Tertiary Pongidae of East Africa: Evolutionary Relationships and Taxonomy

David R. Pilbeam

Bulletin 31

PEABODY MUSEUM
OF NATURAL HISTORY
YALE UNIVERSITY

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BULLETIN 31 • DECEMBER 1969
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT

Bulletins published by the Peabody Museum of Natural History, Yale University, are numbered consecutively as independent monographs and appear at irregular intervals. Shorter papers are published at frequent intervals in the Peabody Museum *Postilla* series.

The *Peabody Museum Bulletin* incorporates the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication after Vol. 19, Article 2 (1967).

Editor: Jeanne E. Remington

Asst. Editors: Nancy A. Ahlstrom, editor of this volume
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Communications concerning purchase or exchange of publications should be addressed to the Publications Office, Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, U.S.A.

Printed in the United States of America

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ABSTRACT

Recently recovered pongid specimens of *Dryopithecus (Proconsul) major* from Moroto and Napak in Uganda are described and compared to material of the same species from Songhor and Koru in Kenya. This species is probably ancestral to *Gorilla gorilla.* Although smaller than the living species, with relatively smaller anterior teeth, less lophodont and hypsodont cheek teeth, shallower palate, less prognathous face, and without a simian shelf, *D. (P.) major* may already have been adapting to the predominantly herbivorous diet typical of the living species. *D. (P.) major* is found in deposits of Early Miocene age dated to around 18 to 20 million years. The species exhibits sexual size dimorphism similar to that shown by its putative descendant. It was a quadrupedal form, probably capable of arm-swinging like some of the Ceboidea.

A second species, *D. (P.) africanus,* from deposits at Songhor, Koru, and Rusinga, is related to *D. (P.) major* and may be ancestral to *Pan troglodytes.* The postcranial remains of *D. (P.) africanus* indicate that this was a lightly built, quadrupedal, mainly arboreal species with some adaptations suggesting arm-swinging behavior.

A third species, *D. (P.) nyanzae,* is discussed. It is the most primitive of the three species and may resemble closely the species ancestral to *D. (P.) major.*

The Late Miocene and Early Pliocene hominids from Kenya and India are described in detail, and it is concluded that they represent a single genus, *Ramapithecus,* and probably the same species. This taxon, although retaining some morphologically primitive features, resembles later hominids in the proportions of its incisors, canines, premolars, and molars, and in its shallow and robust mandible. Hominid species earlier than this are not definitely known, the material classified by Leakey as *Kenyapithecus africanus* being more probably a pongid, perhaps with some relationship to *Dryopithecus fontani* and *D. (Sivapithecus) sivalensis* of Eurasia.

The interrelationships of the living pongids, their Mid-Tertiary ancestors, and the Mid-Tertiary hominids are discussed, and it is concluded that the differentiation of hominids and pongids, and of individual pongid species, occurred earlier in time than is generally supposed.

ZUSAMMENFASSUNG

Neue entdeckte Pongid Exemplare der *Dryopithecus (Proconsul) major* von Moroto und Napak in Uganda werden beschrieben. Sie werden mit Material derselben Art von Songhor und Koru in Kenya verglichen. Diese Art ist wahrscheinlich ein Vorfahr des *Gorilla gorilla.* Obwohl kleiner als die heutige Art, mit relativ kleineren vordern Zähnen, weniger lophodonte und hypsodonte Backenzähne, flacherer Gaumen, weniger vorspringendes Gesicht, und ohne Torus transversus inferior, hat *D. (P.) major* viellicht schon angefangen sich an der vorwiegend pflanzenfressende Ernährung typish von heutige Art anzupassen. *D. (P.) major* wurde in unteren Miocänablagerungen gefunden, die ungefahr 18

bis 20 Millionen Jahre alt sind. Die Art zeigt einen geschlechtlichen Grössendimorphismus ähnlich dem seines vermeindlichen Nachkommen. Es war eine vierfüssige Form die vermutlich in der Lage war die Arme zu schwingen wie einige der Ceboidea.

Eine zweite Art, *D.* (*P*) *africanus,* der in Ablagerungen bei Songhor, Koru, und Rusinga gefunden wurde ist verwahnt mit *D.* (*P.*) *major* und mag eine Vorfahre der *Pan troglodytes* sein. Der hinteren Schädelreste von *D.* (*P.*) *africanus* zeigen dass dieser eine leicht gebaute, vierfüssige, meist auf Bäumen lebende Art war mit einigen Anpassungen, die ein Arm-schwingendes Verhalten vermuten lassen.

Eine dritter Art, *D.* (*P.*) *nyanzae,* wird erwähnt. Es ist die primitivste der drei Arten und mag der vorangehenden Art des *D.* (*P.*) *major* sehr ähnlich sein.

Die obere Miocän und untere Pliocän Hominiden aus Kenya und Indian werden im einzelnen beschreiben. Es wird daraus gefolgert dass sie eine Einzelgattung, *Ramapithecus,* und wahrscheinlich derselber Art darstellen. Obwohl dieser Taxon einige morphologisch primitive Eigenschaften behält, ähnelt es den späteren Hominiden in den Proportionen der Schneide-, Eck-, vordere Backen- und hintere Backenzähne und in seinem flachen und kräftigen Unterkiefer. Frühere Hominidarten sind nicht sicher bekannt. Das Material, das von Leakey als *Kenyapithecus africanus* klassificiert wird, ist vermütlich eine Pongid; etwas Verwahntschaft mit *Dryopithecus fontani* und *D.* (*Sivapithecus*) *sivalensis* von Eurasian ist vielleicht vorhanden.

Die Zusammenhängen der heutigen Pongiden, ihrer mitteltertiären Verfahren, und der mitteltertiären Hominiden werden erwähnt. Es wird deraus geschlossen dass die verschiedenartige Entwicklung von Hominiden und Pongiden, und von einzelnen Pongid Arten früher stattfand als allgemein vermütet wird.

РЕЗЮМЕ

Недавно выкопанные понгидные экземпляры *Dryopithecus (Proconsul) major* из Морото и Напака в Уганде описаны и сравнены с материалом, принадлежащим тому же виду, из Сонгора и Кору в Кении. Этот вид вероятно предок *Gorilla gorilla.* Хотя меньше живущего вида, с релятивно меньшими передними зубами, менее лофодонтными и гипсодонтными коренными зубами, менее глубоким небом, менее прогнатным лицом и без torus inferior transversalis, *D. (P.) major* мог уже приспособляться преобладающе травоядному образу питания, типичном для живущего вида. *D. (P.) major* находят в нижнемиоценовых отложениях; определено, что их возраст — 18-20 миллионов лет. Вид показывает половой диморфизм в величине, подобный тому показуемому его предполагаемым потомком. Он был четвероногим, и вероятно, способным передвигаться качаясь на руках, подобно некоторым Ceboidea.

Второй вид, *D. (P.) africanus,* из отложений в Сонгоре, Кору и Русинге, в родстве с *D. (P.) major* и может быть предком *Pan troglodytes.* Посткраниальные остатки *D. (P.) africanus* показывают, что это был вид легкого строения, четвероногий, преимущественно древесного образа жизни, с некоторыми приспособлениями наводящими на мысль о передвижении, качаясь на руках.

Третий вид, *D. (P.) nyanzae,* тоже рассматривается. Это самый примитивный из трех видов и может быть очень похожим на предка *D. (P.) major.*

Верхнемиоценовые и нижнеплиоценовые гоминиды Кении и Индии описаны обстоятельно и заключается, что они принадлежат одному роду, *Ramapithecus,* и вероятно, одному виду. Этот таксон, хотя он и сохраняет некоторые морфологически примитивные особенности, похож на поздних гоминидов размерами его резцов, клыков, премоляров и моляров, его неглубокой и толстой челюстью. О гоминидовых видах древнее этого не знаем определенно, так как материал, классифицированный Лики как *Kenyapithecus africanus* более вероятно является понгидом, возможно в какой-то форме родства с *Dryopithecus fontani* и *D. (Sivapithecus) sivalensis* Евразии.

Рассматриваются взаимоотношения живущих понгидов, их среднетретичных предков и среднетретичных гоминидов. Заключается, что дифференциация гоминидов и понгидов, а также индивидуальных понгидных видов, совершилась ранее чем это обычно предполагается.

CHAPTER I. INTRODUCTION

In a preliminary study, Elwyn Simons and I (1965) outlined the history of study of the various species of fossil pongids classified in the Dryopithecinae. One problem which concerned us was the great proliferation of specific names, many of which were based on the most fragmentary material. During the course of our analysis, it became clear that the number of valid names was rather small, certainly less than a dozen; these species could be accommodated comfortably in a single genus, *Dryopithecus*. We did not examine at any length the interrelationships of the various species of *Dryopithecus,* nor did we discuss in great detail the evolution of the living pongids from particular *Dryopithecus* species.

Thanks to the generosity of Dr. W. W. Bishop, and through the courtesy of Prof. E. L. Simons, a sample of pongid material from the Miocene of Uganda was made available to me for study. The detailed analysis of these specimens forms the core of this study and has required further work on the extensive series of pongids recovered from the Early Miocene of Kenya. The Ugandan material was classified originally as *Proconsul;* this genus was first diagnosed by Hopwood in 1933 (Hopwood, 1933a). Simons and I (1965) transferred species of *Proconsul* to *Dryopithecus,* and throughout this study these species are described as *Dryopithecus* (*Proconsul*).

