NOTES ON THE EAST AFRICAN MIOCENE PRIMATES.

By D. G. MacInnes, Ph.D.

Introduction.

The material to be described in this paper was obtained from Rusinga Island and Songhor, Kenya, during various scientific expeditions, primarily by members of Dr. L. S. B. Leakey's third and fourth E.A. Archaeological Expeditions, of 1932 and 1935 respectively. Additional material was obtained from Songhor by the author in 1938, and by Dr. Leakey in 1940 and 1942.

Papers dealing with the whole of the collections of mammalian fossils obtained by the earlier expeditions, were prepared for publication some years ago, but unfortunately many unforeseen circumstances have combined to delay publication. The major paper, dealing with the Proboscidea, (MacInnes, 1942), which was submitted for publication in 1937, only appeared in July, 1942, and it has now been decided that detailed descriptions of the remainder of the material should be placed on record without further delay. Owing to the lack of sufficient comparative material, and of much of the relevant literature, these papers must be confined largely to descriptive work, rather than comprehensive systematic discussion.

The present paper deals first—under the heading "Correlation"—with the evidence supplied by the fossil fauna of the area as a whole, in an attempt to determine the geological horizon to which the material subsequently described should be assigned. The remainder of the paper deals with the fossil Primates obtained during the expeditions referred to above. The study of some of the specimens recovered by the earlier expeditions was greatly facilitated by members of the Department of Anatomy at Cambridge University, and I should like particularly to express my thanks to Professor Harris and to Dr. Duckworth, who provided me with comparative material in this connection, and whose help and advice was much appreciated. My thanks are also due to Dr. A. T. Hopwood of the British Museum of Natural History, who enabled me to examine the types of certain fossil specimens, and to Mr. Sam Evans of Songhor, from whose farm much of this interesting material was obtained.

Dr. Leakey's most recent visit to Rusinga Island, in August, 1942, yielded additional anthropoid material, including a nearly complete mandible, and a left astragalus, which are assigned to *Proconsul africanus* Hopwood. I am indebted to Major Hopkirk of the S.R.M.C. for his help in attempting to obtain, by X-ray, the root-cavity formation of this mandible, and certain internal features of the structure of the astragalus. It had been hoped that examination of the trabeculae of the latter might give some indication of the main line of stress, and thus suggest the normal attitude of the animal. Unfortunately, Major Hopkirk found that the cancellous bone was so heavily mineralized, that adequate contrast between the lamellae and the spaces was not obtainable.

Finally, I should like to take this opportunity of expressing my deep appreciation of Dr. Leakey's constant co-operation, and my thanks for his invaluable help in the preparation of this paper, and for placing at my disposal the material upon which so much of the paper is based.

NOTE ON TERMINOLOGY USED IN THIS PAPER.

NOTE.—The terminology of the cusps, used throughout this paper, follows H. F. Osborn, *Evolution of the Mammalian Molar Teeth*, 1907.

Upper Premolars:

Antero-internal=Deuterocone. Antero-external=Protocone.
Postero-internal=Tetartocone. Postero-external=Tritocone.

Upper Molars:

Antero-internal=Protocone. Antero-external=Paracone.
Postero-internal=Hypocone. Postero-external=Metacone.

Lower Premolars:

Antero-internal=Paraconid. Antero-external=Protoconid.
Meso-internal=Metaconid.
Postero-internal=Entoconid. Postero-external=Hypoconid.

Lower Molars:

Antero-internal=Metaconid. Antero-external=Protoconid.
Postero-internal=Entoconid. Postero-external=Hypoconid.
Postero-medial=Hypoconulid.

The explanation of the tooth measurements is as follows:—

Upper and Lower Incisors: Length=maximum antero-posterior length, at right angles to the line of the alveolus. Breadth=maximum breadth at right angles to the long axis of the root, and parallel to the line of the alveolus.

Upper and Lower Canines, and Lower Premolars: Length=maximum length (i.e., following the long axis of the roots). Breadth= maximum transverse breadth, at right angles to length measurement.

Upper Premolars, Upper and Lower Molars: Length=maximum antero-posterior length, parallel to the alveolar border. Breadth= maximum transverse breadth, approximately at right angles.

Text figures and plates are reproduced natural size throughout.

CORRELATION.

The material collected by the various scientific expeditions referred to in the introduction, was obtained from four principal localities in the Kavirondo section of the Victoria Nyanza basin. Of these localities, Rusinga Island proved to have the most extensive fossil beds, and yielded the largest variety of mammalian remains. The deposits of Karungu were previously known from Dr. Felix Oswald's work in 1911, and provided a relatively small variety of fossils. Songhor yielded a small but none the less important selection, whilst Kiboko Island, in some respects the most important of them all, has provided a somewhat puzzling assortment of Mastodon remains and very little besides. The following table gives a list of the genera included in these collections, and the localities from which their remains have been recovered. It will be seen that some thirteen genera are recorded from Kiboko Island which is, in a sense, deceptive, since all but *Trilophodon* and *Climacoceras* are represented by little more than one fragment. The table serves, however, to give an indication as to the distribution of the fossils. The relative isolation of these various localities renders any stratigraphical correlation between them difficult,* but it will be seen from the table that there is no faunal evidence to suggest that any one of these localities represents an appreciably earlier or later geological period than the others.

	Rusinga.	Karungu.	Songhor.	Kiboko.
Deinotherium ...	×	×	—	×
Trilophodon * † ...	×	—	—	×
Rhinoceros † ...	×	×	—	×
Brachyodus * † ...	×	—	—	—
Ancodon ...	—	—	—	×
Hyaenodon ...	—	—	—	×
Amphicyon ...	×	—	—	—
Pterodon ...	×	—	—	×
Herpestes ...	×	—	—	—
Felis * † ...	×	—	—	×
Carnivora indet. ...	×	—	×	×
Macrotherium ...	×	—	—	—
Listriodon † ...	×	—	—	×
Suidae indet. † ...	×	—	—	×
Amphitragulus ...	×	—	×	—
Selenodonta indet. ...	×	—	×	—
Climacoceras ...	—	—	—	×
Pliohyrax † ...	×	—	—	—
Myohyrax * ...	×	—	—	—
Rodentia indet. ...	×	—	×	—
Palaeoerinaceus ...	×	—	—	—
Progalago ...	—	—	×	—
Mesopithecus ...	×	—	—	×
Limnopithecus ...	×	—	×	—
Xenopithecus ...	×	—	×	—
Proconsul ...	×	—	×	×

* This genus has previously been recorded from Karungu.
† This genus has previously been recorded from Losodok.

It has already been pointed out that the deposits of East Africa from which this collection of fossils was obtained, cannot yet be correlated on purely stratigraphical evidence with those of Europe or elsewhere. The study of the fossil fauna is, therefore, complicated by our uncertainty of the exact period to which

*Dr. P. R. Kent is understood to have prepared a paper on this question, which is already in the press.

they belong. A consideration of the existing fauna shows at once that many groups of animals, whose ranges formerly extended over the greater part of the world, are now confined almost solely to the African continent. For example, the remains of an elephant obtained anywhere in Europe, would indicate that the deposit from which they were procured was of Pleistocene age. Clearly, however, the same would not apply in Africa. It seems reasonable to suppose that the variation of altitude and the resultant variations in climatic conditions offers a suitable explanation for the survival of faunas.

Since it is an accepted fact that Africa has existed as a great land mass for a very long period, we may, therefore, assume that for the same reason it has always afforded conditions suitable for survival. The occurrence of *Deinotherium* in the Pleistocene deposits of Southern Abyssinia, Kenya Colony and Tanganyika Territory, proves the validity of such an hypothesis. It is, therefore, of the utmost importance that this possibility should be borne in mind during any attempt to correlate the deposits of East Africa with those of other parts of the world, since in the absence of sufficient stratigraphical evidence we can only compare the fossil remains.

On the other hand, as Dr. Hopwood has pointed out, the determination of the age of any deposit should depend upon the first appearance of new faunal types, and not upon the survival of earlier forms. In this connection, Haug's definition of the Pleistocene, as indicated by the first appearance of any one of the genera *Elephas*, *Bos*, or *Equus*, is well-founded, but at the same time it involves the consideration of "negative evidence." This is always a somewhat unsatisfactory basis, but in the present circumstances the amount of material obtained from the localities concerned, enables us to be fairly confident that a representative collection is at our disposal.

In the area from which the fossils described in this paper were obtained, we have the deposits of Kanam, Kanjera and certain other localities, which have yielded the remains of *Elephas* (in the general sense of the term) (MacInnes, 1942), *Bos* and *Equus*, and which have, therefore, been assigned to the Pleistocene. The fossil beds from which the material under consideration was obtained, have never yielded any of these three genera, and for that reason they are regarded as of pre-Pleistocene age. Comparison of the mammalian remains of these deposits with those of other parts of the world, shows that there is a distinct faunistic resemblance to those of Moghara in Egypt, of Sansan in France, and of the Bugti beds of Baluchistan. The Sansan series is known to be of Burdigalian age, whilst the deposits of Moghara and Bugti have been assigned to the same period on account of the similarity of their mammalian faunas. We have, therefore, a forward and a backward time limit, for we may assume that the fauna of the Victoria Nyanza basin is probably not older than the Burdigalian, and is not as late as the Pleistocene.

A study of the Pontien fauna of Salonika shows that there, at least, a number of new forms, such as *Hipparion, Gazella* and others, which are not represented in the lower Miocene of Europe, and which are not as yet known to occur in the pre-Pleistocene of East Africa, had made their appearance. Thus, even if we admit the possibility of survival, it seems to be improbable that these fossil remains represent a period as late as the Pontien. In the present state of our knowledge, therefore, it will be convenient to regard these deposits as the East African representative of the Burdigalian.

M. Arambourg obtained some fossil remains from the Losodok Hills on the western shore of Lake Rudolf in 1932. The material appears to have been very fragmentary and limited, but since practically all the genera recorded are also included in the Rusinga collection, his suggestion that they should be referred to the lower Miocene is probably correct.

It is clear that further collecting in the East African area would be well repaid, and it is to be hoped that additional specimens will be obtained of those groups which at present are so poorly represented.

ORDER *PRIMATES*.
SUPERFAMILY *LEMUROIDEA*.
FAMILY *ANAPTOMORPHIDAE?*

Progalago gen. nov.

DIAGNOSIS.

A Lemuroid, in which the lower Pm.4 is monocuspid, the hypoconid being practically undeveloped. Greatest depth of horizontal ramus of mandible below M.3. Lower dental formula probably 2 : 1 : 3 : 3.

Progalago dorae sp. nov. (Genotype).

DIAGNOSIS.

A medium-sized Progalago, in which the lower molar series is about 10 mm. in length.

HOLOTYPE.

A fragment of left horizontal mandibular ramus, bearing Pm.4 and M.2. (Plate 23. Figs. 2, 2A and 2B.)

HORIZON.

Miocene.

LOCALITY.

Songhor, Kenya Colony.

DESCRIPTION.

Only the holotype is at present known. This small mandible fragment is broken anteriorly at the level of Pm.2, the posterior root-cavity of this tooth being exposed on the fracture surface. The extreme posterior point of the symphysis is present. Posteriorly the fracture begins immediately behind the M.3 root-cavity, and extends diagonally backwards and downwards, almost to the mandibular angle. The lowest point of the symphysis, which lies below Pm.3, is turned sharply downwards, forming a tubercle which projects well below the lower border of the ramus. The mental foramen is situated in the middle of the ramus, immediately above this tubercle, and below the posterior root of Pm.3. The least depth of the ramus is at the level of Pm.4, and the depth increases posteriorly. By calculation, based on the proportion of the molar-series length to the mandibular length, in modern galagos, the total mandibular length of this specimen must have been about 36 mm.

DENTITION.

Pm.4 is monocuspid, with a large posterior talonid. The longer axis of the tooth is more oblique to the general line of the tooth-row than is usual in the modern galago, owing to the development of the antero-external, and the postero-internal angles. The protoconid is slightly more external than is the case in the modern East African galagos, and from its apex a sharp crest extends to the antero-external angle, while a second crest, directed straight backwards in the same line, extends to the postero-external point. A very faint tubercle is present at the base of this crest, which probably represents the hypoconid. Internally, a third crest is directed inwards and slightly backwards to the middle point of the lingual margin, and a distinct trace of the metaconid may be seen on this crest near the apex of the protoconid. The anterior and internal crests are directly united at their bases by the cingulum, which is produced from the latter into a wide postero-internal loop to the base of the posterior crest, thus enclosing a slightly concave talonid. The barrel of the protoconid is very distinct as a rounded vertical ridge on the external surface, whilst below it, a faint horizontal swelling round the lower margin of the crown, may represent an external cingulum.

M.2 is quadricuspidate, with the external cusps (protoconid and hypoconid) slightly in advance of the corresponding internal cusps (metaconid and entoconid). The protoconid and metaconid are connected by a distinct transverse ridge from their apices, whilst small anterior crests extend from the apex of each to the anterior cingulum, which is very well-developed. From the base of the protoconid, at its postero-internal point, a well-marked crest extends backwards, outwards and upwards to the apex of the hypoconid, whilst another crest from the corresponding point of the metaconid, unites this cusp with the entoconid. The hypoconid and entoconid are also connected, by a transverse crest round the extreme posterior margin of the crown.

The measurements of the specimen, in millimetres, are as follows:—

Total length of fragment	26.4
Calculated mandibular length	36.0
Depth of ramus at Pm.4	7.0
Depth of ramus at M.3	8.8
Maximum thickness of ramus (at Pm.4) ...	3.4
Length of Pm.3—M.3. (approx.)	15.2
Length of molar series (approx.)	10.0

	Pm.3 approx.	Pm.4.	M.1 approx.	M.2.	M.3 approx.
Length ...	2.7	3.4 (long axis)	3.3	3.6	3.7
Breadth ...	—	2.3	—	3.4	—

DISCUSSION.

This fragment, although so incomplete, is of considerable importance, in that it appears to be the first fossil representative of the *Galaginae* to be recorded from East Africa. In size, the animal was very little smaller than the existing *Galago kikuyuensis* Lönnberg, but certain structural characteristics clearly distinguish the fossil from any of the existing East African forms. The main points of difference are as follows:—

(1) The increase in mandible depth from front to back in the fossil, and *vice versa* in the modern animals.
(2) The monocuspidate lower Pm.4 in the fossil, and the relative insignificance of the hypoconid and metaconid.
(3) The oblique position of the long axis of Pm.4 in the fossil.
(4) The wider separation of hypoconid from entoconid in M.2, which in modern animals is about equal to that of protoconid and entoconid.

Unfortunately, no other fossil material is available for comparison and very little of the literature on extinct lemuroids. There appears to be a distinct similarity to *Necrolemur* of Filhol, from the Upper Eocene of Quercy, and it is possible that the new genus might be comparable to *Microchoerus* of Wood, from the Upper Eocene of Hordwell, but the mandible and lower dentition of the latter are at present unknown.

