6.4	7.4	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1824</i>	6.5	6.6	<i>Proconsul nyanzae</i>	p/4	Rusinga	
<i>KNM RU 1947</i>	7.8	8.2	<i>Proconsul nyanzae</i>	p/4	Rusinga	Male
<i>KNM RU 1947</i>	7.9	7.7	<i>Proconsul nyanzae</i>	p/4	Rusinga	Male
<i>KNM RU 1674 B</i>	6.8	10.7	<i>Proconsul heseloni</i>	P3/	Rusinga	Male
<i>KNM RU 1705</i>	5.5	8.6	<i>Proconsul heseloni</i>	P3/	Rusinga	
<i>KNM RU 7290</i>	6.1	10.0	<i>Proconsul heseloni</i>	P3/ left	Rusinga	Female
<i>KNM RU 7290</i>	6.2	9.8	<i>Proconsul heseloni</i>	P3/ right	Rusinga	Female
<i>KNM RU 16000</i>	6.7	10.2	<i>Proconsul nyanzae</i>	P3/	Rusinga	Male
<i>KNM RU 1677 A</i>	7.7	10.8	<i>Proconsul nyanzae</i>	P3/	Rusinga	Male
<i>KNM RU 1718</i>	6.8	10.4	<i>Proconsul nyanzae</i>	P3/	Rusinga	
KNM RU 1874	7.2	11.0	<i>Proconsul nyanzae</i>	P3/	Rusinga	
<i>M 16647</i>	7.8	11.5	<i>Proconsul nyanzae</i>	P3/ left	Rusinga	Male
<i>KNM RU 1705</i>	4.5	8.5	<i>Proconsul heseloni</i>	P4/	Rusinga	
<i>KNM RU 2036 B</i>	4.9	8.5	<i>Proconsul heseloni</i>	P4/	Rusinga	Female
<i>KNM RU 7290</i>	5.2	9.8	<i>Proconsul heseloni</i>	P4/ right	Rusinga	Female
<i>KNM RU 7290</i>	5.5	10.0	<i>Proconsul heseloni</i>	P4/ left	Rusinga	Female
<i>KNM RU 1674</i>	5.8	10.9	<i>Proconsul heseloni</i>	P4/	Rusinga	Male
KNM RU 1733	5.8	9.9	<i>Proconsul heseloni</i>	P4/	Rusinga	
<i>KNM RU 16000</i>	6.1	10.4	<i>Proconsul nyanzae</i>	P4/	Rusinga	Male
<i>KNM RU 1718</i>	6.4	10.6	<i>Proconsul nyanzae</i>	P4/	Rusinga	
<i>M 16647</i>	6.5	11.7	<i>Proconsul nyanzae</i>	P4/ right	Rusinga	Male
<i>M 16647</i>	6.7	11.7	<i>Proconsul nyanzae</i>	P4/ left	Rusinga	Male
<i>KNM RU 1677 A</i>	7.1	10.9	<i>Proconsul nyanzae</i>	P4/	Rusinga	Male
<i>KNM RU 1677 F</i>	7.2	10.7	<i>Proconsul nyanzae</i>	P4/	Rusinga	Male
KNM RU 1715	7.5	11.0	<i>Proconsul nyanzae</i>	P4/	Rusinga	
KNM MW 43	5.9	9.5	<i>Proconsul nyanzae/heseloni</i>	P4/	Mfwangano	
KNM RU 2005	6.1	11.0	<i>Proconsul nyanzae/heseloni</i>	P4/	Rusinga	
KNM RU 2037	6.3	11.0	<i>Proconsul nyanzae/heseloni</i>	P4/	Rusinga	
KNM RU 1719	6.4	10.4	<i>Proconsul nyanzae/heseloni</i>	P4/	Rusinga	

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who created the genus *Ugandapithecus* in order to resolve the problem of one genus containing such a high diversity of morphology. If *Ugandapithecus* is a synonym of *Proconsul*, as was argued recently by MacLachy & Rossie (2005b) and Harrison & Andrews (2009), then the genus once again becomes morphologically heterogeneous. Comparisons of these two species with material from

Rusinga Island attributed to *Proconsul nyanzae* and *Proconsul heseloni* indicate that *P. africanus* is much closer in morphology to the Rusinga species than is *U. major*. Retention of *Ugandapithecus major* as a species of *Proconsul* would therefore result in the genus being paraphyletic. The question of the specific distinction of *P. africanus* and *P. heseloni* needs to be reassessed as a result of our attri-

Table 10.—Comparison of samples of teeth *Ugandapithecus* species and *Proconsul africanus*

Taxon / Collection	Pre-1985 collections	Collected since 1985	TOTAL AS OF 2009
<i>U. gitongai</i>	0	17*	17
<i>U. major</i>	59	32	91
<i>U. legetetensis</i>	57	11	68
<i>U. meswae</i>	28	0	28
<i>P. africanus</i>	37	5	42
TOTAL	181	65	246

* This quantity includes specimens from Moroto, Kipsaraman and Buluk.

bution of the Songhor mandible, KNM SO 1112, to *Ugandapithecus meswae*.

Unlike Senut *et al.* (2000) we no longer retain all specimens previously attributed to *U. major* in a single species. With the recent additions to the available sample made by the Uganda Palaeontology Expedition and the Kenya Palaeontology Expedition (almost 30% of the entire collection [Table 10]), we confirm previous observations (Andrews *et al.*, 1981; Bosler, 1981; Martin, 1981) that there is great metric heterogeneity within the *Ugandapithecus* assemblage. Previous views that this metrically heterogeneous sample reflected a unique expression of sexual dimorphism in *P. major*, can no longer be considered valid, if only on the grounds that if it is unique, then the hypothesis cannot be tested. We prefer to interpret the fossils within a framework that accepts the usual sort of sexual dimorphism that is expressed in extant apes as well as most, if not all, adequately preserved fossil species (Pickford, 1986a; Ruff *et al.*, 1989; Pickford *et al.*, 1999; Patel & Grossman, 2006). This is not to say that the details of the dimorphism, or the degree of dimorphism are the same as that observed in extant apes, but it provides constraints on interpretations of the observable variation, not only in shape but in size, that exists in the collections. We accordingly recognise the presence of two species of *Ugandapithecus* smaller than *U. major* and *U. gitongai*.

Ugandapithecus legetetensis sp. nov., is ca 17% smaller than *Ugandapithecus major* and differs from it in details of dental morphology, whereas *Ugandapithecus meswae* is fully 30% smaller than *U. major*. The genus *Ugandapithecus*, like *Proconsul* and *Rangwapithecus*, was relatively diverse and experienced an increase in body size and relatively minor morphological changes with the passage of geological time (fig. 57).

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