The most comprehensive study of *D.* (*Proconsul*) species is to be found in the monograph by Clark and Leakey published in 1951. These workers expressed the opinion that *D.* (*Proconsul*) species were pongids and that many of the characters in which they differed from the living great apes were merely primitive and should not be used to exclude them from the Pongidae.

Leakey, however, no longer classifies these African Miocene species in the Pongidae, but has proposed a separate family for them, the Proconsulidae. He regards other *Dryopithecus* species as pongids. He has listed in recent publications some of his reasons for advocating a new family. "I have suggested the setting up of this family for certain ape-like fossil creatures which differ from the true Pongidae in lacking a simian shelf, in the structure of their canine teeth, in the position of the root of its molar-process maxillary [*sic*], in the absence of a torus, in the nature of their mandibular condyles and the way their teeth are arranged in the mandible, etc." (Leakey, 1963, p. 40). "By contrast to any living pongid, *Proconsul* has a rounded, smooth forehead and a low, rectangular orbit rather than a high, round one. In not just one but many specimens of four species, *Proconsul* has a relatively small canine with a molar-premolar series converging forward, as opposed to the backward convergence in pongids. . . ." (Leakey, 1965, p. 13).

Leakey therefore regards these species as belonging to a genus distinct from the genus *Dryopithecus* to which the Eurasian species belong. He also believes that the species of *D.* (*Proconsul*) are fundamentally very similar to one another. The present study involves an examination of new material of *D.* (*Proconsul*) *major* and a comparison of this material with other *D.* (*Proconsul*) species; it shows that the subgenus is by no means as homogeneous in some features as Leakey has suggested.

Further specimens of *Dryopithecus* from East Africa distinct from *D.* (*Proconsul*) have been described by MacInnes (1943) and by Clark and Leakey (1951). Clark and Leakey placed these specimens in *Sivapithecus africanus,* a species transferred by Simons and myself (1965) to *Dryopithecus.* Leakey (1967) has since proposed that these specimens, together with other newly described individuals, constitute a new species within the Hominidae. A detailed analysis of Leakey's paper and of the material indicates that this allocation is dubious and that the East African specimens are better classified at the moment in *Dryopithecus.*

The interrelationships of the African *Dryopithecus* species are discussed, as well as the light they throw on the evolution of the African great apes. Their relationship to Eurasian species of *Dryopithecus* and to the earliest hominid, *Ramapithecus punjabicus,* is also examined in some detail.

ACKNOWLEDGEMENTS

Grateful thanks go to the Curator and Trustees of the Uganda Museum for permission to study material in their collections. I should like to thank the following for allowing me access to material under their care: Drs. L. S. B. Leakey, J.-P. Lehmann, J. Biegert, K. P. Oakley, M. Crusafont Pairo, M. C. McKenna, and E. L. Simons. I am most grateful to the following for their advice and help: Drs J. C. Cutbill, D. B. Williams, E. H. Ashton, W. W. Bishop, A. H. Schultz, C. P. Groves, J. R. Napier, B. G. Campbell, and A. C. Walker. Mr L. P. Morley and Rosanne Pilbeam took some of the plates; some were kindly loaned by Sir W. E. Le Gros Clark, others by Dr E. L. Simons and Dr A. C. Walker. Graphs, tables, and figures were drafted by Rosanne Pilbeam. The research was carried out during tenure of Fellowships from the Graduate School of Yale University, and the Wenner-Gren Foundation; a grant was also received from the Boise Fund of Oxford University. This Bulletin has been published with the aid of a National Science Foundation Publication Grant No. GN-475.

Finally, I should like to thank Rosanne Pilbeam, whose help as typist, draftswoman, photographer, and general editor has made the completion of this dissertation possible; and Elwyn Simons, my friend and supervisor, who has guided me through the evolutionary biology of the higher primates and who has made the work involved so enjoyable.

CHAPTER II. MATERIALS AND METHODS

To make a meaningful contribution, adequate comparative material is essential in a study of this type. Since this is predominantly a study of African fossils, the living African apes have been selected for the comparisons. Samples were measured of both sexes of Western gorillas, subspecies *Gorilla gorilla gorilla* (Groves, 1967), and of the chimpanzee subspecies *Pan troglodytes troglodytes.* These are generally referred to as *G. gorilla* and *P. troglodytes* in the text, tables, and appendices. The measurements on their skull and dentitions are included in Appendix I. Some statistics such as means, ranges, standard deviations, and so forth, are available in the literature (Schuman and Brace, 1954; Ashton and Zuckerman, 1950), but more of this sort are included here. However, it is difficult to gain access to raw data and so the measurements used in this study are included in full. Other workers may then calculate, for example, their own indices, correlation coefficients, and regression coefficients, as well as any other statistics they may require.

MEASUREMENTS

Dental and mandibular measurements were taken on 20 male and 20 female gorillas and 14 male and 12 female chimpanzees. Palatal and facial measurements were taken on 20 male and female gorillas and 10 male and female chimpanzees. The facial measurements are either self-explanatory or are explained in the text. Specimens came from the Anthropologisches Institüt der Universität, Zurich; British Museum of Natural History, London; Anatomy Museum and Duckworth Laboratory of Physical Anthropology, Cambridge, England; and the Museum of Comparative Zoology, Cambridge, England.

Dental measurements and their abbreviations are explained below; they were taken to the nearest tenth of a millimeter with engineer's straight-jaw vernier calipers with specially sharpened points. All measurements are in millimeters unless otherwise stated. Good estimates of measurements are marked with one asterisk; poor estimates are marked with two asterisks.

Generally, two basic measurements are given for each tooth, a length and a breadth. The length is usually mesiodistal and is measured between the midpoints of the mesial and distal borders with the calipers held vertical to the occlusal plane. Canines and first lower premolars have maximum lengths. First upper premolars have both a mesiodistal and a maximum projected length. Breadths are measured normal to lengths and are projected; they are termed transverse in the case of canines and lower first premolars, labiolingual for incisors, and buccolingual for upper premolars and molars. These breadths are maxima. Lower second premolars have buccolingual breadths. They also have trigonid and talonid lengths, measured from the midpoint of the talonid basin to the mesial and distal margins. Lower molars have three breadths: trigonid, talonid, and maximum. Heights are measured from the midpoint of the enamel line labially or buccally to the tip of the crown or the midpoint of the occlusal surface or edge.

Certain bilateral measurements have been taken on the tooth row as a whole. Four breadths are listed; between the distal alveolar margins of upper and lower lateral incisors (I^1B and I_1B), and on the crown across canines, second premolars, and third molars (C^1 B, C_1 B; P^4 B, P_4 B; M^3 B, M_3 B). The length of the cheek tooth row from the mesial border of the first premolar to the distal border of the third molar was also taken (P^3–M^3 L, P_3–M_3 L).

The depth of the mandible from the alveolar margin is measured at the mesial margins of the second premolar and third molar (P_4 D, M_3 D). Where possible, mandibular thickness normal to the long axis of the cheek teeth is taken at the mesial border of the second premolar (P_4 T), and at the mesial border of the third molar (M_3 T). The depth of the mental foramen is measured below the alveolar margin (Ment for D).

A maximum of 18 measurements could be taken on upper jaws and teeth and 28 measurements on the lower. As complete a set of measurements as possible was taken on each fossil; extra measurements other than those listed here are explained in the text. Abbreviations for museum numbers are also included here.

ABBREVIATIONS

L	length
B	breadth
H	height
D	depth
T	thickness
MDi	mesiodistal
La	labial
LaLi	labiolingual
Li	lingual
BuLi or BLi	buccolingual
Tri L	trigonid length
Tri B	trigonid breadth
Tal L	talonid length
Tal B	talonid breadth
I	incisor (I^1 = upper incisor, I_1 = lower incisor)
C	canine (C^1 = upper canine, C_1 = lower canine)
P	premolar (P^3 = first upper premolar, P_4 = second lower premolar)
M	molar
dP	deciduous premolar
MNHN	Muséum National d'Histoire Naturelle, Paris
UMP	Uganda Museum, Kampala
BM(NH)	British Museum of Natural History, London
NMK	National Museum Centre for Prehistory and Palaeontology, Nairobi, Kenya
YPM	Peabody Museum, Yale University, New Haven, Conn.

GSI	Geological Survey of India, Calcutta
AMNH	American Museum of Natural History, New York
CGM	Cairo Geology Museum, Cairo

The object of taking morphological measurements is to reflect the genotypic variability in the population. Measurements for bilaterally symmetrical structures are taken on one side of the jaw only; there is no extra information to be gained from taking the length of M_3, for example, on both sides of the jaw, since both teeth are "reflections" of the same genotype. Any differences in size are phenotypic, and statistically speaking can be ignored (Ashton and Zuckerman, 1950, p. 474). Similarly, if statistical constants are calculated for living or fossil populations, pairs of teeth from opposite sides of the same jaw should not be included, since this will mean that one genotype is sampled twice and will therefore bias the calculations.

Measurements can also be altered by wear, weathering, and by compression from adjacent teeth. These are dentally non-genotypic factors. Although the degree of compression, for example, may be an interesting phenomenon and one which should be studied, such factors ought, as far as possible, to be ignored. Attempts have been made here to compensate for tooth wear, rotation, and other variables, thus reproducing best estimates of the measurements of the tooth as it was when newly erupted. Estimates of this sort are also marked with an asterisk.

UNIVARIATE STATISTICS

The standard univariate statistics have been calculated from the gorilla and chimpanzee samples. Calculations were performed on the Titan Computor in the University Mathematical Laboratory at Cambridge University, using a program written by Dr. J. L. Cutbill. The statistics included in Appendix 1 are the mean and its standard error; the standard deviation; the coefficient of variation corrected for small samples (Simpson, Roe and Lewontin, 1960, p. 101–102); the range; and 95 per cent confidence limits. The standard errors in no case exceed 5 per cent of the mean and it can therefore be assumed that samples are of adequate size.