There is also a certain similarity to *Perodicticus* Bennet, in the form of M.2. In this modern genus, however, the posterior point of the symphysis is slightly further back, below Pm.4, and this tooth has retained its primitive form to a greater degree.

The large talonid in Pm.4 of the fossil may well be regarded as an intermediate stage towards the partially molarised Pm.4 of *Galago*, but it could hardly be regarded as ancestral to the simple tooth of *Perodicticus*.

It seems probable that the new fossil may be in the direct ancestral line of the modern galagos, for which reason the name *Progalago* is suggested. The specific name is taken from that of my wife, who found the specimen.

SUPERFAMILY *ANTHROPOIDEA*.
FAMILY *CYNOPITHECIDAE*.

Mesopithecus Wagner sp. ?

MATERIAL.

Part of the right horizontal ramus of a mandible (Plate 23. Figs. 1 and 1A) and some isolated teeth.

REMARKS.

These specimens were recovered from Rusinga and Kiboko Island. Most of the teeth are fairly well-worn, and the condition of the material is such that it cannot well be compared with other examples. Examination of fossil specimens in the British Museum shows that these teeth bear a distinct resemblance to those of *Mesopithecus*, and until better material is forthcoming there seems to be no reason to separate the African fossils from this genus.

DESCRIPTION.

Upper dentition.—Three examples of upper teeth are included in the collection which appear to represent M.2 and M.3. By measurement M.2 is very slightly broader than it is long, though in the unworn condition it appears to be relatively longer owing to the proximity of the outer and inner cusps. Four cusps are present, arranged in two lobes, and the cingulum is well-developed at either end of the tooth and absent on either side. The protocone gives rise to three crests, one of which is directed antero-externally to merge with the cingulum at the antero-median point, a second is directed transversely to the paracone, while the third extends postero-externally to the metacone. The hypocone has a very small antero-external crest which unites with that between the protocone and metacone at its middle point, while a second crest on the posterior surface of the hypocone curves outwards and merges with the cingulum. The protocone and metacone each have an anterior and a posterior crest. The lateral walls of the tooth converge sharply towards the apex, so that the breadth between the extremities of the cones is less than half the total breadth of the tooth. The posterior lobe is slightly narrower than the anterior.

M.3 is smaller than the preceding tooth and shows a greater constriction of the posterior lobe on account of the reduction of the metacone. In other respects the structure appears to be identical with that of M.2. The measurements of these upper teeth in millimetres are as follows:—

		Breadth		
	Length.	Anterior.	Posterior.	Index.
M.2 ...	7.5	8	7	106
M.3 ...	6	6.5	5	108
M.3 ...	6.5	7.5	5.5	115

The mandible fragment has Pm.4—M.3 in place, in all of which the length exceeds the breadth. The ascending ramus begins as a slight horizontal ridge below the anterior border of M.2 which curves sharply upwards and is nearly vertical at the level of the posterior part of M.3. The lower border of the ramus is slightly concave antero-posteriorly, but the specimen is fractured at either end, and the full extent of this concavity is not apparent. The mental foramen is single and lies below Pm.4. The anterior fracture is oblique and extends backwards on the lower border to the level of M.1, so that it is impossible to determine the backward extension of the symphysis.

The mandibular dimensions in millimetres are as follows:—

Depth of ramus at M.1.	15
Depth of ramus at M.3	16
Thickness of ramus at M.2	7.5
Length of tooth row, Pm.4—M.3	25

Lower dentition.—Pm.4 is bicuspid, with two subequal cones closely united by a transverse crest. Anteriorly the cingulum is developed into a distinct shelf which bounds a small fovea anterior, while posteriorly it surrounds the large basin-shaped talonid. The wear is such that the structure of the talonid is obscured, but it appears that the hypoconid and entoconid were developed into distinct tubercles. The tooth is set obliquely in the alveolus, extending outwards towards the front. The broken roots of the preceding tooth are present from which it is clear that Pm.3 was larger and even more oblique than Pm.4.

M.1 is oblong with four cusps arranged at the four corners. The two outer cusps, protoconid and hypoconid, are much worn and have a somewhat selenodont pattern, by reason of the antero-internal and postero-internal crests of each cusp. The anterior crest of the protoconid and the posterior crest of the hypoconid unite with the cingulum at the middle point of the anterior and posterior borders of the tooth. The other two crests unite in the middle line of the tooth to form a distinct median longitudinal ridge. The metaconid and entoconid are fairly high and pointed, and each has a slight external crest which extends transversely across the tooth to the opposite external cusp. The hypoconulid is absent, and the cingulum is only developed at the ends and not at the sides. M.2 is slightly larger than M.1 but is identical in structure.

M.3 differs from the preceding molars by the presence of a well-developed hypoconulid. This is situated immediately behind the hypoconid and in the same straight line with the hypoconid and protoconid, and the tooth thus has a more elongated appearance. The protoconid is still selenodont, while the hypoconid is more bunodont, with a small antero-internal crest which unites with the posterior crest of the protoconid. The median longitudinal ridge is thus retained, while the postero-internal crest is replaced by a very small projection connecting the hypoconid with the hypoconulid. The cingulum is developed anteriorly and on the postero-internal border between the entoconid and the hypoconulid. The measurements of these teeth in millimetres are as follows:—

	Length.	Breadth.	Index.
Pm.4	5	4	80
M.1	6	5	83
M.2	7	6	85
M.3	7.5	6	80

DISCUSSION.

The structure of these teeth is almost exactly similar to that of *Mesopithecus pentelici* Wagner, but the lower molars are somewhat smaller than those of the latter species, and they are also relatively narrower. There is at present insufficient material for any close comparative study, and the material is, therefore, referred to this group.

In Europe, *Mesopithecus* first appears in the Pontien, where its remains are fairly frequent, and it is also known from China. Arambourg pointed out that the genus appears to have African rather than Asiatic affinities, and if this is so we might expect to find fossil remains of an earlier date in Africa. It has already been shown that no exact correlation has yet been made between the deposits of Africa and those of Europe, but there is a general concensus of opinion that the pre-Pleistocene deposits of the Victoria Nyanza basin from which these fossils were obtained, are Lower Miocene (Kent, 1941), or at least older than Pontien. It is thus particularly unfortunate that this material is so incomplete, for it seems very possible that it may represent an ancestral form from which the European *Mesopithecus* was derived.

By comparison with a modern *Colobus* monkey from East Africa we find that the lower dentition differs in certain features. Pm.4 of the fossil is fairly sharply oblique to the axis of the tooth row, whilst in the modern form the longer axis of the tooth continues the line of the molar series. In the molars the outer cusps are more distinctly selenodont in the fossil, and the two transverse crests of each tooth appear to be more united by reason of the median longitudinal ridge, whereas in *Colobus* Illiger, the crests are sharper and more distinct. It seems probable, however, that in the more worn condition the teeth of the latter would approximate more closely to those of the fossil. The most marked difference in the molar series is the development of the hypoconulid in the third lower molar of *Colobus*. It is in the same straight line with the protoconid and hypoconid, as in the fossil, but it is a much larger cusp, and is entirely detached from the hypoconid projecting backwards as a distinct posterior lobe.

FAMILY *SIMIIDAE*.

Limnopithecus legetet Hopwood.

TYPE LOCALITY.

Koru, Kenya Colony.

MATERIAL.

Four fragments of mandible from Songhor and Rusinga, with examples of the last premolar and the molar series.

DESCRIPTION.

The largest specimen consists of a right horizontal ramus with half of Pm.3 and Pm.4—M.1 complete (Plate 23. Figs. 3 and 3A). The teeth are very low-crowned, although only slightly worn. The bone of the ramus is deep and fairly narrow. On the external surface the ascending ramus begins to rise at the level of the anterior part of the third molar. A low but distinct ridge continues the line of the ascending ramus in a downward and forward curve which reaches its lowest point below M.1 and subsequently rises again to Pm.3. The mental foramen is single and is situated below the interval between Pm.3 and Pm.4, slightly below the middle point of the ramus. On the internal surface a shallow groove is present near the base which extends anteriorly into the simian pit.

DENTITION.

Pm.3 is too incomplete for the structure to be seen. Pm.4 is rather broader than it is long, and is slightly bicuspid. The outer cusp, which is the larger, is situated almost in the middle line and is connected by a distinct crest to the smaller, inner cusp on the lingual margin. These two cusps are rather in advance of the middle point, and posteriorly the cingulum forms a wide flat shelf. Anteriorly the cingulum is also present, connecting the bases of the two cusps to form a distinct fovea anterior.

The three molars all show a similar structure of five cusps arranged round the periphery, and they differ only in their proportions. The protoconid and metaconid are united by a crest similar to that connecting the cones of the premolar, while the anterior cingulum bounds the fovea anterior. A very slight crest connects the protoconid with the hypoconid, while the entoconid and the hypoconulid remain almost isolated. The latter cusp is situated practically in the middle line on the posterior margin. The cingulum is well-developed, particularly between the cusps on the anterior, external and posterior surfaces, but it is absent internally. M.1 is approximately oblong, being rather longer than broad. M.2 is slightly broader in front than behind, whilst in M.3, the hypoconulid is extended well backwards and produces an almost triangular outline.

The measurements of this specimen in millimetres are as follows:—

MANDIBLE:	
Depth of ramus below Pm.3	17.5
Depth of ramus below M.3	17
Thickness of ramus below M.1	8
Length of tooth row Pm.4—M.3	22

TEETH:	Pm.4.	M.1.	M.2.	M.3.	M.1.	M.2.	M.2.	M.3.
Length ...	4.0	5.5	6.0	6.5	5.5	6.5	6.0	5.5
Breadth ...	4.8	5.0	5.7	5.2	4.5	6.0	5.0	4.8
Index ...	120	90	95	80	81	92	83	87

DISCUSSION.

The genus to which these specimens are most obviously comparable, is *Limnopithecus* Hopwood, originally described from material obtained at Koru. One example of M.1, and two of M.2 in this collection, correspond almost exactly both in dimensions and also in structure, with the genotype of *L. legetet*, and the breadth index is necessarily very similar. Other specimens, however, whilst showing structural similarity, disagree in the length-breadth index. In spite of this, the material is regarded as belonging to *L. legetet* Hopwood, for reasons which are discussed in greater detail in the discussion on the two species.

Limnopithecus evansi sp. nov.

DIAGNOSIS.

A species of *Limnopithecus,* in which the molars are slightly larger than those of the genotype. Lower Pm.4 appreciably longer than broad. Length-breadth proportion of molars generally less than 90. Horizontal ramus of mandible lower than that of genotype.

HOLOTYPE.

A fragment of right mandibular ramus, with Pm.4—M.3 in position (M.3 damaged). (Plate 23. Figs. 4, 4A and 4B.)

PARATYPE.

A right mandibular ramus and symphysis, showing the whole premolar—molar series, and with the roots of the incisors and canines in the alveolus. (Plate 23. Figs. 6, 6A and 6B.)

HORIZON.

Miocene.

LOCALITY.

Songhor, Kenya Colony.

MATERIAL.

Holotype, paratype, and one other fragment of left mandible bearing M.1 and M.2. (Plate 23. Figs. 5, 5A and 5B.)

DESCRIPTION.

Holotype (Plate 23. Figs. 4, 4A, 4B). This fragment is broken anteriorly in the middle of Pm.3, the crown of which is lost, and posteriorly about 2 mm. behind M.3. Pm.4—M.2 are in excellent condition, while M.3 lacks the posterior half of the crown. The body of the ramus is more slender and less deep than that of the specimen of *L. legetet* already described from the same locality. There is no apparent decrease in depth from front to back. The ascending ramus begins to rise at the level of the anterior part of M.3, as in *L. legetet*, but there is no trace of the ridge referred to in the description of the latter species, continuing the line onto the labial surface of the horizontal ramus.

The paratype (Plate 23. Figs. 6, 6A and 6B) consists of the right horizontal ramus, the symphysis, and a small portion of the left ramus. The right ramus is broken immediately behind M.3, and the left immediately behind Pm.4. The crowns of all the incisors, both canines and the right Pm.3 are broken, leaving the roots in the alveolus. The remaining teeth are largely complete, but the enamel is lost in parts, and weather action has obscured the finer structural details. The ramus is fairly low and stout, and the decrease in depth from front to back is very marked, especially on the lingual surface. With the alveolus set horizontally, the posterior point of the symphysis lies immediately below the principal cusp of Pm.4. The mental foramen is single, and lies below the middle of Pm.3. The line of the premolar—molar series is more sharply oblique to the axis of the ramus, than in the holotype, and the two series appear to have been almost parallel, while the rami converge at a fairly sharp angle. As a result of this arrangement, M.3 is situated well over from the middle line of the ramus, onto the lingual surface: thus the contrast in the depth of the ramus from front to back is very much more apparent on the lingual aspect than on the labial. As in *L. legetet,* a shallow groove is present in the lingual surface of the horizontal ramus, which passes from the middle point of the ramus below M.3, forwards and downwards to end in the simian pit.

The third mandible fragment (Plate 23. Figs. 5, 5A and 5B) has the left M.1 and M.2 very well-preserved, but no other teeth are present. The body of the ramus is much damaged, but it appears to have been more slender and is distinctly less deep than that of *L. legetet.*

No maxilla fragments or upper teeth were obtained.

Lower dentition.—Incisors. The crowns of all the incisors are missing, but the teeth appear to have projected at an angle of 20°—25° from the vertical.

Canine. The roots show considerable lateral flattening, and suggest that the crown was fairly high and slender.

Pm.3, which is present only on the left side of the paratype, is monocuspid, with one anterior, and two posterior crests from the apex of the protoconid. The anterior crest follows the line of axis of the premolar—molar series, and ends in a distinct tubercle arising from the cingulum. The other two crests extend to the postero-internal and postero-external angles respectively, leaving an intervening flat area, forming a posterior shelf. The longer axis of the tooth lies obliquely, and the cingulum is well-developed round the inner and posterior margins of the crown.

Pm.4. Three examples of this tooth are present, all of which differ in one important character from the corresponding tooth of *L. legetet,* namely, the length-breadth index (see table of measurements). In all three the length is appreciably greater than the breadth, while in the latter species the breadth exceeds the length. The tooth is very slightly oblique to the general tooth-row axis, and is bi-cuspid, the outer cusp being the larger. In the paratype, the two cusps are united by a distinct crest, while in the holotype this is less well-developed. The two main cones are well in advance of the middle point of the tooth, and a small fovea-anterior is present, bounded in front by the well-developed cingulum. At the postero-external angle, a small tubercle occurs, which may represent the hypoconid. This is connected by a distinct crest, to the apex of the protoconid, while a similar crest from the apex of the metaconid, extends round the postero-internal angle. to the hypoconid, bounding a deeply concave talonid. Externally the cingulum is distinct.