ABBREVIATIONS

n	sample size
$\bar{x}$	mean
SE	standard error
SD (or s)	standard deviation
V_{cor}	corrected coefficient of variation
OR	range
95%CL	95 per cent confidence limits

Sample standard deviations are calculated using the formula,

$$s = \sqrt{\frac{\sum |x - \bar{x}| 2}{n - 1}} ,$$

where x is any individual sample variate. The corrected coefficient of variation is calculated using the formula,

$$\left(\frac{s}{\bar{x}}\right) \times \left(\frac{4n + 1}{4n}\right) \times 100.$$

The sample confidence limits are calculated using the formula $\bar{x} \pm ts$, where t is Student's t and has $n - 1$ degrees of freedom at the appropriate level of probability, in this case 0.05. Other workers may calculate their own confidence limits using this formula; all other necessary information is given in Appendix 1.

The comparative tables in the text include means and confidence limits for raw measurements, and means and ranges for indices and ratios. Strictly speaking, ratios and indices cannot be treated as single variates for the purposes of calculating confidence limits.

Simpson, Roe and Lewontin (1960, p. 164) give a method for calculating confidence limits when numerator and denominator are uncorrelated. "If the upper and lower limits for the numerator are written A_U and A_L and the limits for the demoninator symbolized as B_U and B_L, confidence limits for the ratio are given by A_L/B_U and A_U/B_L. The confidence value for this interval is the product of the individual confidence levels. If the confidence limits for numerator and denominator are those for a 95 per cent interval, the confidence interval for the ratio has a confidence level of 90.25 per cent ($.95^2$). If a 95 per cent level is wanted for the ratio, the confidence limits for numerator and denominator must represent the 97.5 per cent limits ($\sqrt{.95} = .975$)." However, since ratios and indices are only of use when the variates involved are correlated, they should not be used if numerator and denominator are uncorrelated (in such cases, ratios contribute no more information than the original variates). When variates are correlated, ratios are less variable than the raw measurements and confidence limits calculated in the manner outlined above will then be conservative, a desirable property.

In all the cases in which ratios have been calculated from fossil material, the samples involved are very small. For this reason, no attempt has been made to test the significance of differences between ratios. The smallness of the samples should constantly be borne in mind when evaluating the fossil data.

In a few cases, equiprobability ellipses have been calculated according to the method outlined by Defrise-Gussenhoven (1955). These ellipses encompass any desired percentage (in this case 95 per cent) of a bivariate population. Accurate confidence limits for ratios can be calculated by noting the points on the ellipse at which the values of the ratio are highest and lowest. The positions of these points vary with the slope of the major axis of the ellipse and the product moment correlation coefficient between the two variates. These in turn depend on the variances of the variates, and their covariance.

In cases of fossil samples smaller than eight, ranges rather than confidence limits have been given and standard deviations have not been calculated.

MULTIVARIATE ANALYSIS

It was considered desirable to use a multivariate technique which dealt with individuals rather than with samples, one which sorted individuals into groups rather than one which required individuals to be placed *a priori* into groups before analysis could begin. In this particular case where the sorting of individuals is important, and where fossil sample sizes were small and in some cases clearly biased towards one sex of a size dimorphic species, such a technique has been particularly useful (see Chap. VI).

The type of analysis used was Principal Coordinates, a modification, by J. C. Gower (1966), of Principal Components Analysis. The computer program was written by Dr. J. L. Cutbill, for whose help (and mathematical tuition) I am greatly indebted.

Principal Components can most easily be explained in two dimensions. Consider a bivariate sample plot surrounded by, say, a 95 per cent equiprobability ellipse. The original individual points are in x, y space. If each point is now projected onto the major and minor axes of the ellipse, the points can be given new coordinates along these axes (say, a and b) instead of along x and y. If x and y were originally fairly strongly correlated, the coordinates along the major axis will account for most of the variance in the sample. The coordinates along the minor axis will account for the remainder of the variance. As a general case $s_x^2 + s_y^2 = s_a^2 + s_b^2$, where s_x^2 is the sample variance of x, etc. The sum of the original variances is equal to the sum of the new variances.

The total variance remains unchanged, although the distribution of the variances changes, the tendency being to "squeeze" as much of the variance into one dimension as possible. The new variances are the latent roots or eigenvalues of the 2×2 covariance-variance matrix of the original variates. One valuable property of the new coordinates a and b is that they are orthogonal and the new variates are uncorrelated.

This model can now be considered in more than two dimensions. If p measurements are taken on each of n individuals, the sample can be represented as a swarm of n points in p-dimensional space. This swarm can be surrounded by a p-dimensional hyperellipsoid. The major axis, or first principal component, of this ellipse can then be found, and this axis will account for "most" of the variance in the system. The next axis, or second principal component, will account for "most" of the remaining variance and so forth. Thus, the original n points can now be represented along the first few new coordinates, and the sample can be plotted on one or more two-dimensional graphs. Using the first few axes only, some accuracy is inevitably lost, since only a certain percentage of the total variance is accounted for by the first few dimensions. However, if this total percentage is reasonably high, the remainder can be safely ignored.

Principal Components Analysis generally takes the p sets of raw data on n individuals and produces a $p \times p$ matrix of variances and covariances. This matrix is then manipulated to produce the new axes and coordinates along these axes. This is known as an R mode method of analysis, in which attention is concentrated on the relationships between *variables*. The type of Principal

Coordinates Analysis used here differs from most Principal Components Analyses in that it is a Q mode method, utilizing relationships between *individuals.* This type of analysis is ideal for sorting individuals and groups of fossils.

In any multivariate method it is important to standardize the variates used. If this is not done, large dimensions like P_3–M_3 L will dominate smaller ones such as MDi L P_4. Generally, variates are transformed to dimensionless quantities by dividing by the sample standard deviation. However this has no mathematical superiority and other normalizers can be used, for example, the mean or the range.

In Principal Components Analysis the product moment correlation coefficient is used as a measure of association between variates (R mode). Principal Coordinates uses here a similarity coefficient for the Q mode analysis of individuals. This coefficient is calculated according to the following formula,

$$s_{yz} = \frac{\left(p - \sum_{1}^{p} \frac{|a_y - a_z|}{OR_a}\right)}{p}$$

The similarity coefficient s_{yz} between individuals y and z is obtained as follows. The difference between the values of variate a for individuals y and z is calculated ($|a_y - a_z|$) and standardized by dividing by the sample range for character a (OR_a). This operation is performed for each of p characters and the total summed from the first to the pth character. The total is subtracted from p and this value is then divided by p to give the coefficient. When two individuals have identical values for each variate,

$$\sum_{1}^{p} \frac{|a_y - a_z|}{OR_a}$$

will be zero, and the coefficient will then be 1. When two individuals in a sample are at the opposite extremes of the range for every variate, the coefficient is 0.

The similarity coefficients can be regarded as a measure of distance between each pair of points. These n individuals can be represented in $n - 1$ dimensions without distorting the inter-individual distances. The problem is to produce $n - 1$ new dimensions, so that the first m dimensions, where $m < n - 1$, contain "most" of the variance. The program produced new values for each individual in each of the new coordinates and also produced the percentage of the total variability accounted for by each coordinate. The assemblage was then plotted in these m dimensions with a minimum of distortion.

The amount of time taken to extract latent roots from an $n \times n$ matrix is proportional to n^3. In order to save machine time and to deal with large sample sizes, the program used extracted only the first four latent roots and hence coordinates are available only in the largest four dimensions. Graphs have been plotted in the first two dimensions, these accounting normally for between 60 and 70 per cent of the variability. The third and fourth dimensions contribute two or three per cent only and are not used on these graphs.

The variates used are the 28 mandibular dimensions described above and listed in Appendix 1. The program was tested first with data from living material, to discover whether or not it could sort individuals of known species into specific groupings; this it did. In the case of gorillas and orangutans it sorts according to sex, too. Fossils were introduced into the analysis and the amount of clumping or scattering noted; this was then compared with the range of variation to be found within and between living species (see Figs. 4–6).

Since fossil material is rarely so complete as to provide a full complement of 28 mandibular variates, the program was adapted to cope with gaps in the data. By experimentation it was noted that for adequate comparison between two individuals, they should share values for at least two-thirds of the variates.

Measurements on fossil and Recent specimens are listed in the Appendices. Where necessary, measurements have been utilized to illustrate various points.

CHAPTER III. GEOLOGIC AND PALEOECOLOGIC CONSIDERATIONS OF THE EAST AFRICAN SITES

The African pongid material discussed in subsequent chapters is derived mainly from five areas in East Africa: Moroto and Napak in Uganda; and Rusinga, Songhor, and Koru in Kenya (Fig. 1). During the Miocene these deposits were associated with a number of volcanic centers. Those at Rusinga contain material from the Rangwa volcano and those at Songhor and Koru material from Tinderet volcano. The sites at Moroto and Napak take their names from the respective volcanoes on the slopes of which the sites are found.

These sites have been dated as Early Miocene or "Burdigalian", although the application of European faunal stage names is probably not strictly appropriate (Andrews, 1911; Clark and Leakey, 1951; Bishop, 1962). It is, however, unlikely that all these sites are contemporaneous. The potassium-argon dating of the sites will be discussed briefly later (p. 17). The geology of the Uganda deposits has been covered most adequately by Bishop (1962, 1963a, 1964, 1966, and 1967) and Bishop and Whyte (1962). This description draws heavily on their work. Bishop is now working on a monograph on the stratigraphy and paleoecology of the Uganda sites which will cover more thoroughly the subjects of this chapter.

MOROTO II

Karamoja District, Northeastern Uganda

This site was first discovered in 1961 by Bishop and Whyte (1962) and has yielded an excellent pongid palate, UMP 62–11. The fossiliferous deposits consist of water-laid sediments infilling steep-sided valleys cut into the Precambrian basement gneisses. Most of the sedimentary material is derived from the gneisses, although some is of volcanic origin; fossiliferous horizons have a calcareous cement. Bishop (1966, p. 157) noted that some of the lavas at Moroto II may be later than Early Miocene in age. One potassium-argon date on the capping lavas has been obtained by Bishop, Fitch, and Miller (1969, in press). It is $14.3 \pm 0.3 \times 10^6$ years. This gives a latest possible date for the deposits.

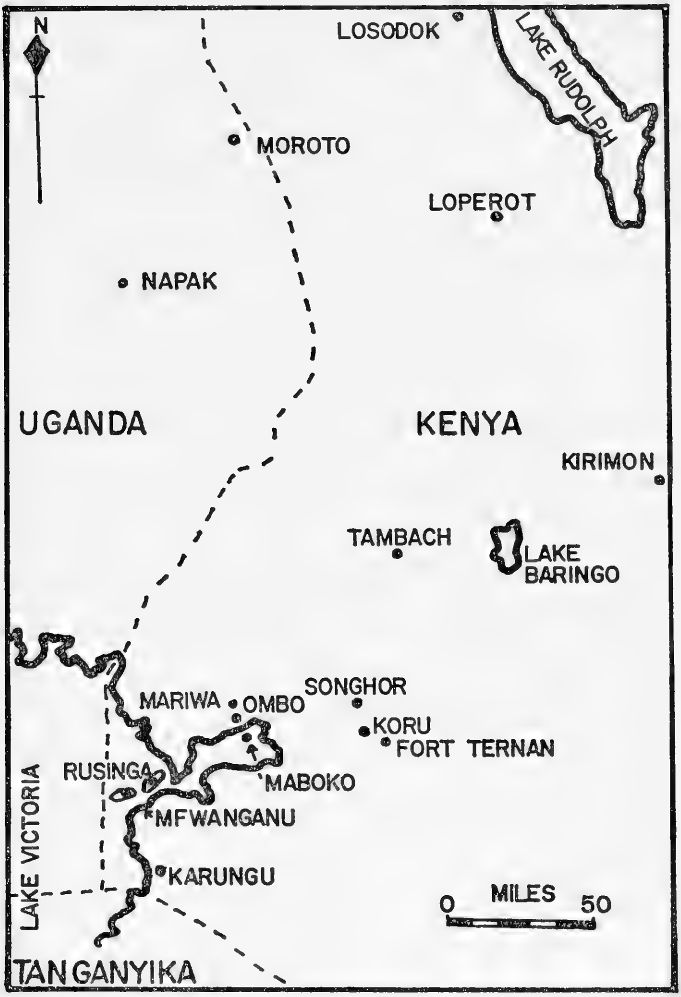
The associated fauna is rather sparse and poorly preserved, and apparently does not differ from that at the other Miocene sites (Bishop, 1967). However, as noted, the potassium-argon date is a latest age estimate and so there is a possibility that the site is somewhat younger than the other sites discussed, perhaps middle Miocene.

NAPAK

Karamoja District, Northeastern Uganda

A number of fossil sites have been found in the vicinity of the dissected remnant of the Napak volcanic cone, some 55 miles southwest of Moroto. The sites have

FIGURE I. FOSSILIFEROUS LOCALITIES



After Bishop (1963)

been divided by Bishop into two groups on the basis of lithology (Bishop and Whyte, 1962). The first includes sediments made up of sands, gravels, and tuffs occurring beneath volcanic sediments and resting on basement rocks (sites II, III, VI, VII, and VIII). Moroto II is also a site of this type. The second group consists of bedded tuffs and agglomerates within the volcanic pile, approximately 500 feet above the basement (sites I, IV, V, IX, and X). The pongids from Napak come only from sites I, IV, and V; these sites are treated as a contemporaneous group. The pyroclastic sediments are usually medium to fine tuff and the fauna is generally very well preserved due to its burial in such sediments.

The high incidence of teeth, jaws, and cranial fragments, some with signs of rodent and carnivore gnawing, suggests that these faunas largely represent less edible bones left by predators on the temporary land surfaces. Fortunately, secondary calcification has meant that the fossils have been remarkably well preserved. Resistant fossils were secondarily concentrated in patches as they were weathered out. The fauna has been discussed by Bishop (1964, 1967) and appears to be broadly similar to those from Rusinga and Songhor in Kenya. Detailed analysis of faunas from the various sites at Napak shows interesting differences between the faunas, presumably due to ecological variation between contemporaneous assemblages (Bishop, 1967).

Bishop (1964, p. 1331) reported a date of 19.0 ± 2.0 × 10^6 years for biotite from Napak I. A further sample from the same site yielded an age of 17.8 ± 0.4 × 10^6 years for three age determination runs [Bishop, Fitch, and Miller, 1969 (in press)]. The second age however is perhaps less accurate; the Napak deposits are probably latest Early Miocene. As stated above, it is possible that the Moroto II material is a little younger than that from Napak.

KORU

Kavirondo District, Kenya

Primate material from Koru was first reported by Hopwood (1933a and b). The deposits are mainly of subaerial volcanics like those of Napak I, IV, V, and IX.

SONGHOR

Kavirondo District, Kenya

The main site was discovered in 1932 by Leakey and MacInnes. Like Napak I, IV, V, and Koru, the primate-bearing deposits at Songhor consist of subaerial pyroclastics.

Both Koru and Songhor occur at the base of the same pyroclastic sequence, and they may be regarded as contemporaneous. Sediments in these sites originated from the same volcanic crater. Like Napak I, IV, and V, the deposits at Songhor and Koru probably represent a relatively short period of time. The following radiometric dates have been obtained from material collected at Koru and Songhor (Bishop, Fitch, and Miller, 1969, in press): Koru, 19.5 ± 0.3 × 10^6 years and 19.6 ± 0.3 × 10^6 years; Songhor, 19.7 ± 0.5 × 10^6 years and 19.9 ± 0.6 × 10^6 years.

The two sites can be treated as contemporaneous. They fall at the end of the Early Miocene.

RUSINGA ISLAND

Lake Victoria, Kenya

Leakey and MacInnes first located hominoids on Rusinga Island on the south side of the Kavirondo Gulf of Lake Victoria in 1931. Since then the island has been searched extensively for fossils and a large amount of material has been recovered. The island is 170 miles south of Napak and 75 miles west-south-west of Songhor. These deposits have yielded faunas, including primates, more extensive than those from the other East African sites. Their geology has been described by Shackleton (1951), Whitworth (1953), Bishop (1967), and Van Couvering and Miller (1969).

Recent stratigraphical work on Rusinga Island has been completed by John Van Couvering (Van Couvering and Miller, 1969). Briefly, he concludes that the main fossiliferous horizons at Rusinga are some 18 million years old. Some specimens may date back to 20 or 22 million years, but most of the pongid material is probably between 18.5 and 17.5 million years old.

PALEOECOLOGY

The various East African Early Miocene sites are almost certainly not exactly contemporaneous; more careful faunal collecting and radiometric dating should in the future enable us to build up a chronological sequence of sites in East Africa. The known potassium-argon dates are set out in tabular form in Table 1. Dates for the European sequence are drawn from von Koenigswald (1962),

Table 1 Potassium -argon dates (10^6 years)

EUROPE	EAST AFRICA					
	Moroto II	Napak	Fort Ternan	Koru	Songhor	Rusinga
12 -						
12.5±0.4						
SARMATIAN						
			14.0			
14 -	>14.3±0.3		14.0±0.2			
14.0±0.4			14.7±0.7			
- - - - - - - - - ?						
14.6±0.5						
14.7±0.5						
16 -						
16.2±0.4						
VINDOBONIAN						
		17.8±0.4				
18 - - - - - - - - ?						18.0-18.5
		19.0±2.0		19.5±0.3		
19.8±1.0				19.6±0.3	19.7±0.5	
20 -					19.9±0.6	
BURDIGALIAN						
22 -						
24 -						

and those for East Africa from Evernden *et al.* (1964), Van Couvering and Miller (1969), and Bishop, Fitch, and Miller (1969, in press).

The faunas of the earlier Miocene sites are broadly similar, although careful studies have emphasized differences in relative frequency of various groups (Whitworth, 1958; Bishop, 1967). With the sites arranged in chronological order, no doubt evolutionary changes within lineages will be detectable. Studies of this sort, however, are not possible with the present state of knowledge of these faunas.

The faunal differences between sites are generally interpreted as being due more to ecological contrasts between more or less time-synchronous assemblages than to faunal evolution. Bishop (1967) has shown marked fluctuations in the relative abundance of rodents, proboscideans, and artiodactyls at four of the Napak sites (I, IV, V, IX). These differences, he assumes, are due to variations in local ecologic conditions between contemporaneous sites which are geographically close together. Whitworth (1958, p. 46–47) compared the well-known faunas of Rusinga and Songhor. The differences between the two generally take the form of the presence of one species at Rusinga and its absence from Songhor. For example, the ruminants *Dorcatherium chappuisi, D. pigotti,* and *D. parvum* are abundantly present at Rusinga but absent from Songhor. Conversely, *D. songhorensis* is absent from Rusinga and present at Songhor. Another large ruminant *Propalaeoryx nyanzae* is present at Rusinga and not at Songhor. The lagomorph *Kenyalagomys* (two species, *K. rusingae* and *K. minor*) is likewise present in abundance at Rusinga yet absent from Songhor; *Megalohyrax championi* and other hyracoids follow this same pattern.