Molar series.—The molars agree fairly closely with those of the genotype, but are slightly larger, and differ in their length-breadth proportions. M.1 is consistently the smallest of the series, and is distinctly more rhomboidal in outline than the M.1 of *L. legetet,* and also more so than M.2. The protoconid is larger than in the genotype, and is subequal in size to the hypoconid. As a result, the two pairs of cusps, protoconid-metaconid and hypoconid-entoconid are more nearly opposite than is the case in the Songhor specimen of *L. legetet*, in which the hypoconid is almost alternate with the metaconid and entoconid. The hypoconulid is large and median. The greatest breadth of the tooth is at the posterior lobe.

M.2 is very similar in structure to M.1, but the outline is less rhomboidal, and the protoconid and metaconid are more widely separated.

The posterior end of M.3 is missing in the holotype, while in the paratype the weather action and wear have largely obscured the structure. It is clear, however, that the talonid was produced backwards, though it appears that it was somewhat wider and less constricted than in M.3 of *L. legetet*.

The first and second molars present in the third specimen show certain structural differences from the holotype and paratype. In M.1, the protoconid is large, and is situated rather further forward, which gives a more irregular outline to the tooth. The hypoconid is correspondingly further forward, and thus more nearly alternate to the metaconid and entoconid. In both M.1 and M.2, the hypoconulid is slightly more external. In spite of these differences, the specimen appears to be more similar in general to *L. evansi* than to *L. legetet*.

The measurements of these specimens, in millimetres, are as follows:—

HOLOTYPE:

Depth of mandible at M.1.	14.5
Thickness of mandible at M.1.	6.0
Length of tooth-row (Pm.4—M.3)	23.0

	Pm.4.	M.1.	M.2.	M.3.
Length	5.0	6.2	6.5	6+
Breadth	4.0	4.9	5.6	5.2
Index	80	79	86	—

PARATYPE:

Depth of mandible at Pm.3	18.5
Depth of mandible at M.1	16.0
Depth of mandible at M.3	15.2
Thickness of mandible at M.1	7.2
Length of tooth-row (Pm.4—M.3)	22.8
Length of symphysis	22.2

	Left		Right				(Roots.)		
	Pm.3.	Pm.4.	Pm.4.	M.1.	M.2.	M.3.	(I.1	I.2	C.)
Length	6.0	5.2	5.2	6.0	6.4	7.0	(4.0	5.0	7.0)
Breadth	4.2	4.0+	4.1	4.4+	5.5	5.3	(2.2	3.0	5.0)
Index	70	76.9+	78.8	73.3+	85.9	75.7	(—	—	—)

LEFT RAMUS:

Depth of mandible at M.3	15.7
Thickness of mandible at M.1.	6.8

	M.1.	M.2.
Length	6.6	7.1
Breadth	5.2	6.0
Index	78.7	84.5

Comparative measurements of M.1 and M.2 in *L. legetet* and *L. evansi* are as follows:—

	L. legetet type.	*L. legetet* Songhor.			*L. evansi*.		
M.1:							
Length ...	5.3	5.5	—	5.5	6.2	6.6	6.0
Breadth ...	4.9	5.0	—	4.5	4.9	5.2	4.4+
Index ...	92.5	90	—	81	79	78.7	—
M.2:							
Length ...	6.2	6.0	6.0	6.5	6.5	6.4	7.1
Breadth ...	6.0	5.0	5.7	6.0	5.6	5.5	6.0
Index ...	96.8	83	95	92	86	85.9	84.5

It is clear from the above table, that the first and second molars of *L. evansi* are slightly larger, and tend to have a rather lower length-breadth index than those of *L. legetet*.

DISCUSSION.

Although it is apparent that these specimens are closely allied to *Limnopithecus legetet* Hopwood, the various differences of structural detail noted above seem to indicate that they do not belong to the same species. Dr. Hopwood, in his original description pointed out the following characters as being diagnostic of the genus:—

(1) Very low-crowned lower cheek-teeth.
(2) Length-breadth index of lower molars exceeding 90.
(3) Presence of distinct internal cingulum between the cusps.

The material at present under consideration may be said to agree with the first character, though the limits are not easily defined. It is decidedly opposed to the second character, while the third is a general characteristic, found in many other genera. Thus, superficially this new material, and also the Songhor specimens obtained in 1932, should be excluded from the genus *Limnopithecus,* since they disagree with the one definite diagnostic character. There is, however, no other genus with which the material bears close comparison, and to follow the literal interpretation of the diagnosis of *Limnopithecus* would necessitate the formation of a new genus. On the material available, such a course would be undesirable, and it would still be impossible to make an adequate generic diagnosis in anything but general terms, since all the specimens are so clearly comparable, in essentials, to *Limnopithecus*. For these reasons, the material collected at Songhor and on Rusinga Island in 1932, has, after comparison with the type, been included with the species *L. legetet,* despite the fact that some of the molars show a length-breadth index as low as 80, while in four out of the seven molars obtained, the index is below 90.

The new material, as already shown, exhibits several other minor points of difference, both from the type, and also from the 1932 specimens. These may be summarized again as follows:—

(1) The slightly larger size, and corresponding greater length of the Pm.-M. series.

(2) The lower and more slender horizontal ramus of the mandible.

(3) The tendency to a decrease in the depth of the ramus from front to back.

(4) The difference in the proportions of the cusps in the molars.

This material has, therefore, been distinguished as a separate species, for which the specific name *L. evansi* is employed, in recognition of Mr. Sam Evans' kind help and co-operation which has resulted in the discovery of so much interesting and important material on his farm at Songhor.

General Discussion.

In comparison of *Limnopithecus* Hopwood, with Fourteau's *Prohylobates*, we find that the total length of the molar series is the same, but whereas in the latter the three molars are all of equal length, those of *Limnopithecus* show a gradual increase in length from M.1 to M.3. The teeth also differ from those of *Prohylobates* by the presence of a distinct cingulum, although they show a certain resemblance in the distribution of the principal cusps, and in the central position of the hypoconulid.

The molars of *Limnopithecus* differ from those of *Hylobates* Illiger, in the greater development of the cingulum, and the higher breadth index. The position of the hypoconulid, on the other hand, appears to be very similar to that of *Hylobates*, except in M.3, where in the fossil it is produced as a backward lobe. In *Limnopithecus*, M.1 is the smallest of the molar series, while M.3 is less quadrate in outline, owing to the backward extension of the hypoconulid. In *Hylobates*, M.1 tends to be the largest of the series, and M.3 may be fully as quadrate in outline as the preceding molars.

The most striking feature in which the mandible of *L. legetet* differs from that of *Hylobates*, is the great depth of the horizontal ramus, and the sharp angle at which the ascending ramus rises. Moreover, the lower margin of the ramus is very slightly concave, and the depth is almost equal at either end, whereas in the recent form the lower border of the ramus is convex, and the depth increases appreciably from front to back. These points seem to suggest that *L. legetet* is a more primitive animal, if the low horizontal ramus, and wide angle of the ascending ramus be regarded as indicative of specialization. In these respects *L. evansi* is somewhat more similar to *Hylobates*.

The mandible of *Limnopithecus* compares more favourably with that of *Propliopithecus* Schlosser, from the Oligocene of the Fayum. The latter is a rather smaller animal, but the relative depth of the horizontal ramus is very similar. The teeth, however, differ in certain respects; the breadth index is higher, the cingulum less developed, and the hypoconulid more central in position in the earlier form. In comparison with *Pliopithecus* Gervais, these new specimens are rather smaller, and the depth of the mandibular ramus is relatively greater, while the teeth, with the exception of M.3, are very similar. The latter tooth is more elongate in the African form, whilst in the European genus the posterior end of the tooth is more square.

SUMMARY.

Comparison with these other genera suggests that *Limnopithecus* might well have been derived from the Fayum anthropoid *Propliopithecus,* but that it was probably not in the direct line to *Pliopithecus.* It seems possible that the three genera *Limnopithecus, Pliopithecus* and *Prohylobates,* may represent contemporary (Miocene) stages in divergent lines of development from the *Propliopithecus* stock. If the original form spread from the source of origin into other parts of the world, the migrating descendants would probably continue to develop along different lines, according to their different climatic conditions. Thus it would come about that at any given stage, representatives of the original stock taken from different geographical positions, would show varying combinations of primitive and specialized characteristics.

Xenopithecus koruensis Hopwood ?

TYPE LOCALITY.

Koru, Kenya Colony.

MATERIAL.

A single upper molar (Plate 23. Fig. 12) and some mandible fragments from Rusinga and Songhor (Plate 23. Figs. 7—11).

REMARKS.

The identification of this material is somewhat doubtful and should be regarded as only provisional. The specimens are distinguished from *Limnopithecus* on account of their larger size, but they are clearly too small for *Proconsul.* The presence of only one upper molar is unfortunate since it renders adequate comparison with the type of *Xenopithecus* impossible. In addition, there is no definite association between the one upper tooth and the lower teeth, and they can only be grouped together by reason of their size. The upper tooth appears to be M.1 in which case it agrees fairly closely in size with the corresponding tooth of the type specimen. Certain differences of structural details are, however, apparent, and it is possible that when more complete material is available this example will prove to represent a different species. The lower molars are mostly in a poor state of preservation with the exception of a mandible fragment recently discovered by Dr. Leakey, and in any case it is impossible to make direct comparison, since the lower molars of *Xenopithecus* have not yet been described. The specimens appear to be approximately the size one might expect for the latter genus, and until further material is available it would be undesirable to make any distinction.

DESCRIPTION.

Right upper M.1 ? (Plate 23. Fig. 12).

This tooth is slightly-worn and very low-crowned. The primitive trigon is very distinct, with clearly-marked crests joining the three cusps. The internal surface of the protocone is somewhat worn, but it does not appear that the two ridges noticed by Hopwood in the first molar of *Xenopithecus* were ever present. In other respects the tooth answers Dr. Hopwood's description of the type specimen fairly closely. At the antero-external angle of the protocone a double crest is present, the anterior arm of which is derived directly from the protocone and slopes down to unite with the anterior cingulum. The posterior arm is less clear and appears to be an offshoot of the paracone. The postero-external crest of the protocone is directed diagonally across the tooth to the metacone and is equally derived from each cusp. A small crest uniting the protocone with the hypocone is apparently derived from the latter. On the external surface of the tooth a crest connects the paracone and metacone, which is equally derived from both cusps. In the valley between the metacone and hypocone a longitudinal crest is present which is apparently an offshoot of the postero-external crest of the protocone. The cingulum is present all round the protocone, and also between the two principal cusps on all four sides of the tooth, producing four foveae. The protocone, metacone and hypocone are subequal in size while the paracone is rather smaller.

The measurements of this tooth, in millimetres, compared with those of M.1 in the type specimen, are as follows:—

	Length.	Breadth.	Index.
Rusinga M.1 ...	7.0	8.1	116
Koru M.1 ...	6.8	8.3	122.1

Mandible.—A fragment of a right horizontal ramus from Rusinga has parts of Pm.4, M.1 and M.2 in place, but most of the enamel has been lost and the structure, therefore, cannot be determined. The bone of the ramus is relatively rather less deep than that of *Limnopithecus* and is slightly stouter. The mental foramen is single and is again situated below the interval between Pm.3 and Pm.4. The ascending ramus begins to rise at the level of the anterior part of M.3, but it rises more gradually, and the line is not continued by an external U-shaped ridge as in *L. legetet*. The simian pit is shallow and the groove at the base of the internal surface is almost absent.

The measurements of this specimen, in millimetres, are as follows: —

Depth of ramus at Pm.4	22
Depth of ramus at M.1	22
Thickness of ramus at M.1	9

Another mandible fragment from Songhor (Plate 23. Fig. 8), which is provisionally assigned to this species, shows the whole of the symphysial area, but no teeth are present. The posterior point of the symphysis lies below the interval between Pm.3 and Pm.4, and is above the simian pit. The latter is very deep, and its lower margin, which is also the lowest point of the symphysis, is well in advance of the upper margin when the specimen is set with the alveolus horizontal. This lowest point is produced downwards into a distinct tubercle. From the upper border of the simian pit, the symphysis slopes upwards in a straight line to the incisor root-cavities. Anteriorly, the line of the symphysis is a gradual curve from the alveolus to the basal tubercle, the general line making an angle of about 55° with the alveolus. The mental foramen in this case is situated below the C.-Pm.3 interval.

The measurements of the specimen, in millimetres, are as follows: —

Depth of ramus at Pm.4	22.0
Thickness of ramus at M.1	10.0
Length of symphysis (I.1—basal tubercle)	27.3
External breadth at canines	24.7

Root cavities.	C.	I.2.	I.1.	I.1.	I.2.	C.
Length ...	9.0	6.0	5.1	4.8	6.0	8.5+
Breadth ...	6.0	3.1	3.0	2.9	3.5	6.0

Dentition.

A fragment of left horizontal ramus from Songhor (Plate 23. Fig. 10) has Pm.3—M.1 in place in a somewhat damaged condition. The anterior part, and the apex of Pm.3 are missing, but the tooth appears to have consisted of a large central cone and a very small talonid. The posterior wall of the main cusp shows a slight vertical groove which suggests that there was a tendency for the tooth to be bicuspid. The long axis of the tooth is sharply oblique to the axis of the tooth row as a whole, sloping forwards and outwards from the postero-internal angle.

Pm.4 is also damaged anteriorly, but it appears to have been more distinctly bicuspid, though less so than the corresponding tooth of *Limnopithecus*. The external cusp is the larger, while the internal cusp is little more than a subsidiary tubercle of the main cusp. Parallel posterior crests slope down from each cone to the cingulum at the posterior end, enclosing a fairly deep talonid basin. Anteriorly, the cingulum is also developed into a small shelf. The long axis of the tooth is again oblique, but less so than that of Pm.3.

The first molar of this specimen is damaged at either end, but it is clear that it was composed of the usual five cones, with the hypoconulid in an almost median position at the posterior end. The cingulum is well-developed except on the internal margin.

Another example of left horizontal ramus (Plate 23. Figs. 9 and 9A) has the two premolars fairly well-preserved. Pm.3 is very oblique, the long axis making an angle of 55° with the line of the ramus. The apex of the protoconid is slightly damaged, but the tooth appears to have been monocuspid, with perhaps a very small trace of the metaconid. From the apex, a single anterior crest passes down to the well-developed anterior cingulum, while a postero-external crest continues the line of the anterior crest backwards to the postero-external angle. A third, more distinct crest from the protoconid to the postero-internal cingulum, encloses a small talonid basin. Pm.4 is bicuspid, the metaconid being slightly smaller than the protoconid, to which it is united by a well-defined transverse ridge. Anteriorly, from the apex of each of the principal cones, a ridge extends to the anterior cingulum, enclosing a distinct fovea anterior. Posteriorly, similar crests extend to the postero-external and postero-internal angles, enclosing a deep, concave talonid basin. The roots of the tooth are set even more obliquely in the alveolus than are those of Pm.3, and the longer axis of the tooth makes an angle of about 60° with the line of the ramus.