Whitworth believes that these differences are best regarded as ecologic and concludes (1958, p. 46) that the "fossil assemblage at Rusinga seems to be a representative savannah fauna, and it has been suggested . . . that in early Miocene times Rusinga was principally an area of parkland and steppe. At Songhor, we are dealing with the fauna of an associated, but more restricted, habitat, perhaps analogous to the isolated, tree-clad jebels which rise, here and there, above the Recent African savannahs, and support a mammal fauna distinct from that of the surrounding parklands."

While sympathizing with this general viewpoint, Leakey has recently (1967, p. 163) suggested an alternative explanation. "It is, however, possible that the Songhor beds may only represent the upper part of the Rusinga series, and that both may be of Middle Miocene age, leaving the main Rusinga deposits in the Lower Miocene." As we have already seen, this thesis is unlikely, the radiometric dates weighing against it.

Chesters (1957) has studied the available palaeobotanical material from the East African Miocene. Most of her material comes from Rusinga and the neighboring island of Mfwanganu. The majority of her Rusinga material consists mainly of fruits rather than leaves. This has made comparison with other Tertiary African floras difficult, since they have been composed predominantly of leaves. The flora of tropical Africa apparently has changed relatively little during the Tertiary. That of the East African Miocene shows that the ecology and climate of East Africa would not have differed greatly from the present day. Considering those species most similar to living forms, and for which habitat can be inferred, the setting suggested to Chesters by the flora is one of a tropical rain forest with tall trees and a multiplicity of climbers. Many of the trees are species which grow close to, or at, the forest margin. Fruits adapted for water dispersal are also present in large numbers in the deposits. The flora is indicative of a gallery forest overhanging lakes, rivers, and streams, with trees covered with climbers. The fauna at Rusinga contains forest, marshland, and savannah elements, and presumably the savannah forms inhabited the local grasslands. Gallery forest was present along water courses and around lakes and marshes. The slopes of the volcano were probably thickly wooded. Animals characteristic of the various habitats are found as fossils in lake-shore deposits presumably because they would have visited the lake for water and died there. The larger primates certainly would have inhabited the wooded slopes of the volcanoes. Here, as Bishop (1963a, p. 259) has said, "one is tempted to draw analogies with the present habit of the mountain gorilla in Kigezi, southwest Uganda. . . . This is between 7,500 and 9,500 feet above sea level (1,500–3,500 feet above the surrounding country) on the slopes of volcanoes which have been active until very recently and which are in areas where lakes impounded by volcanic activity abound." This description would probably fit the sites at Songhor and Koru, Napak and Moroto; regions of tree-clad relief standing above local areas of savannah and open woodland.

Verdcourt (1963) has studied the nonmarine Mollusca in a valuable contribution to the paleoecology of the area. Fortunately, land mollusca are good indicators of climatic conditions. Like the flora, the Miocene mollusc fauna is similar to that of the Recent, emphasizing the fact that this area has been climatically stable. The majority of the specimens studied by Verdcourt again came from Rusinga. Verdcourt concludes (1963, p. 35) that the predominant type of vegetation represented in these Early Miocene deposits is evergreen rain forest receiving a fairly heavy annual rainfall (35–70 inches), heavier than that of the present. Evidence from Rusinga indicates that climatic fluctuations also occurred, for some of the molluscs are indicative of drier habitats such as riverine forest and savannah woodland. The aquatic habitats evidently consisted of swamps and rivers, although not necessarily lakes. "The impression gained is that the area around Rusinga and Karungu was covered with a series of swamps." (Verdcourt, 1963, p. 35).

The predominant vegetation at the Koru and Songhor sites is said by Verdcourt to have been evergreen forest, with an implied rainfall of 40–80 inches, hardly surprising for elevated areas. Similar habitats and climatic conditions probably obtained at Napak and Moroto, too.

In conclusion, the Rusinga sites contain faunal elements from a variety of habitats. The hominoids found in these sites may have lived near the rivers and swamps, in the savannah, or on the forested slopes of the nearby volcanoes. The sites at Songhor, Koru, Napak, and Moroto are more likely to contain a homogeneous fauna, representative of the local habitat. This habitat would have been not dissimilar to that of the presentday mountain gorilla, *Gorilla gorilla beringei.*

CHAPTER IV. *DRYOPITHECUS (PROCONSUL) MAJOR* FROM MOROTO II, UGANDA

PRESENTATION OF MATERIAL

The next three chapters contain descriptions of the Miocene ape *Dryopithecus major* from Uganda and Kenya. First I shall discuss the morphology and possible relationships of the excellent material from Moroto II in Uganda. Next, in Chapter V, I shall attempt to demonstrate that all pongid specimens from another Ugandan site, Napak (see Fig. 1), are best assigned to a single species, and that this material is conspecific with that from Moroto II. Finally in Chapter VI I attempt to show that the Ugandan apes belong in the species *Dryopithecus* (*Proconsul*) *major,* first described from Songhor and Koru in Kenya. This species is gorilla-like in a number of features and exhibits—like the gorilla—a high degree of sexual dimorphism in dental, facial, and mandibular characters.

HISTORY OF MOROTO DISCOVERIES

The history of recovery of the material from Moroto II in Uganda is of particular interest. In August 1961, Dr. W. W. Bishop and Mr. F. Whyte, while investigating a number of mid-Tertiary sites in Uganda and Kenya, discovered the locality known now as Moroto II (Bishop and Whyte, 1962). They recovered part of the left maxilla of a large hominoid, lacking tooth crowns (specimen UMP 62–11), and a fragment of right mandibular horizontal ramus (UMP 62–10), also of a large hominoid.

Four months later, in December 1961, Prof. David Allbrook led a party of students from Makerere University College to the same site. They found a right maxilla and two other fragments of upper jaw, all from the same individual as UMP 62–11. The reconstructed specimen was described by Allbrook and Bishop (1963) and provisionally assigned by them to *Proconsul major.* Allbrook's party also recovered a left upper canine of this species (UMP 62–12) and some more mandibular fragments.

Collecting ceased until Bishop returned to the site in December 1963. Sieving surface material downslope from the original point of exposure of UMP 62–11 resulted in the collection of 25 further pieces, including most of the teeth and parts of the inferior facial region. To judge from the sharp edges of the broken pieces and the lack of weathering, the maxilla had evidently only recently been exposed on the side of the erosion gulley.

Seven further mandibular fragments were also found. One of these belonged to the specimen previously numbered UMP 62–10. The other six made up a rather weathered portion of a left mandibular horizontal ramus (UMP 66–01) belonging to the same individual as UMP 62–10.

The fragments of the upper jaw and face, UMP 62–11, came from one side of the gulley, the mandibular fragments, UMP 62–10 and 66–01, from the other.

The mandibular fragments show a higher degree of weathering, suggesting that they had lain rather longer on the surface before collecting. It is possible that the maxillary and mandibular remains come from the same individual.

SPECIMENS

UMP 62–11

(FIGS. 18 AND 19)

This is one of the most complete specimens of a mid-Tertiary dryopithecine known, and has been described and figured by Allbrook and Bishop (1963) and Bishop (1964). One especially pleasing feature is the almost total absence of postmortem deformation. The maxillae, premaxillae, nasals, palatines, and dentition have been reconstructed from a total of 36 fragments found over a period of two and a half years. A further 17 fragments cannot be fitted into place.

Most of the lateral walls of the maxillae are missing, as are the lateral parts of the nasal meatus, and the maxillary sinuses are exposed. The premaxillae are complete as are the adjacent parts of the maxillae as far as the distal border of P^4. Narrow strips of the maxillary frontal processes are preserved superiorly between the infraorbital foramina and the lacrimal fossae, but they do not reach the frontal. The nasals, which are deficient inferiorly, run superiorly as far as the nasofrontal suture above which is preserved a tiny strip of frontal. A number of isolated fragments can be identified. These include the lateral margin of the left orbit and a portion of what is possibly the left inferior malar region. The dentition is complete except for the right central incisor.

FACE

NASALS AND NASAL REGION

The nasofrontal suture is convoluted. Superior to this, the frontal is represented only by a very small fragment of bone which does not reach the level of glabella. The fragment continues the smooth sagittal curve of the nasal.

The nasals are preserved superiorly, but are extremely fragmentary inferior to the level of the infraorbital foramina. The contour of the internasal suture is concave anteriorly. A tangent drawn to the curve at the level of nasion makes an angle of approximately 60 degrees with the occlusal plane of the premolars and molars. At the level of reconstructed rhinion the angle is approximately 30 degrees. (The occlusal plane of the cheek tooth is used here as the plane of orientation since none of the accepted planes are available.)

The nasomaxillary sutures are not convoluted and diverge slightly inferiorly. The distance between the two sutures at the nasofrontal suture is approximately 10 mm and at the level of the infraorbital foramina 12.5 mm (a vertical distance of some 40 mm). The sutures continue to diverge and about 15 mm below the level of the infraorbital foramina the sutures are 16 mm apart. The inferior parts of the nasals are not preserved, although the premaxillary part of the nasopremaxillary suture is preserved at its most superior point. The distance between the sutures at this level—assumed to be approximately equivalent to the level of rhinion—is about 25 mm. The length of the nasals from nasion to rhinion has been estimated at about 65 mm, within the range for *Gorilla gorilla* and outside that of *Pan troglodytes.*

In cross-section the nasals form an almost flat plane at the level of nasion but are convex anteriorly at the level of the lacrimal fossae and at this point are set at an angle of approximately 160 degrees to each other. The nasals are therefore long, rather narrow bones, gradually expanding inferiorly from nasion to between the infraorbital foramina and rhinion, and then rather more rapidly as far as their inferior border. In general shape they resemble those of the Cercopithecidae rather than Pongidae, although in size they are matched only by the gorilla. Chimpanzees tend to have approximately parallel nasomaxillary sutures like this specimen, although this is a variable feature. In *Gorilla gorilla,* the nasals are often constricted superiorly, then expanded greatly in their inferior half (Vogel, 1965, p. 308).

Superiorly the margins of the nasal aperture are not preserved. Laterally, the crista nasalis is smoothly rounded. Premaxillary-maxillary sutures are present 3.5 mm lateral to the lateral borders. These sutures diverge inferiorly to the alveolar border. The crista nasalis on each side curves gently towards the midline, so that the outline of the inferior half of the border of the piriform aperture is shaped like a half-circle when viewed anteriorly. There is a flattened prenasal area anteroposteriorly some 10 mm long, running from the anterior margin of the incisive fossa to the superior margin of the nasoalveolar clivus. There are no traces of nasal spines. This area shows superficial similarities to that of male gorillas, although in gorillas the prenasal area is much more extensive and a nasal spine is present.

Tables 2 and 3 contain some nondental measurements of UMP 62–11, together with means and ranges of small samples of male gorillas, female gorillas, and chimpanzees. Some of these measurements are rather unorthodox, because the fragmentary nature of parts of the specimen means that standard reference points are lacking. Appendix 1 contains full details of all measurements taken, together with the statistics calculated from these samples.

Nasal height, listed in Table 2, is a convenient measurement of the height of the superior part of the face. In the Ugandan specimen it is 98.5 mm. Such values are found only in male gorillas, and this value is in fact above the mean (95.8 mm) for ten male lowland gorillas. The nasal index is low and in this feature the fossil resembles gorillas rather than chimpanzees. However, the high value of the index in *Pan troglodytes* is due to the low value of *nasal height,* whereas the difference between the values in male gorillas and the fossil are due to differences in *nasal breadth.* In the case of female gorillas differences are due both to height and breadth. (This illuminates one of the dangers of using the absolute value of an index too uncritically.) The low nasal breadth, 30.2 mm is a reflection of general upper facial narrowness in this specimen, presumably a primitive feature correlated with small anterior tooth size.

INTERORBITAL AREA AND ORBITS

Only the anterior parts of the interorbital region are preserved. Neither maxillofrontale nor dacryon are present, and therefore an unorthodox inter-

Table 2 Facial measurements of UMP 62-11, Gorilla and Pan

	UMP 62-11		G. g. gorilla		P. troglodytes (n=10)
			males (n= 10)	females (n=10)	
Nasal height	*98.5	$\bar{X}$	95.8	77.7	54.0
		OR	89.5-106.3	68.6-85.2	42.1-59.8
Nasal breadth	30.2	$\bar{X}$	37.9	32.6	25.2
		OR	33.4- 40.7	28.0-39.7	21.0-28.6
Index B/H x 100	33.4	$\bar{X}$	39.6	42.2	46.6
		OR	35.7- 43.9	33.7-50.7	41.7-61.7
Breadth across anterior lacrimal crests	*20.0	$\bar{X}$	26.9	19.7	20.6
		OR	16.9- 34.9	15.3-23.4	13.6-26.3
Thickness of lateral orbital margin	*6.0	$\bar{X}$	15.8	11.0	9.1
		OR	13.0- 17.3	6.7-14.8	7.6-10.8
Orbital height from zygomaticofrontal to inf. border	*29.0	$\bar{X}$	28.9	29.4	21.6
		OR	23.2- 34.5	27.1-31.4	17.7-25.8
Nasospinale-alveolare	16.7	$\bar{X}$	34.1	28.1	29.3
		OR	29.5- 42.1	21.3-37.5	25.0-39.2
Breadth across infra-orbital foramina	40.0	$\bar{X}$	61.9	53.2	50.2
		OR	53.3- 69.2	49.0-59.6	42.9-57.0
Left infraorbital for. to left anterior lacrimal crest	*30.0	$\bar{X}$	39.7	34.0	27.0
		OR	34.5- 43.7	29.1-41.4	21.8-31.9

Table 3 Alveolar and palatal measurements of UMP 62-11, Gorilla and Pan

	UMP 62-11		G. g. gorilla		P. troglodytes (n=10)
			males (n=10)	females (n=10)	
Alveolar L	95.8	$\bar{X}$	104.3	85.0	67.7
		OR	98.5-109.0	80.6-89.5	63.0-75.9
Alveolar B at M^2	62.5	$\bar{X}$	72.7	65.7	58.0
		OR	68.2-76.2	62.1-69.1	54.8-63.2
Alveolar B at C^1	66.5	$\bar{X}$	75.2	58.2	56.2
		OR	64.4-84.5	52.2-64.1	50.3-62.4
$\frac{\text{B at M}^2}{\text{Alv L}} \times 100$	65.3	$\bar{X}$	70.1	77.4	85.8
		OR	64.5-73.8	74.4-81.4	81.2-93.8
$\frac{\text{B at M}^2}{\text{B at C}^1} \times 100$	94.0	$\bar{X}$	97.4	113.4	103.5
		OR	86.3-108.2	103.0-125.7	95.7-116.4
Palatal D at C^1 -P^3	*4.0	$\bar{X}$	9.7	10.3	6.2
		OR	6.3- 16.2	8.2-14.4	2.0- 9.0
Palatal D at M^2	*7.5	$\bar{X}$	16.9	15.9	12.4
		OR	11.0- 24.3	11.0-22.4	10.0-14.8

orbital breadth measurement has been taken, utilizing terminals on the anterior lacrimal crest at the level of the most superior part of the lacrimal fossa. Table 2 includes this measurement for UMP 62–11, as well as for gorillas and chimpanzees. The fossil yields a value of approximately 20.0 mm and falls therefore very close to the means of chimpanzees and female gorillas and within the range of male gorillas.

In living gorillas, particularly males, the interorbital breadth increases posteriorly. This is associated with the pneumatization by the frontal sinuses of the interorbital area. In UMP 62–11 there is a tiny indentation behind the posterior lacrimal crest on the left side which is probably part of the frontal sinus, suggesting that interorbital width would have increased posteriorly.

Anterior and posterior lacrimal crests are preserved superiorly on the right side and delimit the superior part of the lacrimal fossa. On the left both crests remain and surround a small fossa which opens into the nasolacrimal duct. The lacrimal fossa is small compared to that of modern pongids. The maxillolacrimal suture is preserved in each fossa.

The only other fragment of orbit is an isolated piece from the left lateral margin. The fragment is broken superiorly at the zygomaticofrontal suture and inferiorly at the inferolateral corner internally and externally on the frontal process of the zygomatic externally. Table 2 includes two measurements on this fragment: the thickness of the lateral border taken at the (presumed) midpoint between the superior and inferior orbital margins, and the vertical distance from the zygomaticofrontal suture to the horizontal plane of the most inferior part of the inferior orbital margin. The fragment resembles most closely in size and morphology a gracile female gorilla. It is in fact very similar to the homologous area of a female lowland gorilla Pr 52.0.4 in the Duckworth Laboratory of Physical Anthropology at Cambridge, England. The lateral margin of UMP 62–11 is even more slender than in the living form. As far as can be inferred, the orbit was probably relatively high with respect to breadth as in many female gorillas.

MAXILLAE AND PREMAXILLAE

The maxillae and premaxillae are well preserved anteriorly. The alveolar processes are intact, although their most posterior portions, the maxillary tuberosities, are deficient superiorly. Alveolar bone adherent to tooth roots and not invaded by sinuses is intact. Thus on either side of the piriform aperture and nasals remains of the maxillae extend superiorly above the canines and premolars almost as far as the inferior margin of the orbits. However, these frontal processes are confined to narrow strips, as the majority of the bone forming the lateral walls of the maxillary sinuses has broken and been lost, although a number of pieces from this lateral maxillary area remain among the unattached pieces.

The anterior part of the face is dominated inferiorly by the alveolar juga of the canines which extend superiorly as prominent ridges lateral to the nasal aperture. In UMP 62–11, these juga are associated with large canine roots and so are relatively large and massive. At the level of the upper part of the nasal aperture, the juga disappear and the frontal processes of the maxillae become gently concave. The architecture of this part of the face is strongly reminiscent of that of male gorillas, although built on a somewhat smaller scale.

The premaxillary area is short from nasospinale to alveolare (see Table 2) and this may be regarded as a lack of alveolar prognathism alone or as part of the general shortness of the maxillary alveolar processes. In Recent Pongidae, the alveolar processes project inferiorly to a greater extent (note the dimensions of palatal depth in Table 3), while as part of the general increase in size of the dentition the incisors have been carried far anterior to nasospinale. Thus in modern Pongidae the great length from nasospinale to alveolare is a function of two related factors. Apparently, neither factor was important in UMP 62–11. The slope of the nasoalveolar clivus is at an angle of 30 to 40 degrees to the occlusal plane of the cheek teeth, somewhat steeper than that of most male gorillas, and about as steep as that of females. The difference is apparently correlated with the fact that the length of the clivus is less than in male gorillas.