Another fragment of left horizontal ramus has Pm.4—M.2 in place (Plate 23. Fig. 11). The teeth in this case are complete, but seriously affected by weather action which has produced a severe pitting of the enamel. Pm.4 is very much more distinctly bicuspid than that just described, and is almost oblong in outline. The two cusps are separated by a deep groove and the cingulum is developed on all but the internal surface.

M.1 and M.2 show the usual molar structure with five cusps. The hypoconulid is median, and in M.1 extremely small. The cingulum is well-developed except on the internal border, and the enamel is very deeply wrinkled. This latter feature has probably been accentuated by the weathering. The breadth index of these teeth is distinctly lower than that of *Limnopithecus*.

Two very badly preserved fragments have the remains of the second and third molars in place, from which it can be seen that the hypoconulid of the third molar is again extended backwards, resulting in a somewhat attenuated appearance to the tooth. Much of the enamel is missing from both these specimens so that the details of structure are obscured.

The measurements, in millimetres, of all these lower teeth are as follows:—

	Pm.3.	Pm.4.	M.1.	M.2.	M.3.
Length ...	7.5	6.0	7.0	8.0	9.0
Breadth ...	4.0	4.5	6.0	6.5	6.5
Index ...	53	75	85	81	72

	Pm.3.	P.m.4.	Pm.4.	M.1.	M.2.	M.1.	M.2.	M.2.	M.3.
Length ...	8.6	7.0	6.0	8.0	9.0	7.0	8.0	8.0	7.5
Breadth ...	5.2	5.2	5.0	6.0	7.5	6.0	7+	10.0	8.0
Index ...	60	70	83	75	83	85	87	80	93

It will be seen from the table of measurements that there is a certain variation in the size and in the proportions of these teeth. It is possible that these differences will eventually prove to be of specific or even of generic significance. On the other hand differences in sex might account for the extent of variation which is found, since the material may be divided approximately into two groups, one of which shows distinctly more slender structure than the other. [In the table these groups are shown with the more slender above, and the more massive (male ?) below.] On the evidence of such badly preserved material, I am inclined to adopt the latter view, since any specific separation would necessarily be based upon an exceedingly imperfect type.

The poor condition of these specimens renders any critical comparison with other forms a matter of great difficulty. The teeth are larger than those of *Propliopithecus,* and comparison with figures shows that Pm.3 is relatively larger and more simple. Pm.4 has a larger talonid, and the molars show an increase in size from before backwards, while those of the latter genus are subequal. The structure of Pm. 3 appears to be a primitive character, while the other features seem to show a greater specialization.

It is possible that *Xenopithecus* represents another offshoot of the *Propliopithecus* stock, but there is still insufficient evidence on which to base such conclusions.

Since the above was written, an additional mandible fragment has been recovered from Rusinga Island by Dr. Leakey, in September, 1942. Pm.4—M.3 of the left side are preserved, and, unlike any of the other teeth already assigned to this species, the enamel is in excellent condition (Plate 23. Figs. 7 and 7A).

Structurally, these teeth appear to be essentially similar to those already described, but the poor state of preservation of the latter renders exact comparison impossible. In size and proportions the teeth do not agree, and it is possible that when

PLATE 23. All figures natural size.

Fig. 1. *Mesopithecus* sp. Right ramus of mandible. Lingual.
Fig. 1A. *Mesopithecus* sp. Right ramus of mandible. Occlusal.
Fig. 2. *Progalago dorae*. (Genotype.) Left ramus. Occlusal.
Fig. 2A. *Progalago dorae*. (Genotype.) Left ramus. Buccal.
Fig. 2B. *Progalago dorae*. (Genotype.) Left ramus. Lingual.
Fig. 3. *Limnopithecus legetet* Hopwood. Right ramus. Lingual.
Fig. 3A. *Limnopithecus legetet* Hopwood. Right ramus. Occlusal.
Fig. 4. *Limnopithecus evansi*. (Holotype.) Right ramus. Occlusal.
Fig. 4A. *Limnopithecus evansi*. (Holotype.) Right ramus. Buccal.
Fig. 4B. *Limnopithecus evansi*. (Holotype.) Right ramus. Lingual.
Fig. 5. *Limnopithecus evansi*. Left ramus. Occlusal.
Fig. 5A. *Limnopithecus evansi*. Left ramus. Lingual.
Fig. 5B. *Limnopithecus evansi*. Left ramus. Buccal.
Fig. 6. *Limnopithecus evansi*. (Paratype.) Occlusal.
Fig. 6A. *Limnopithecus evansi*. (Paratype.) Right lateral.
Fig. 6B. *Limnopithecus evansi*. (Paratype.) Left lateral.
Fig. 7. *Xenopithecus koruensis* Hopwood. Ramus of mandible. Left lateral.
Fig. 7A. *Xenopithecus koruensis* Hopwood. Ramus of mandible. Occlusal.
Fig. 8. *Xenopithecus koruensis* Hopwood. Symphysial area. Occlusal.
Fig. 9. *Xenopithecus koruensis* Hopwood. Left lower Pms. Buccal.
Fig. 9A. *Xenopithecus koruensis* Hopwood. Left lower Pms. Occlusal.
Fig. 10. *Xenopithecus koruensis* Hopwood. Fragment of left ramus with Pm.3-M.1. Lingual.
Fig. 11. *Xenopithecus koruensis* Hopwood. Left lower Pm.4-M.2. Occlusal.
Fig. 12. *Xenopithecus koruensis* Hopwood. Right upper M.1 ?. Occlusal.

PLATE 23.

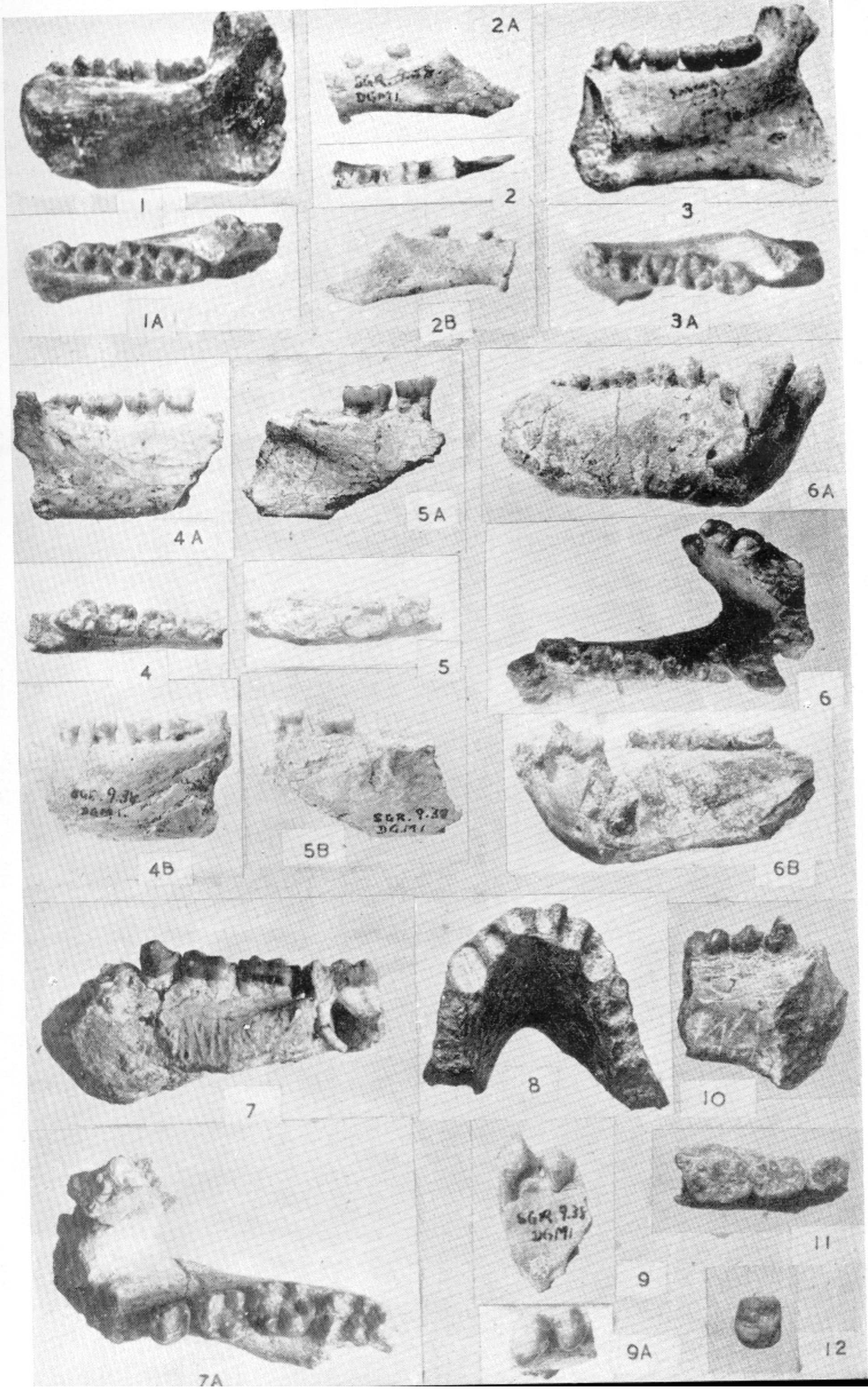

PLATE 24. All figures natural size.

Fig. 1. *Proconsul africanus* Hopwood. Palate.

Fig. 2. *Proconsul africanus* Hopwood. Left upper Pm.3-M.1.

Fig. 3. *Proconsul africanus* Hopwood. Right upper M.1.

Fig. 4. *Proconsul africanus* Hopwood. Left upper M.2.

Fig. 5. *Proconsul africanus* Hopwood. Right upper M.3.

Fig. 6. }
Fig. 7. } *Proconsul africanus* Hopwood. Associated upper and lower teeth.*

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*The left lower Pm.3 (Fig. 7) should probably have been set at more oblique angle, when the teeth were mounted in plaster.

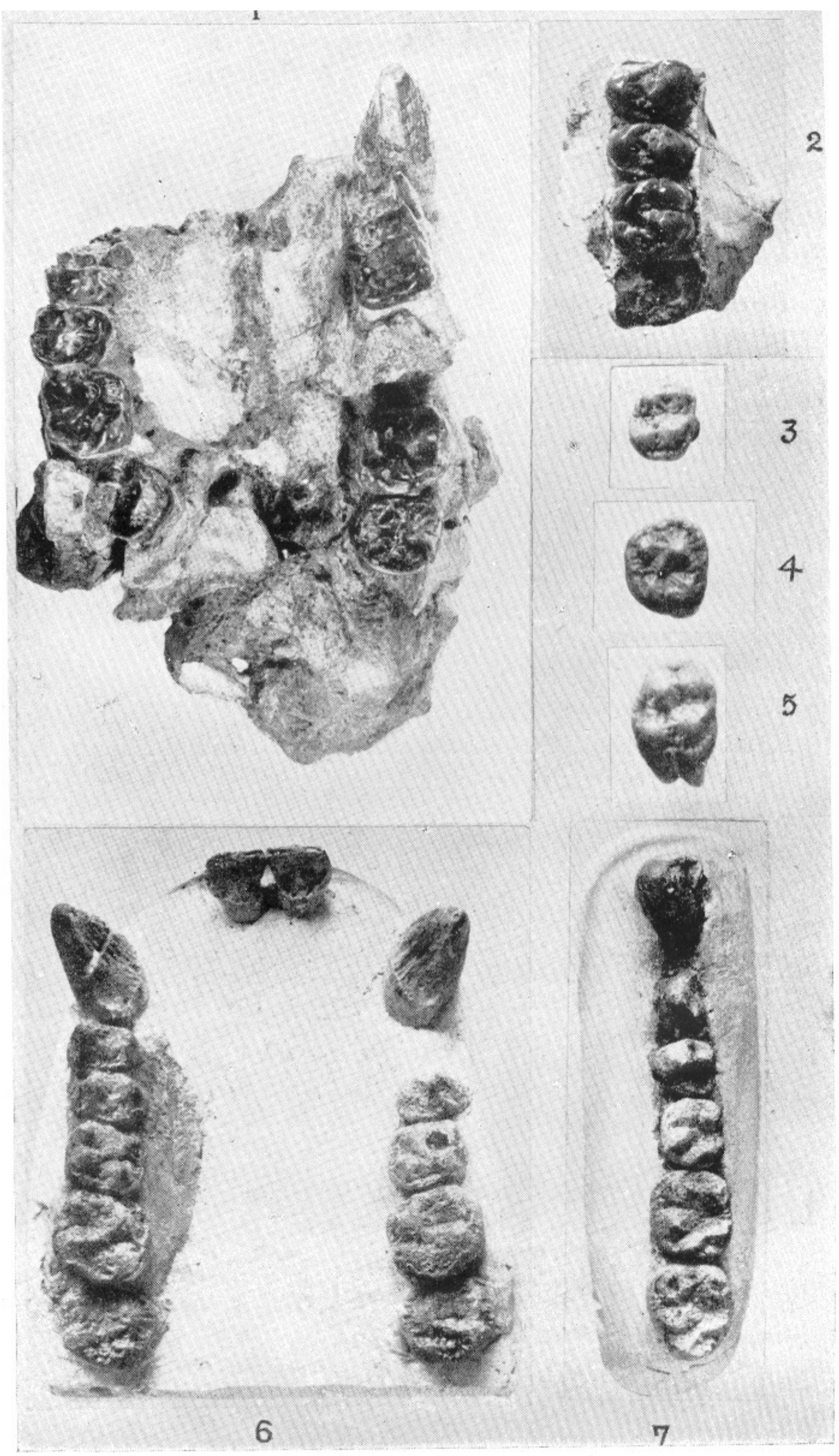
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PLATE 25.

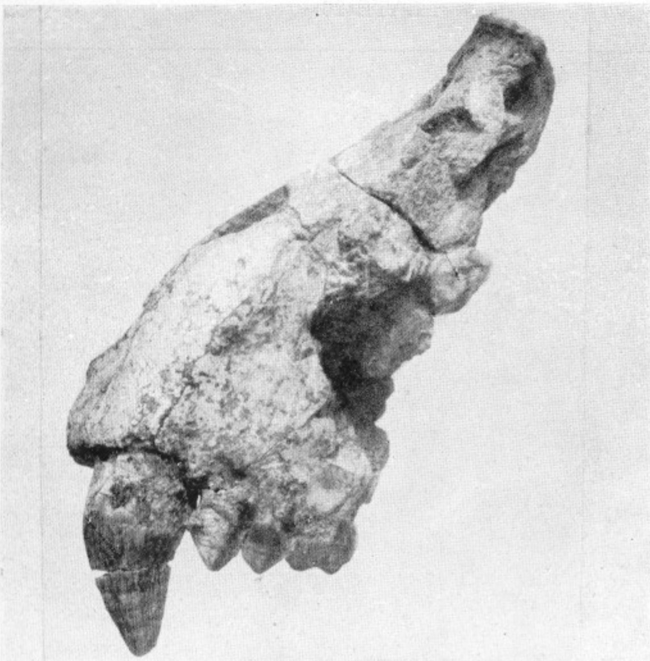


Fig. 1.