A rather strong jugum is associated with the root of the left central incisor (the right had been lost some time before death). The area between this and the ipsilateral canine jugum is rather flattened. Similar juga are associated with the mesiobuccal roots of the anterior premolars. These juga merge superiorly with the canine juga. Immediately posterior to the premolar juga are slightly depressed areas—the canine fossae. Although the relevant parts of the face are missing, it is unlikely that the depressions were of any great extent posteriorly, for the zygomatic processes of the maxillae begin at the level of the posterior border of M^1. Regions immediately below the infraorbital foramina were probably predominantly flattened, although a slight groove perhaps ran inferiorly from the infraorbital foramen to the fossa.

The zygomatic processes of the maxillae are broken off, but eversion of the maxillae some 10 mm above the alveolar margins indicates that the inferior margins of the zygomatic processes were situated at about the level of M^2.

An isolated fragment of what is probably the left zygomatic bone consists of a small fragment of the inferior border, some 15 mm long, including the zygomatic surface of the zygomaticomaxillary suture. Superiorly, 10 mm from the inferior border there is part of the zygomatic process of the maxillary sinus. The inferior margin of the fragment is roughened for the origin of the superficial laminae of the masseter. The area is not excavated as in many gorillas, nor even as greatly roughened as in many living chimpanzees (and some gorillas), suggesting that the portion of the masseter originating therefrom was relatively poorly developed. Anteromedial to this is a tuberosity, in size and morphology gorilla- rather than chimpanzee-like. Although the fragment is small, it indicates that in all probability the part of the zygomaticomaxillary region represented was similar in build to that of a small female gorilla.

The medial margins of the infraorbital foramina are bilaterally preserved as "lipping" on the lateral margins of the broken maxillary frontal processes. As a measurement of facial breadth, the distance between the mediosuperior edges of the infraorbital foramina has been taken. This is not a particularly satisfactory measurement, but is the only one which can be taken. It is impossible to measure the depth of the foramina below the inferior orbital margin, so the distance between the infraorbital foramen and the superior end of the anterior lacrimal crest has been measured on the left side. Both measurements are listed in Table 2.

The distance between the infraorbital foramina is less than that for 20 gorillas and 10 chimpanzees. The specimen clearly had a rather narrow face. One gets the impression of a long, gorilla-like upper face above a dentition which is a little smaller than that of a female gorilla, except for the canines. The large canines, and the relatively massive portions of the facial buttress system associated with these, suggest that UMP 62–11 is a male. The specimen probably resembled a "scaled-down," long-snouted male gorilla, with a gracile upper face rather like those of female gorillas.

The nasal floor is formed by the palatine processes of the maxillae. Just posterior to nasospinale the maxillae drop 5 mm or so to the nasal floor. The inferior nasal meatus is restricted anteriorly. The incisor fossa is almost 10 mm broad and takes up the entire width of this anterior part. The incisive canal slopes forward at a very oblique angle to the plane of the cheek teeth (and to the nasal floor). Part of the posterior lip of the incisive fossa is broken, thus increasing the anteroposterior fossa length, but even so the incisive canals were very large, much larger than is the case in the living African apes. This is probably a primitive feature.

Traces of the intermaxillary crest are present along the midline of the nasal floor. The lateral walls of the fossa are present as far back as the distal borders of the posterior premolars. Posterior to this the thin septum separating the fossa and the maxillary antrum has been broken leaving only ridges inferiorly. The palatine bone is deficient and the most posterior parts of the nasal floor are therefore absent. The inferior conchal crests are present on the lateral walls at the front of the nasal fossa some 13 or 14 mm above the floor, extending approximately 20 mm posteriorly.

The fragmentary remains of the nasal bones and associated parts of the maxillary frontal processes do preserve some features of interest on their posterior surfaces. On each side the medial half of the lower 10 mm of a single infraorbital canal is preserved. Medial to this is part of the roof of a superior lobe of the maxillary sinuses. Farther medial still to this on each side, but best preserved on the left, is the nasolacrimal canal. This is a delicate bony tube, some 4–5 mm in diameter. On the left side it is 25 mm long. The canal runs anteriorly as well as inferiorly from the lacrimal fossa towards the nasal floor at an angle of approximately 50 degrees to the cheek tooth row. At its broken inferior end the canal is 25–30 mm above the nasal floor. Just superior to the break the canal becomes part of the lateral wall of the nasal fossa. Unfortunately, the manner in which the nasolacrimal duct opens into the inferior meatus is unknown, but it is unlikely that it would have expanded into the dilated nasolacrimal bulb typical of *Gorilla gorilla*. In adult gorillas the bulb forms almost immediately inferior to the lacrimal fossa (Cave, 1961). In the chimpanzee the expansion is much less marked, but in neither does one find 25–30 mm of undilated nasolacrimal canal. The specimen is in general less pneumatized than are living pongids of comparable age and the absence of an expanded nasolacrimal bulla may be another manifestation of this general underdevelopment.

Medial to the nasolacrimal canal are low ridges corresponding to the broken middle conchae and the superior portion of the bony nasal septum.

SINUSES

MAXILLARY

Fortunately, the surface of the nasal fossa and the lining of the sinuses have a distinctive pink color, thus enabling the extent of sinuses to be judged from the isolated identifiable fragments.

The maxillary sinus occupies the body of the maxilla from the level of the distal border of P^4 anteriorly to some 30 mm behind and 40 mm above the distal border of M^3 posteriorly. The mesiodistal root of M^3 is bilaterally exposed in the sinus. Inferiorly, the sinus floor is depressed slightly between M^1 and M^2, and between M^2 and M^3. However, the antrum cannot be termed multilocular as it is in Recent pongids. In living apes, with the extension inferiorly of the alveolar processes, the sinus fills deep recesses between the roots of the cheek teeth and these recesses are often separated by sharp partitions. In UMP 62–11 the alveolar processes are relatively poorly developed and the sinus is not expanded.

In living apes, since the lengthening alveolar processes have carried the floor of the maxillary sinus inferior to the palatine processes, the palatine processes in turn become pneumatized. This has not occurred in UMP 62–11.

Superiorly, there is at least one anterior process of the sinus. The sinus extends superiorly to the lacrimal fossa. It seems therefore to have been as extensive superiorly as in living pongids. The sinus has invaded the zygomatic process at least as far as the lateral border of the orbit. Both the lateral orbital and the inferior zygomatic fragments preserve patches of the distinctive pink sinus lining on their inferior and superior aspects respectively.

FRONTALETHMOIDAL

A multilocular frontalethmoidal sinus was present at the level of the frontomaxillary suture and below and posterior to this. It extended medial to the lacrimal and ethmoid bones. The bone surrounding the sinus was probably a little thicker, and the sinuses themselves less extensive, than in living African pongids.

Alveolar Processes

The alveolar processes of the maxillae are preserved intact. The external or buccal and labial portions of the processes will be considered first. The external alveolar margins diverge anteriorly. This is undoubtedly correlated with the large size of the canines. Table 3 gives some external dimensions of the alveolar region. In the sample of gorillas, bicanine breadth exceeds that across the ectomolaria (at M^2) only in males. The relative breadths of the alveolar processes at the level of canines and second molars has been expressed by the ratio (Bimolar B/Bicanine B) × 100. In UMP 62–11 the value of this ratio is 94.0, indicating that bicanine breadth exceeds bimolar breadth. In male gorillas this ratio varies from 86.3 to 108.2, in females from 103.0 to 125.7. The value of this ratio is governed almost entirely by the size of the canine roots, which affects the bicanine breadth. In the mountain gorilla, *Gorilla gorilla beringei,* this tendency to anterior expansion in males is often even more marked. Thus a specimen of a young adult male mountain gorilla in the Duckworth Laboratory has a bicanine breadth of 83.7 mm and a bimolar breadth of 64.7 mm, giving a ratio of 77.3.

The length of the alveolar region from prosthion to the plane of the posterior edges of the maxillary tuberosities had to be estimated for UMP 62–11 since the tuberosities are deficient posteriorly. The estimated length is

95.8 mm which exceeds that of 10 gorilla females (range 80.6–89.5) and falls short of the range for 10 male gorillas (98.5–109.0). The ratio (Bimolar B/Alveolar L) × 100 has been calculated as an expression of relative alveolar length. The ratio ranges from 64.5 to 73.8 for the male gorillas and from 74.4 to 81.4 for the female gorillas. Male gorillas therefore have relatively longer and narrower alveolar regions than do females. In UMP 62–11, the value of this ratio is 65.3, indicating a long narrow muzzle. As far as proportions are concerned, the specimen is once again best interpreted as a male.

PALATE

A few palatal measurements are included. Palatal length cannot be taken, since staphylion is lacking. The palatal breadth between endomolaria at M^2 is 33.4 mm and at P^4 between 33 and 34 mm. Palatal depth has been taken from the plane of the alveolar margin to the midline of the palate (Table 3). At M^2 the depth is about 7.5 mm and between C^1 and P^3 about 4 mm. The alveolar processes project considerably less than in gorillas and less than in many chimpanzees.

The intermaxillary suture is still visible, but the premaxillary-maxillary suture is almost entirely obliterated. On the left side, a small portion of the horizontal part of the palatine is preserved, and the maxillopalatine suture is just visible.

The greater palatine foramen is present on the left side. Anteriorly the incisive canals open in a broad palatine incisive fossa. The median partition has been broken and is absent. Broad, shallow grooves run anteriorly from the fossa on either side of the midline.