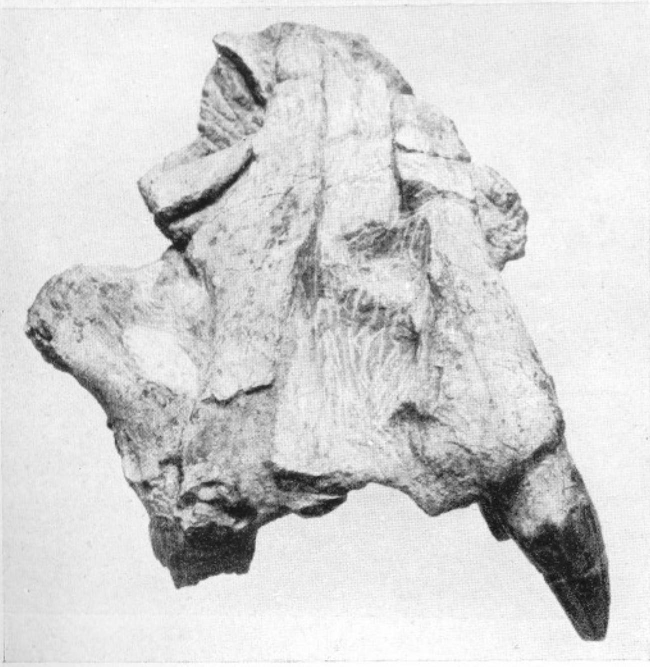


Fig. 2.

PLATE 25. Figures natural size.

Fig. 1. *Proconsul africanus* Hopwood. Facial fragment. Left profile.
Fig. 2. *Proconsul africanus* Hopwood. Facial fragment. Facial aspect.

PLATE 26.

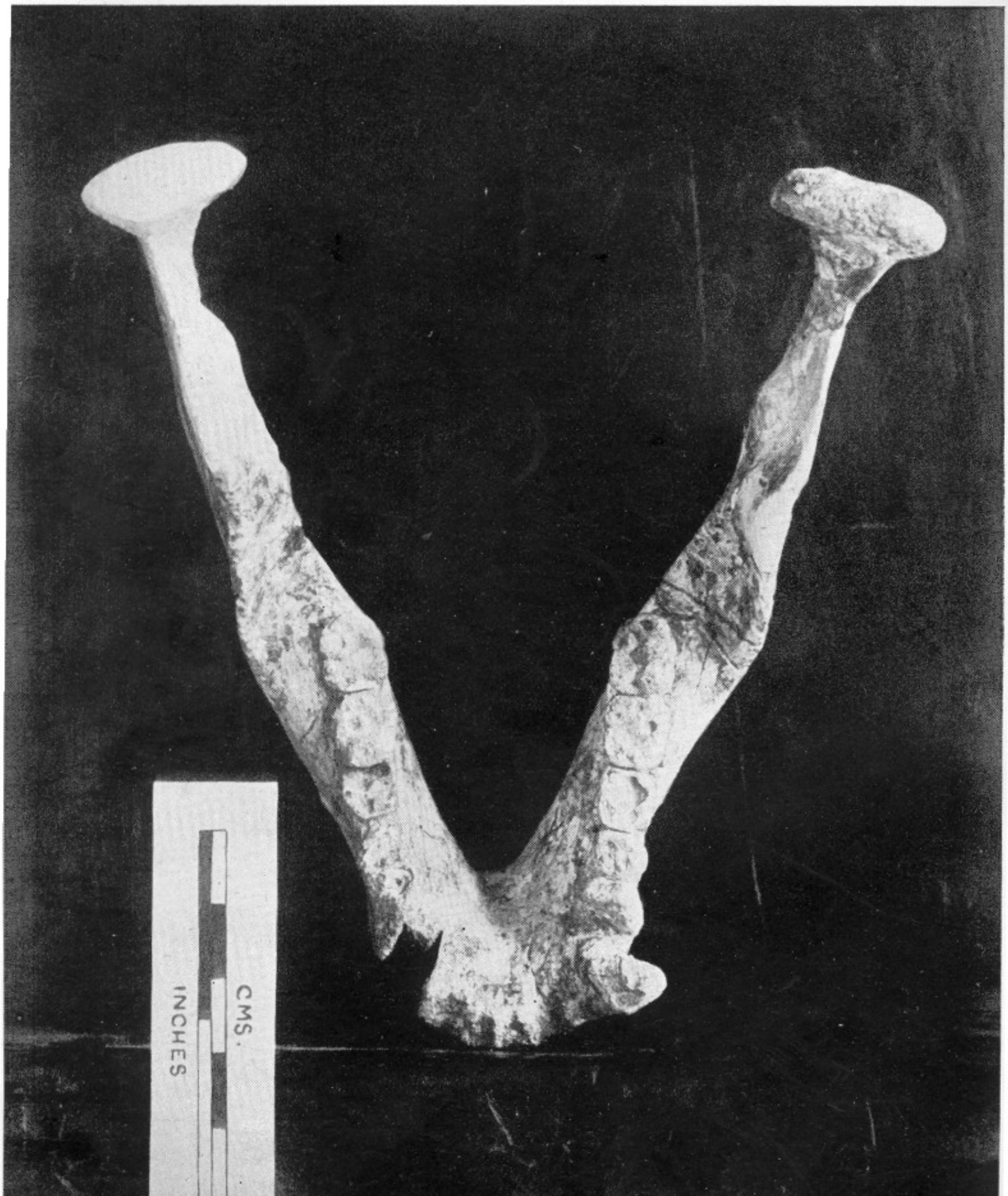
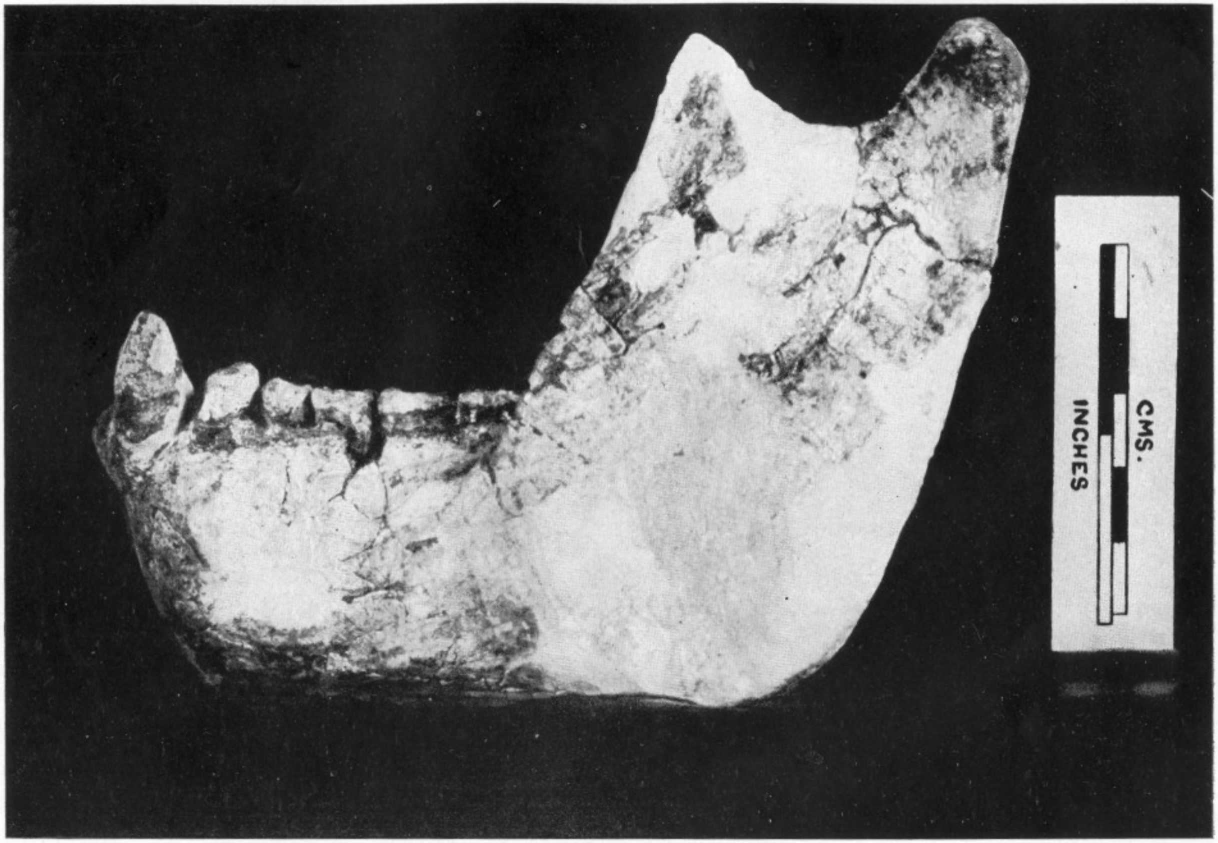


PLATE 26.
Proconsul africanus Hopwood. Rusinga mandible. Occlusal. Natural size.

PLATE 27.



FLATE 27. *Proconsul africanus* Hopwood. Rusinga mandible. Left lateral. Natural size.

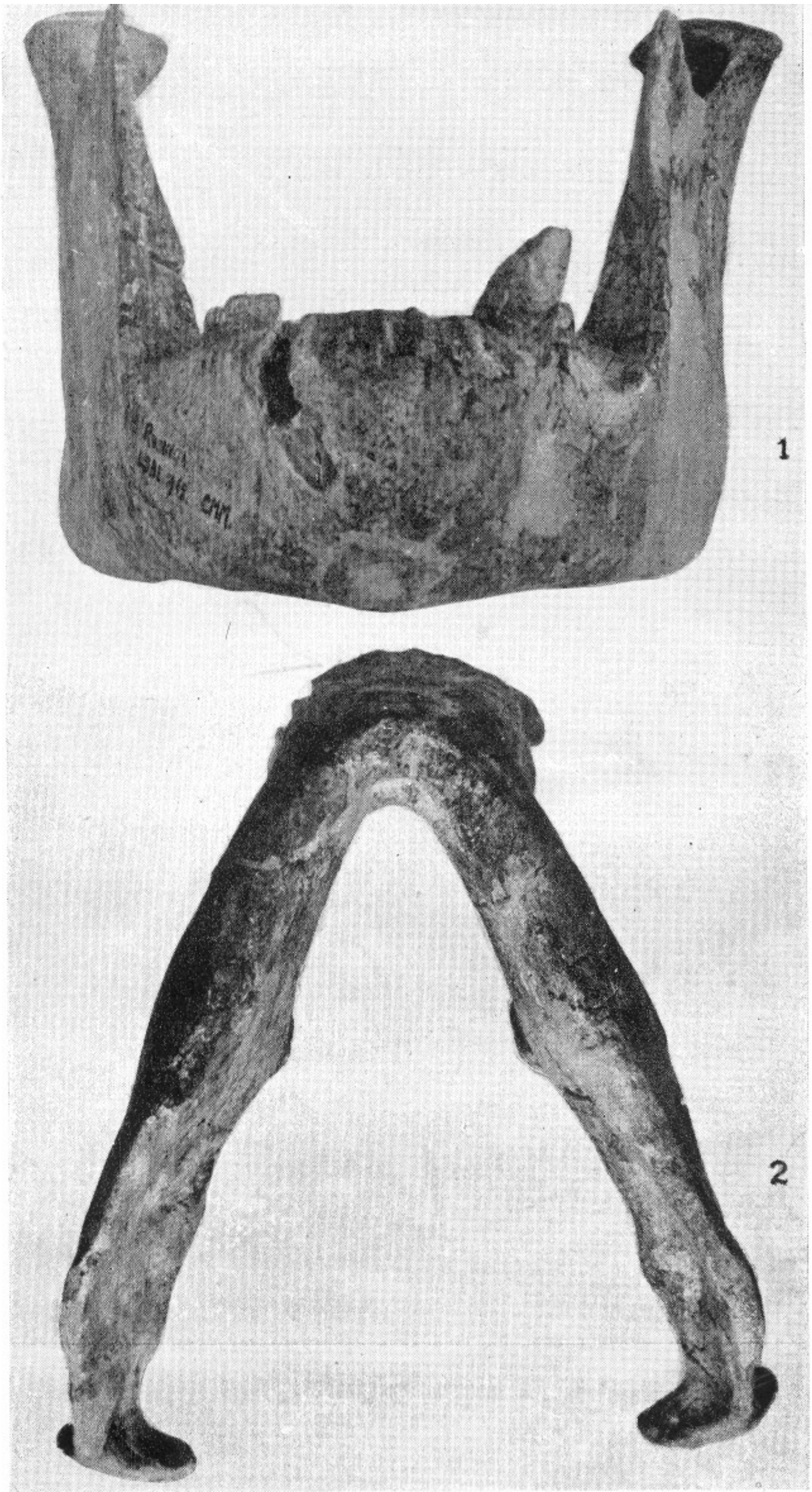


PLATE 28. Figures natural size.
Fig. 1. *Proconsul africanus* Hopwood. Rusinga mandible. Frontal.

more complete material is available, particularly of associated upper and lower dentition, it may be found necessary to separate this larger variety, at least specifically, from *X. koruensis*. On the basis of this single specimen, however, it is not considered advisable to found a new species, and for this reason the mandible in question is provisionally assigned to *Xenopithecus koruensis* Hopwood.

The fragment consists of the upper part of the left horizontal ramus, from M.3 on the left side, to the middle of the root of Pm.4 on the right side, thus including the greater part of the symphysis. The lower border of the ramus is nowhere complete, so that the total depth cannot be ascertained. Anteriorly, the alveolus is considerably eroded between the roots of the two canines, so that the true form of the symphysis is obscure. On the internal surface there is a deep simian pit, and it appears that below this a simian shelf extended at least to a greater degree than in *Proconsul*.

Pm.4 is markedly bicuspid, with the metaconid well-developed. The cingulum is not very clearly defined.

The structure of M.1 and M.2 is so similar to those already described, that no additional description is required. In M.2, the hypoconulid is perhaps slightly more external in position.

M.3 has lost a portion of the enamel of the outer side, so that the maximum breadth of the tooth cannot be determined with accuracy. The hypoconulid is set well back, and almost in the same line as the protoconid-hypoconid. The tooth is very slightly worn anteriorly, whilst the talonid is quite unworn, and the enamel shows considerable crimping. The crown is supported by two roots, the anterior of which carries the protoconid and metaconid. This root is almost vertical for about $\frac{2}{3}$ of its length, while the lower third curves sharply backwards. The posterior root shows a more gentle curve throughout.

The measurements of these teeth, in millimetres, are as follows:—

	Pm.4.	M.1.	M.2.	M.3.
Length ...	6.2	8.1	9.8	11.0
Breadth ...	6.0	7.2	8.3	8.3+
Index ...	96	88	84	75+

N.B.—The maximum breadth of the first and second molars is across the talonid.

Proconsul africanus Hopwood.

TYPE LOCALITY.

Koru, Kenya Colony.

MATERIAL.

A crushed palate and part of the facial region of a fully adult animal, in which the incisors, one canine and one premolar are missing. (Plate 24. Fig. 1. Plate 25. Figs. 1 and 2). Some associated upper and lower teeth of a single individual (Plate 24. Figs. 6 and 7). A juvenile mandible: a number of isolated fragments, including additional examples of upper and lower teeth (Plate 24. Figs. 2 to 5); and an almost complete mandible of a fully adult animal (probably a male) (Plates 26 to 28). The majority of this material was obtained from Rusinga Island. In addition, two tarsal bones from Songhor, and one from Rusinga, are also described as probably belonging to this species.

DESCRIPTION.

The palate and facial fragment has undergone considerable post-mortem deformation, but the greater part of the palate itself is complete. On the left side, the canine, premolars and first molar are undisturbed, while the second and third molars are displaced upwards for 30 mm. and 40 mm. respectively. The incisors are missing from both premaxillae. On the right side, the canine and Pm.3 are damaged; Pm.4 and M.1 are present and undisturbed; M.2 is displaced upwards about 5 mm., and M.3 is split longitudinally, the outer-half being twisted to face almost directly outwards, whilst the inner-half is forced upwards about another 10 mm. All the teeth are well-worn (Plate 24. Fig. 1).

On the upper surface, the premaxillary area is damaged, and it is impossible to determine the degree of prognathism. A very striking feature of the anterior view is the great length and relative narrowness of the nasal aperture and the nasal bones (Plate 25. Fig. 2). The base of the aperture seems to lie only just above the alveolus, but this may be partly due to the distortion. In profile (Plate 25. Fig. 1), the facial angle appears to be fairly steep, but again much may depend upon the distortion. The anterior part of the zygomatic arch has its origin very near the alveolar border over M.1. In another detached maxilla fragment, it is situated over Pm.4. The nasal bones are slightly displaced downwards by two parallel fractures which appear to follow the lines of the sutures. The two bones are fused together and have a flat surface with no median keel. If the two fractures are really along the lateral sutures as they appear to be, the bones themselves are even longer and more exactly parallel than those of the orang utang, and very considerably more so than those of the chimpanzee.

The teeth are severely worn, and will be described in greater detail from other specimens in which the structure can be more clearly seen. The premolars are bicuspid, the trigon of the molars is very distinct and the cingulum is well-developed. The canine is in closed series with the cheek teeth, while anteriorly a diastema of 5 mm. separates it from the socket of the lateral incisor.

The approximate measurements of this specimen, in millimetres, are as follows:—

Length of nasal aperture	37
Breadth of nasal aperture	19
Length of nasal bones	34
Breadth of nasal bones	10
Internal breadth of palate between canines ...	30
Internal breadth of palate between M.1 ...	34

Teeth (left side).		Length.	Breadth.	Height (external).
C.	...	15	12	24
Pm.3	...	8	11	11
Pm.4	...	6	11.5	8
M.1	...	9	11	6
M.2	...	12	13	6
M.3	...	11	14	6

Upper dentition.—I.1. The root and base of the crown of the first incisor is roughly trihedral in section, with a flat surface to the front. The apex of the crown is sharply constricted from front to back, the anterior surface being gently convex from above downwards, while the posterior surface is rather sharply concave, producing a flat chisel edge. The median surface shows a pressure facet produced by contact with the first incisor of the other side, which lies at right angles to the cutting edge of the tooth, while the outer angle of the cutting edge is more rounded. From each of these two angles a very distinct crest curves downwards, backwards and inwards, the two uniting posteriorly. From the middle point of the posterior surface a massive enamel buttress extends from the base of the crown to a point about half way to the cutting edge. The enamel is considerably wrinkled, particularly on the posterior surface.

I.2. The root of the second incisor is nearly oval in section, with the longer axis from front to back. The anterior surface of the crown is somewhat expanded laterally, and is gently convex from above downwards and also from side to side. On the posterior surface the convex form of the root is produced almost to the apex where it becomes flattened across the top and sides into a distinct flange. The cutting edge of the tooth is more rounded, and there are no posterior crests from the apex. The enamel is again considerably wrinkled.

The measurements of some of the incisors are given below in millimetres. The term length, as applied to these teeth denotes the maximum distance from front to back. Owing to the inward curve of the alveolus this measurement is at right angles to the line of the alveolus instead of parallel to it as in the cheek teeth. Similarly, the breadth measurement of the incisors is along the line of the alveolus instead of transversely across it. The term height denotes the maximum external enamel height of the crown.

	I.1.				I.2.
Length ...	7	7.5	7	7	4.5
Breadth ...	8	10	9.5	8.5	8
Height ...	10	11	11	12	9

Canine. The root of the canine is oval in section, with the longer axis from front to back. The crown consists of a single massive cone, with a sharp crest from the apex to the posterior point of the base. Anteriorly, a second, more rounded rib, extends to the anterior point of the base. On either side of this rib a distinct groove is present which produces a partial isolation of the rib itself from the main cone. The cingulum is well-developed at the base of the crown on the lingual side. The enamel shows extensive vertical wrinkling, particularly on the lingual surface.

Pm.3 is bicuspid, with a massive protocone and a smaller deuterocone. From the apex of the protocone crests extend to the antero-external and postero-external corners of the tooth. The deuterocone has similar crests which curve sharply across the tooth along the anterior and posterior surfaces, to unite with those of the protocone at the external corners. It is probable that these crests merge into the cingulum on the anterior and posterior surfaces, but the distinction is not apparent. The inner surface of the protocone, and the outer surface of the deuterocone, are considerably wrinkled, so that the valley between the two cusps shows a complex enamel pattern of irregular ribs and grooves. The external and internal surfaces of the tooth show a much finer wrinkling of the enamel.

Pm.4 is rather smaller than the preceding tooth, and is more nearly symmetrical about the longitudinal axis. The deuterocone is larger and the protocone smaller, so that the two cones are subequal in size. The same crests are present, but in this case the external extensions of those of the deuterocone are distinctly formed by the anterior and posterior cingulum. The latter is produced in a small shelf round the postero-internal surface of the deuterocone. The enamel is again coarsely ribbed in the valley between the cusps, while the outer and inner surfaces are more smooth.

M.1 is roughly square in outline, with four subequal cusps. The cingulum is developed in different degrees in all the specimens. In some it is present only on the anterior and posterior surfaces, and is entirely absent on the internal and external margins. In others it corresponds exactly to Hopwood's description of the type specimen, in which he says "the crown is surrounded by a beaded cingulum which is discontinuous at each of the angles except the antero-internal." In the first molars of the palate already described it is only discontinuous for a very short distance on the external surfaces of the paracone and metacone.

The cusps of the trigon are united by very distinct crests. From the apex of the protocone an anterior crest extends antero-internally, and merges with the cingulum at the middle point, of the anterior surface. A crest from the paracone is directed inwards to unite with the anterior crest of the protocone at its middle point. A second crest from the protocone is directed postero-externally towards the metacone, to meet an antero-internal crest from the latter cusp at the middle point of the tooth. The external crest, uniting the paracone and metacone, is also equally derived from either cusp. The hypocone is the largest of the four cusps and is practically isolated, but a faint crest affords a partial connection with the metacone, and bounds a small fovea posterior. A very slight projection on the anterior wall connects in wear with the postero-external crest of the protocone.

M.2 is larger and somewhat more rhomboidal than M.1 owing to the greater backward extension of the hypocone. The general structure of this tooth is almost identical with that of the first molar. The slight transverse crest is again apparent uniting the hypocone with the metacone. This can scarcely be traced in some of the more worn examples, but it is quite distinct in one unworn tooth. The cingulum shows the same varying degrees of development noticed in M.1.

M.3 is smaller than M.2 and is more rounded posteriorly owing to the great reduction of the hypocone and the partial reduction of the metacone. Most of the examples of this tooth in the collection are either greatly worn, or severely affected by weather action. A single unworn, and probably unerupted crown shows the same general structure as that of the preceding molars, with distinct crests uniting the three cones of the trigon. The enamel at the bases of the cusps is strongly crimped, and the cingulum, though weak on the external surface, is unbroken.

Amongst the upper molars a number of isolated examples are included (Plate 24., Figs. 2 to 5) which show distinct variation in size. In all the unworn examples, the crests uniting the cones of the trigon are more or less divided in the middle, especially those of the first and second molars. The unworn teeth also show a considerable crimping of the enamel both of the cingulum, and more particularly round the bases of the principal cusps. It appears that even a slight degree of wear eliminates most of the crimping, and also causes the crests of the trigon to appear more unbroken than is actually the case. The breadth of the premolars and molars exceeds the length in every case.

The measurements of the upper teeth, in millimetres, are as follows:—

	Right.				Left.			
	Lgth.	Bdth.	Hgt.	Ind.	Lgth.	Bdth.	Hgt.	Ind.
Associated upper teeth—								
C. ...	14	11	20	78	14	10.5	19	75
Pm.3 ...	8	10.5	11	131	—	—	—	—
Pm.4 ...	7	10.5	7	150	7	10	6.5	143
M.1 ...	10	11	6	110	9.5	11	5	115
M.2 ...	12.3	13	6	104	12	14	5	115
M.3 ...	11.5	13.5	5.5	117	11	14	5	127

	Length.	Breadth.	Height.	Index.
Left maxilla fragment—				
Pm.3	8.5	12	8	142
Pm.4	7	11.5	7.5	164
M.1	10	11	6	110
Associated right upper teeth—				
Pm.3	6.5	10	7.5	169
Pm.4	6	10	7	166
M.1	8	9.5	5	118
M.2	11	12	6	109
Isolated upper teeth—				
M.2	12	15.5	9.5	129
M.3	12	14.5	4	120

Lower dentition.—The lower dentition is less well-represented, and practically all the specimens have been subject to such extensive weather action that the smaller details of structure are lost.

Incisors. Only one example of a lower incisor is included which can with some degree of certainty be regarded as belonging to this species. This tooth is unerupted in the alveolus of a mandible fragment, and is clearly the second incisor. The crown is narrow, and flat on the inner surface. The anterior and posterior surfaces also are almost flat, and converge towards the apex to form a chisel edge. This specimen measures 11 mm. in height anteriorly, 6 mm. in length from front to back at the base, and 4 mm. in breadth across the cutting edge.

The canine consists of a single massive cone from the apex of which crests slope down to the antero-internal and postero-internal corners. Thus in transverse section the internal face of the crown is flat, while the remainder is rounded. A very faint vertical groove is present on the anterior surface. The cingulum is well-developed at the base of the internal surface, but it is absent elsewhere. The transverse section of the root is roughly triangular with rounded corners, having a flat surface to the front.

Pm.3 consists of a single somewhat caniniform cone, from the apex of which sharp crests slope down to the internal and posterior angles, whilst the antero-external angle is rounded. At the base of the antero-internal crest, there is a small tubercle apparently derived from the cingulum. In the middle of the postero-internal crest a distinct swelling is present, which probably represents the metaconid. The two posterior crests are separated by a deep groove. The base of the postero-external crest is slightly damaged, but it appears that a very faint trace of the hypoconid was present. The cingulum forms a posterior shelf which unites the bases of the two crests, and it is also developed on the anterior part of the internal surface. Anteriorly, the enamel is produced downwards on to the anterior root.

Pm.4 is bicuspid, the outer cusp being the larger. The talonid is well-developed and has a pronounced hypoconid and a smaller entoconid. The cingulum is developed at either end. The protoconid and metaconid have slight anterior and posterior crests, which extend anteriorly to the cingulum, and posteriorly to the hypoconid and entoconid respectively. Transversely, they are united towards their bases to divide a small fovea anterior from the larger talonid basin.

M.1 is somewhat oblong in shape, with five cusps. The presence of a well-developed hypoconulid verifies Dr. Hopwood's view that this cusp was probably present in the first molar, although lost in all the examples originally described. The protoconid and metaconid are close together and are united by a transverse crest. The hypoconid is massive and isolated. The hypoconulid is almost in the middle line on the posterior border, and is united to the entoconid by a slight crest. The entoconid and metaconid are widely separated. The cingulum is developed between all the cusps except the entoconid and metaconid, on the internal surface. By analogy with the second molars it is possible that it was continuous round the protoconid, but the weathering is such that all trace of it at this point is lost.

M.2 is considerably larger and is relatively broader, with the five cusps arranged in the same manner. The crest between the hypoconulid and entoconid is much more distinct, and there is also a slight crest uniting the entoconid with the metaconid. The cingulum is present round the protoconid and between all the principal cusps except those of the internal margin.

M.3 is considerably narrower posteriorly, on account of the backward extension of the hypoconulid, which is practically in a straight line with the hypoconid and protoconid. In other respects the same general structure is retained. The cingulum again surrounds the protoconid and is faintly visible on the outer wall of the hypoconid. The crest between the entoconid and metaconid is quite distinct.

In all these lower molars the enamel of the basin enclosed by the five cusps is strongly crimped, as in the upper teeth. The outer surface appears to have been almost smooth. The length of the lower molars slightly exceeds the breadth.

The measurements of these teeth, in millimetres, are as ollows: —

	Length.	Breadth.	Height.	Index.
Associated lower teeth—				
C.	12	9.5	19	79
Pm.3	10	7	9	70
Pm.4	8	8	7.5	100
M.1	10	8.5	6.5	85
M.2	13	11	6	84
M.3	14	12	6	85
Mandible fragment—				
Pm.4	7	6.5	7	92
M.1	9	8	5	88
M.2	11	9.5	5	86
Mandible fragment—				
Pm.4	7	7	—	100
M.1	10	8	—	80

A juvenile mandible, which is in a very bad state of preservation, and which has lost most of the teeth, is included in the collection. Pm.4 is present on each side, the posterior-half of M.1 on the left, and M.2 on both sides. All the teeth anterior to Pm.4 are broken at the alveolar level. M.1 is fully erupted, while Pm.4 is a little below the same level, and thus appears to have been incompletely erupted. The posterior part of M.2 is still embedded in the alveolus, and the germ of M.3 can be seen in the crypt behind M.2 where the ramus is fractured. Another fracture in the region of the symphysis exposes the crown of the permanent canine deep in the alveolus. The fragment measures 49 mm. from the alveolar border between the first incisors, to the posterior margin.

A left horizontal ramus represents an older animal, though still apparently immature. Pm.4-M.2 are present, while posteriorly the socket for M.3 is visible, but the general condition of the bone and the absence of a posterior pressure facet on M.2 suggests that the last molar was incompletely erupted. The ascending ramus begins to rise at the level of the posterior part of M.2. Anteriorly, the fragment is fractured through the root of the canine which is very massive, but it is impossible to determine the backward limit of the symphysis. The mental foramen is single, and is situated below Pm.4 about 10 mm. above the lower margin of the ramus.

The measurements of this fragment, in millimetres, are as follows: —

Depth of ramus below Pm.3	29
Depth of ramus below M.2	24
Thickness of ramus at M.1	13

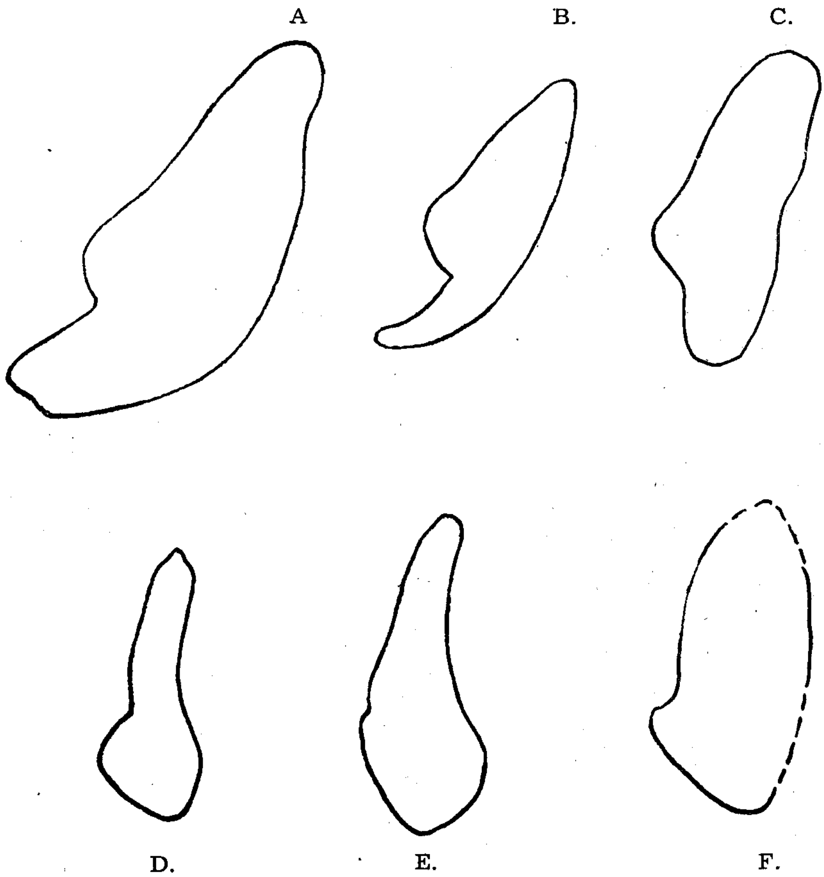
Another mandible fragment is very much more massive. The roots of the canine and the premolars are in place, but the crowns are lost. The canine root is very stout and almost vertical. The symphysis appears to have been very upright, with practically no backward extension. The mental foramen is below Pm.4, 12 mm above the base of the bone. Above it, on the external surface, there is a large shallow depression, so that in transverse section at M.1, where the specimen is fractured, the ramus curves sharply outwards towards the base. The depth of the ramus at Pm.3 is 40 mm.

A mandible discovered by Dr. Leakey on Rusinga Island, in September, 1942, is of particular importance, since it is the most complete fragment hitherto recorded of *Proconsul,* or indeed of any of the fossil examples of the great apes.

The preserved portions of the specimen are as follows: The condyle, a large part of the coronoid process, and some of the body of the left ascending ramus; the whole of both horizontal rami, including the canine and all the cheek-teeth of the left side, and the three molars of the right side; the symphysis, intact, and the anterior border of the right ascending ramus. The missing portions are the right condyle and coronoid, the bulk of the ascending ramus of that side, and the mandibular angles of both sides. The teeth are unfortunately severely affected by weather action, so that the finer details of structure are obscured, but it is clear that they are well-worn, and that the animal was fully adult.

The condyle measures 23 mm. transversely, by 10 mm. antero-posteriorly, with the long axis almost exactly at right angles to the general plane of the ramus. A sharp crest connecting the condyle with the coronoid, projects from the anterior edge of the articular surface at about 6.5 mm. from the external point. The general form is remarkably similar to that of the human condyle, and very different from that found in the few specimens of recent apes available for comparison. It is unfortunate that apparently no example of any simian condyle has hitherto been preserved as a fossil, so that the significance, or otherwise, of this feature cannot at present be determined.

The coronoid process appears to have been low, and rather close to the condyle, the apex being separated from the mid-point of the condylar articulation by a distance of 34 mm. The sigmoid notch is shallow, the lowest point being only about 13 mm. below a line connecting the apices of the condyle and coronoid, but since it has been necessary to reconstruct part of the latter, these observations cannot be regarded as exact. The anterior border of the ascending ramus appears to be almost parallel to the posterior border, but here again the latter is largely reconstructed, and thus not exact. The anterior border forms a sharp, straight crest from the apex of the coronoid process, to a point opposite the middle of M.3, and thence curves gently forwards as a rounded ridge, to merge into the corpus below M.2. The external surfaces of both horizontal rami show very distinct concavities below the Pm.3-M.1 areas, which tend to accentuate the rather massive ridge produced by the canine root. The exact position of the mental foramen is obscured on both sides. The anterior part of the symphysial area hardly projects beyond a line connecting the front part of the two canine ridges. Thus, externally, the two horizontal rami are united by a nearly flat symphysial area, forming distinct angles with the bodies, and not by a rounded curve (Plate 28. Fig. 1). There is practically no decrease in the depth of the corpus from front to back. The form of the symphysis is best shown by the diagramatic section (Text Fig. 1). .When set with the occlusal surface of the cheek-



Text Figure 1.

A.=Gorilla.
B.=Chimpanzee.
C.=*Proconsul africanus*.
D.=Modern African (Somali).
E.=Prehistoric African.
F.=Heidelberg mandible.

Text Figure 1.—Antero-posterior section through the mid-line of the symphysis of *Proconsul africanus* (C.), compared with similar sections of the modern Old-World Apes (A. and B.), and with those of three types of human mandible (D., E. and F.).

teeth horizontal, the most posterior point of the symphysis is the ridge above the simian pit, while the lower lip of the pit is almost vertical, and the simian-shelf wholly absent. This is a somewhat surprising condition for a primitive anthropoid, since the simian-shelf is much more pronounced in *Dryopithecus*, and even in *Eoanthropus*.

The measurements of the mandible, in millimetres, are as follows: —

Total length	121
Height of condyle	81
Antero-posterior breadth of ascending ramus (left side)	49
Vertical height of symphysis	38
Maximum length of symphysis	40.8
Depth of ramus at Pm.3	34
Depth of ramus at M.2	32
Depth of ramus at M.3	33
Length of tooth-row Pm.3-M.3	45.3
Length of tooth-row C.-M.3	58
Alveolar breadth at canine	35
Alveolar breadth at M.1	41.8
Alveolar breadth at M.3	49.8
Bicondylar width	112
Thickness of ramus at M.1	15
Condylar length	23
Condylar breadth	10

There is a distinct convergence of the Pm.-M. series from back to front, which is most clearly shown by the above measurements of the alveolar breadth (external) across the canines (35 mm.) and across the third molars (49.8 mm.).

Dentition.

Incisors. All the incisors are unfortunately missing, but it appears that they were fairly vertical.

Canine. The left canine is present, and nearly complete, but like all the other teeth, the enamel surface is severely eroded. The apex is damaged, but the tooth was certainly fairly low, probably projecting not more than 15 mm. above the alveolus. The cingulum appears to have been developed on the antero-internal border. The longer axis of the root-cavity lies at an angle of about 30° from the line of the symphysis. The canine is separated by small diastemata, both from the incisors and from the premolars, the former measuring 3 mm. at the alveolus, and the latter 2 mm.

Premolars. Only the left premolars are present, in which the details of structure are almost entirely obscured, but they appear to agree fairly closely with those already described. The longer axis of Pm.3 makes an angle of about 45° with the general line of the Pm.-M. series, whilst that of Pm.4 is slightly less oblique.

Molars. All the molars are present on both sides. M.1 shows considerable wear, that on the left side having a continuous lake of dentine, formed by the uniting of the metaconid, entoconid and hypoconid. M.1 of the right side reflects an abnormality which must have existed in the corresponding upper tooth. From a line connecting the extreme postero-internal point of the hypoconid to the posterior border of the metaconid, the whole of the posterior part of the crown is worn down at a sharp angle, the wear extending almost to the alveolus on the postero-external root. In structure, all the molars appear to resemble those already described in all essential features. The type of wear in the molars is perhaps of some importance, since they are all distinctly flattened, suggesting a somewhat lateral movement of the mandible in mastication, rather than the more vertical movement of the modern anthropoids. Another significant feature is that the greatest width of the first and second molars is across the talonid (entoconid-hypoconid) and not across the anterior lobe (protoconid-metaconid). According to Gregory and Hellman, this is a character which should indicate a development towards the human dentition.

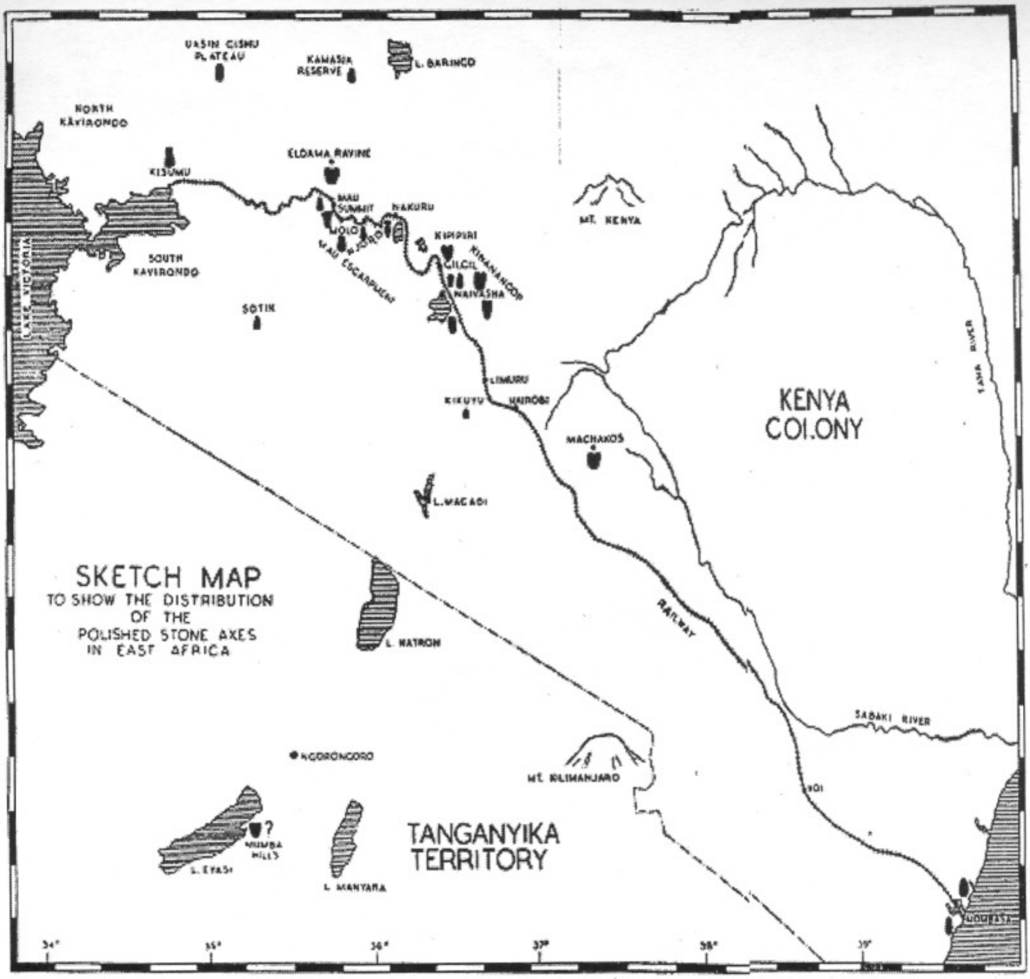
The tooth measurements are as follows:—

		Left side.			Right side.	
	Length.	Breadth.	Index.	Length.	Breadth.	Index.
I.1 ...	6.6	4.0	60	6.8	4.0	79
I.2 ...	7.4	4.5	60	8.0	4.5	56
C. ...	11.0	8.7	79	—	—	—
Pm.3 ...	8.9	6.6	74	—	—	—
Pm.4 ...	8.5	6.5	76	—	—	—
M.1. ...	8.7	8.0	92	—	—	—
M.2 ...	10.3	9.2	89	10.8	9.3	86
M.3 ...	12.3	9.2	74	11.6	9.5	81

N.B.—The incisor measurements are taken from the root-cavity at the alveolus in each case.

A significant feature of all the worn molars in this collection, is the nature of the attrition, which is remarkably flat throughout. This implies a grinding movement in mastication, which in turn suggests the presence of a distinct glenoid cavity and articular eminence—a character usually associated with the hominids, and regarded as more advanced than the condition found in the temporo-mandibular articulation of all the known members of the *Simiidae*.

In addition to the material already described, Dr. Leakey obtained at Songhor a right astragalus and os calcis of a single individual, and on Rusinga Island a left astragalus, all of which clearly belong to a large primate, and which are of a size approximately equivalent to *Proconsul*. At both these sites teeth were found which can definitely be attributed to this genus, and



SKETCH MAP
TO SHOW THE DISTRIBUTION
OF THE
POLISHED STONE AXES
IN EAST AFRICA
UASIN GISHU PLATEAU
KAMASIA RESERVE
L. BARINGO
NORTH KAVIRONDO
KISUMU
ELDAMA RAVINE
MAU SUMMIT
NAKURU
MOLO
NJORO
MAU ESCARPMENT
KIPIPIRI
KINANGOP
GILGIL
NAIVASHA
MT. KENYA
SOUTH KAVIRONDO
LAKE VICTORIA
SOTIK
LIMURU
KIKUYU
NAIROBI
MACHAKOS
KENYA
COLONY
TANA RIVER
L. MAGADI
L. NATRON
RAILWAY
SABAKI RIVER
NGORONGORO
MT. KILIMANJARO
VOI
MUMBA HILLS
L. EYASI
L. MANYARA
TANGANYIKA
TERRITORY
MOMBASA
34°
35°
36°
37°
38°
39°

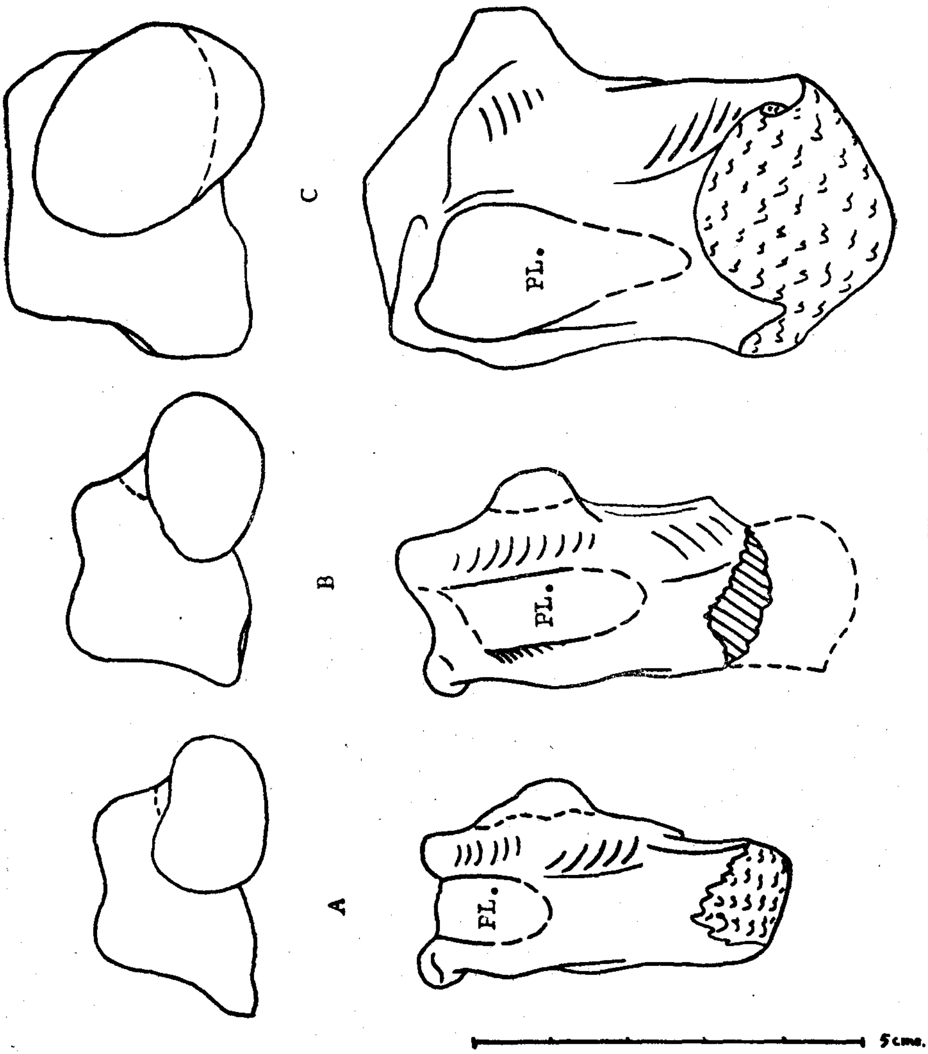
there can thus be little reasonable doubt that these bones are, in fact, the tarsals of *Proconsul*.

The upper surface of the astragalus has a large trochlear facet for the articulation of the tibia. This is convex from front to back, and concave from side to side, and it is slightly wider in front than behind. From the antero-internal angle of this facet the large rounded head projects obliquely forwards and inwards. The distal part of the head shows the articulation with the navicular, while the posterior part of the lower surface articulates with the calcaneum. The external part of the lower surface has an elongate facet which affords the principal articulation with the calcaneum. This is rather sharply concave from front to back, and it is separated from the lower facet of the head by a very deep channel. On the external surface a facet for the fibula is present, and internally another facet shows the point of contact of the internal malleolus of the tibia. The bone is only slightly compressed from above downwards, and expands in width towards the distal end.

By comparison with the astragalus of the chimpanzee, the most striking feature is the great depth of the body of the bone, and its relative compactness. The lower flange on the fibula side is relatively more massive and less extensive. The length of the head is rather greater than that of the modern animal which is distinctly a more primitive feature, but in other respects this bone appears to be almost intermediate between the chimpanzee and man, and it must, therefore, be regarded as more specialized than the former.

The tuber calcis of the calcaneum is broken, but it does not appear to have been very massive. The inner part of the upper surface has a large proximal facet which is oval in shape, and convex from front to back along the longer axis. This articulates with the astragalus, and is the converse of the large facet on the lower surface of that bone. On the anterior part of the upper surface a smaller facet is present which articulates with the lower part of the head of the astragalus. This is elongated longitudinally, hollowed at either side, and concave from front to back. The distal end of the bone shows a flat crescentic facet for articulation with the cuboid. The horns of the crescent are directed inwards, and between them the smooth surface of the facet curves over onto the inner surface of the bone.

The plantar surface is of particular importance since it shows a massive longitudinal ridge for the attachment of the plantar ligaments. This is very much larger than the corresponding region of the chimpanzee, which implies that the ligaments were stronger. In man, where these ligaments have to support a well-arched foot suitable for an erect posture, this ridge extends almost throughout the whole length of the bone.



Text Figure 2.

Text Figure 2 shows, above, the distal aspect of the right astragalus, and below, the plantar aspect of the os calcis from Songhor (B.), compared with similar aspects of these bones of chimpanzee (A.), and man (C.).

In view of Dr. Hopwood's suggestion that *Proconsul* is directly ancestral to the modern chimpanzee, the form of these tarsal bones is significant, if they are correctly assigned to that genus, for they appear to show a more hominoid, and, therefore, presumably a more advanced condition than would naturally be expected in any ancestral link.

DISCUSSION.

The teeth of this collection differ somewhat in their dimensions from those of the type specimen and other examples originally described by Dr. Hopwood. The variation of the breadth index cannot be regarded as a very reliable character, and in comparison of the relative sizes of the teeth in the two collections, we must take into consideration the sexual differences which might naturally be expected. Dr. Hopwood points out that his holotype is the maxilla of a very much smaller animal than that to which his mandible fragment belonged. Moreover, comparison of these Rusinga specimens with the original material shows that the mandible fragment of this collection corresponds almost exactly with the holotype, whereas the palate, and the group of associated upper teeth which clearly represent larger animals, occlude perfectly with the Koru mandible.

It will be seen from the table of measurements of the first specimen of *Proconsul* to be described in this paper (i.e., the palate and facial fragment), that the Pm.3-M.3 series must have measured approximately 46 mm. In the Rusinga mandible, this measurement is found to be 45.3 mm., which indicates that the two animals were practically identical in size. These measurements agree more closely with Dr. Hopwood's paratype than with the holotype, and for this reason both animals are regarded as being probably males. It is also clear that the distortion of the facial fragment has not materially affected the facial angle, which adds weight to the view that *Proconsul* was a remarkably short-faced animal.

Some associated lower teeth in this collection which clearly belong to a single individual correspond to the larger form, and may, therefore, be more directly compared with the teeth of the Koru mandible. The most striking difference is in the proportions of Pm.3 which is considerably shorter in the Rusinga specimen, though almost the same in breadth, resulting in a higher breadth index. Pm.4, on the other hand, is rather longer and narrower, so that the index is lower. M.1 and M.2 in the Rusinga specimen are again longer and narrower. These differences of dimensions are, however, relatively slight, whilst the more important structural characters of the Rusinga material are, on the whole, very similar to those originally described.

Consideration of these points, and in addition, of the fact that this new collection was obtained within a comparatively short distance of the type locality, seems to show that there is sufficient justification for regarding the differences of size, as characters of individual and of sexual significance rather than of generic or specific value.

The upper teeth of the larger, or male variety are very similar in size to those of *Dryopithecus* Lartet, but with regard to structure they differ in the same features referred to by Hopwood, namely, the strong cingula, the large hypocones, and the relative sizes of the cusps of the premolars. In the lower teeth, Pm.3 is relatively smaller, and shows the extension of the enamel on to the anterior root, which is a feature not found in any species of *Dryopithecus*. Pm.4 has a distinct hypoconid, and in the molars the anterior transverse crest is less pronounced. In M.3, the protoconid, hypoconid and hypoconulid are arranged almost in a straight line, and the cingulum is well-developed.

Dr. Hopwood distinguished the upper teeth of *Proconsul* from those of the gorilla on account of:—

(*a*) Their smaller size.
(*b*) The greater width and smaller length of the premolars.
(*c*) The greatly-reduced M.3.
(*d*) The pronounced cingula.
(*e*) The stronger crista transversa and crista obliqua.

These distinctions are equally applicable to the Rusinga specimens, and we may also add:—

(*f*) The more slender form of the first incisors.
(*g*) The lower and relatively stouter canines.

In discussion of the lower dentition, he pointed out that Pm.3 of *Proconsul*, in comparison with that of gorilla, was:—

(*a*) Smaller.
(*b*) Narrower.
(*c*) Shallower in the talonid basin.
(*d*) Less developed as regards the metaconid.

The last point does not apply to the Rusinga tooth, in which the metaconid appears to be as well-developed as that of the gorilla. The lower canine is again relatively lower and has a pronounced internal cingulum which is absent in the gorilla, while the lower molars differ in their smaller size, lower crown, and greater relative breadth.

Discussing the comparison with the chimpanzee, Dr. Hopwood gives the following list of characters in which *Proconsul* is found to differ in its upper dentition:—

(*a*) The anterior premolar is more caniniform.
(*b*) The premolars, especially Pm.4, are shorter.
(*c*) The molars have a prominent cingulum.

(*d*) The ridge joining the metacone and hypocone is present only in the first molar, and that tooth alone has a definite fovea posterior.
(*e*) The chimpanzee has the enamel more wrinkled.
(*f*) The entire premolar-molar series is cut at about the same time in *Proconsul*, whereas in the chimpanzee, the first molar erupts in the sixth year, and the third not before the fifteenth year (Zuckerman, 1928).

The Rusinga material agrees with the first three points, and shows, in addition, that the first incisors are more slender and that the third molar is very little smaller than the second, whereas in the chimpanzee, it may be considerably reduced. Point (*d*), however, does not apply to this collection, since the ridge connecting the metacone to the hypocone is visible in M.2, particularly in the unworn condition, while on the other hand, it does not appear to be a constant feature in the chimpanzee. With regard to the fifth point (*e*), some of the unworn teeth show a remarkable wrinkling of the enamel, but this feature appears in some cases to be obscured by quite a small degree of wear.

A fragment of maxilla has the third molar not quite completely erupted, though very nearly so, whilst the remainder of the teeth are in place, yet scarcely worn. This is in accordance with Hopwood's last point, that the entire premolar-molar series is cut at about the same time in *Proconsul*.

In the lower dentition represented by this collection, Pm.3 is a more slender tooth than that of the chimpanzee, and it is apparently more specialized on account of the greater development of the metaconid. Pm.4 is relatively narrower, and has both the hypoconid and the entoconid very much more distinct than the corresponding tooth of the chimpanzee. In the molar series of the fossil, M.1 is relatively smaller, and the two succeeding molars show a progressive increase in size, whilst in the existing genus they tend to be more nearly equal. This point is, however, a variable feature, and, therefore, not perhaps of very great significance. In consideration of the structure of the lower molars, it is found that the hypoconulid is more central in position, which must be regarded as an indication of the greater specialization of the fossil form.

From the foregoing discussion, it will be clear that there is at present no reason to separate this new material from *Proconsul*, since it agrees essentially both with Dr. Hopwood's original specimens, and also with the summary of the diagnostic characters as given by Gregory, Hellman and Lewis. For this reason all the *Proconsul* material described in this paper, although diverging in several respects from Dr. Hopwood's diagnosis of *P. africanus*, is, nevertheless, included in that species.

Owing to the present lack of comparative material, and also of literature, it is not proposed to enter into any detailed discussion, based on this material, on the relationship of *Proconsul* to other fossil examples of the great apes. Clearly, however, it is a somewhat generalized genus, in which a number of primitive characters are combined with some specialized developments. Amongst the latter, the following appear to be of some significance:—

(1) The short mandibular symphysis, and absence of the simian shelf.
(2) The reduced size, and high breadth index of the premolars and first molar.
(3) The increased width of the talonid in M.1 and M.2, which results in the maximum breadth being across the talonid.
(4) The shortening of the Pm.-M. series, indicating a relatively short-faced animal.
(5) The forward convergence of the Pm.-M. series.
(6) The flat type of wear of the molars, suggesting a somewhat human type of temporo-mandibular joint.
(7) The apparently hominoid development of the astragalus and os calcis.

This combination of characters appears to be incompatible with Dr. Hopwood's suggestion that *Proconsul* is in the direct ancestral line to the chimpanzee, since all the features enumerated show more of an approach towards the human condition than do the corresponding features of the modern animal. Gregory and Hellman express the view (*Ann. Transv. Mus.*, 1939, p. 350) that whereas Dr. Hopwood considered that *Proconsul* was "ancestral only to the chimpanzee," they regard it as "near to the stem of the entire ape-man stock" From this, it seems that they do not disagree fundamentally with Hopwood's view, but merely consider that *Proconsul* may have been ancestral not only to the chimpanzee, but possibly to many other genera as well. On the evidence of this new material, it seems unlikely that an animal which shows so many apparently hominoid characters, could have given rise to the modern genus, except by retrogressive evolution. Thus it becomes necessary to postulate either that the ancestral chimpanzee diverged from the common stock at a pre-Miocene date, or that the ancestral form which gave rise to *Proconsul* diverged at an earlier date, and happened to develop certain characters which we now regard as hominoid, whilst the main stem retained its more generalized characteristics, subsequently giving rise to the chimpanzee and other genera. The former hypothesis appears to be the more logical.

There is at present little material which is directly comparable with the South African genera, *Australopithecus,* Dart, *Plesianthropus* Broom, and *Paranthropus* Broom, and the evidence does not suggest any close affinities with them.

In conclusion, it would appear that this new material does not support the contention that *Proconsul* is directly ancestral to the chimpanzee, but rather suggests a position nearer to the main ancestral line from which man was ultimately derived.

It is perhaps of interest to note that all the three genera of East African Miocene *Simiidae* at present known, where mandibular fragments showing the lower part of the symphysis are preserved, appear to have a poorly-developed simian shelf. This is most marked in *Proconsul,* where the shelf is entirely absent. In *Xenopithecus* it is indistinct, while in *Limnopithecus,* although apparent, the shelf is less clearly developed than in most of the *Simiidae.* The significance of this characteristic cannot at present be assessed, but it would seem that if the modern African Apes were in any way derived from the Miocene genera, the simian shelf can only be a comparatively recent development.

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