PTERYGOID AREAS

The right and left pterygoid areas are preserved posteriorly. The medial and lateral plates have been broken off. Their basal thickness is similar to that in female gorillas, although the lateral plate lamina was probably thicker than the medial.

DENTITION

CENTRAL INCISORS

The left central incisor is intact, although it had been broken at the alveolar border. The crown is heavily worn, the pulp cavity being exposed in an area of 5 mm by 1 mm. The tooth is rather procumbent, its long axis forming an angle of approximately 45 degrees to the plane of the cheek teeth, and resembles male rather than female gorillas in this respect. Just below the cervix there is a thickening of the enamel which represents the cingulum.

To facilitate comparison with the living great apes, incisor crown measurements have been taken using the methods described by Ashton and Zuckerman (1950). The dimensions taken are the labial mesiodistal and labiolingual diameters. These are compared in Table 4 with those of adult gorillas and chimpanzees which had worn dentitions.

Table 4 Measurements of central incisors of UMP 62-11, *Gorilla* and *Pan*

	UMP 62-11		*G. g. gorilla*		*P. troglodytes*	
			males (n=12)	females (n = 11)	males	females
MDi L	10.8	$\bar{x}$	12.4	11.1	10.0 (n=13)	9.9 (n=8)
		95%CL	7.0-17.8	8.2-14.0	5.2-14.8	5.4-14.3
LaLi B	9.1	$\bar{x}$	10.6	9.2	8.9 (n=18	8.8 (n=13)
		95%CL	6.0-15.2	8.5-11.0	6.3-11.2	6.2-11.4

The tooth is closest in size to those of female gorillas. Morphologically, there are no particularly distinctive characters, the tooth being similar to those of gorillas, although smaller.

The root is approximately 20 mm long and appears as a rounded ridge on the nasoalveolar clivus. Just above the cervix, the root has a mesio distal diameter of 9.4 mm and a labiolingual diameter of 8.7 mm. Similar dimensions can be found in small specimens of *Gorilla gorilla.*

The right central incisor was lost during life and the root socket filled with cancellous bone.

LATERAL INCISORS

Both lateral incisors are present and in both the roots are missing for a few millimeters inferior to the alveolar margin. On each root there is a large elliptical wear facet on the lateral (distal) side which in its lower part has eroded the cervical margin of the crown. The facets were formed by the lower canines and are a little unusual.

In male gorillas facets are sometimes found in a similar position, but rarely are these facets as well developed as in UMP 62–11. In the male gorilla, as the lower jaw moves laterally from centric occlusion, one upper canine occludes with the ipsilateral lower canine; this acts as a stop preventing further lateral movement. The contralateral lower canine may or may not have reached the contralateral lateral incisor and so the presence or absence of wear facets is variable. The factor affecting presence or absence is the relative breadth across the outside of the lower canines compared to the distance from the internal margin of one upper canine to the distal margin of the contralateral lateral incisor. The distance across the outside of the lower canines will depend on the bicanine breadth at the cervical margin and on the relative divergence of the axes of the crowns. Thus very divergent lower canine lingual borders, as in many male gorillas (e.g. Duckworth Pr 62.0.1), may prevent formation of wear facets on the upper incisors.

As the tip of the lower canine occludes with the distal border of the upper incisor, the anterior margin of the upper canine occludes with the distal and labial surface of the lower canine, forming there a characteristic wear facet. Very approximately, the distance between the midpoint of the upper lateral incisor wear facet and the midpoint of the upper canine anterior wear facet corresponds to the distance between the tip of one lower canine and the midpoint of the labiodistal wear facet of the other lower canine. This distance in UMP 62–11, measured on the upper dentition, is approximately 48 mm. This gives us some guide to the dimensions of the lower dentition.

The incisor crowns are moderately worn, more so on the left where the occlusal wear facet is approximately 5 mm by 2 mm. On the right the facet is about 3 mm by 1 mm. The loss during life of the right central incisor resulted in the exposure of the front teeth to differential chewing and thus to differential wear.

On the left, the mesial border of the crown is vertical, while the distal border slopes distally to the cervix. The labial border is smoothly convex, the enamel being rather heaped up just below the cervix. The labial surface of the tooth is set at a less acute angle to the plane of the cheek teeth than is the root, the values being approximately 60 and 40 degrees respectively. The lingual border (which strictly speaking also includes the distal aspect) is coarsely wrinkled as in *Gorilla gorilla* and is almost parallel to the plane of the cheek teeth. The lingual surface is thickened at the cervix and from there an enamel "pillar" extends to the occlusal surface. The pillar gets thinner occlusally. Measurements are given in Table 5.

Table 5 Measurements of lateral incisors of UMP 62-11, *Gorilla* and *Pan*

	UMP 62-11			*G. g. gorilla*		*P. troglodytes*	
	L	R		males	females	males	females
MDi L[1]	8.6	8.7	$\bar{X}$	10.6	9.0	8.7	8.8
				(n=11)	(n=13)	(n=5)	(n=5)
			95%CL	8.7-12.5	4.5-13.5	6.9-10.5	7.0-10.6
LaLi B[1]	10.2	10.1	$\bar{X}$	10.7	9.0	8.3	7.9
				(n=11)	(n=13)	(n=18)	(n=13)
			95%CL	7.5-13.9	5.6-12.4	6.1-10.5	5.7-10.1
Breadth across lateral alveolar margins (I[1] B)		39.1	$\bar{X}$	41.7	37.7	37.5	36.2
				(n=19)	(n=20)	(n=14)	(n=12)
			95%CL	38.6-46.7	32.7-42.6	33.8-41.1	32.9-39.5

[1] Comparative data from Ashton and Zuckerman (1950).

Metrically, the lateral incisors are relatively narrow mesiodistally but broad labiolingually. In the second character the teeth resemble those of *Gorilla gorilla,* particularly males. The relatively small mesiodistal diameter is but one reflection of the fact that a number of this specimen's teeth have relatively short mesiodistal diameters when compared to those of the living African apes.

Table 5 also includes measurements taken between the external borders of the lateral incisors at the alveolar margin. Measurements are taken at the incisor alveolar margin to facilitate comparisons between living and fossil material in which the incisor crowns are often lost. The fossil falls between the means for male and female gorillas. Considering the overall small size of UMP 62–11 when compared to the male gorillas we may conclude that, relative to overall size, the fossil has a rather broad incisor region. This suggests again that the specimen is a male.

Small diastemata are present on each side. At the level of the alveolar margin the left diastema is 5.2 mm long. The measurement cannot be taken on the right.

CANINES

The left canine is broken approximately at the level of the cervix although part of the crown is preserved in the distal part of the tooth. The mesial part of the tooth is broken above the cervical margin. Distally, the portion of the root between the cervix and interdental septum is missing.

A slight cingulum is present distolingually. The inferior distal 15 mm of the tip of the labial section of the crown was recovered. The root of the right canine is broken at the alveolar margin. However, part of the crown is preserved —the proximal two-thirds—and this reaches as far proximally as the cervical margin on the mesial half of the lingual side of the crown. Since the middle section of the canine crown, missing on the left, is present on the right, and the tip, although absent on the right, is present on the left, both crowns can be restored with some accuracy.

The reconstructed canines are typically pongid, resembling those of gorillas. A well-marked mesial groove runs almost to the tip of the crown. There are smooth areas of wear on either side of the groove and running parallel to it. Measurements are given in Table 6. In all three dimensions UMP 62–11 falls within the 95 per cent confidence limits for male lowland gorillas and outside the limits for females. For labiolingual breadth and labial height, the fossil falls very close to the means for males; in mesiodistal diameter the fossil is relatively small. The difference in proportion is reflected in the length-breadth index, the Uganda specimen being relatively short mesiodistally. We have already noted that the mesiodistal length of the lateral incisors is also relatively short.

The roots of the canines are approximately 40 mm long and are relatively massive. Associated with the large roots are the strong canine juga described above. Morphological and metrical features of the crown and roots indicate that UMP 62–11 represents a male.

Table 6 C^1 measurements of UMP 62-11 and *Gorilla*

	UMP 62-11		*G. g. gorilla*	
			males	females
Max L	*18.6	$\bar{X}$	21.2	14.5
			(n=20)	(n=20)
		95%CL	18.3-24.1	12.8-16.2
Trans B	*15.7	$\bar{X}$	16.0	11.2
			(n=20)	(n=20)
		95%CL	13.7-18.2	9.5-12.8
La H	*27.6	$\bar{X}$	29.1	17.1
			(n=7)	(n=11)
		95%CL	19.8-38.4	14.4-19.8
Index L/B x 100	118.4	$\bar{X}$	133.2	130.1
			(n=20)	(n=20)
		OR	115.4-151.3	112.5-145.4

FIRST PREMOLARS

The protocone is broken away in the left P^3. The crown is broad buccolingually and the roots well-developed. There are two buccal roots and a single lingual root. A premolar jugum is associated with the mesial buccal root and extends superiorly 18–20 mm above the cervical border.

The mesiobuccal angle slopes sharply inferiorly and distally and bears a wear facet from the distal face of the main cusp of P_3. This same tooth has left a wear facet in the middle of the mesial border of P^3. A wear facet for the mesial face of P_3 can just be seen on the distal aspect of the cervical region of the left upper canine. In normal centric occlusion, the paracone-protocone crest of P^3 generally lies directly superior to the line of contact of P_3 and P_4. The distance from the paracone-protocone crest of P^3 to the distal wear facet on C^1 is between 7 and 8 mm. This is approximately equivalent to the distance between the tip of the main cusp of P_3 and its distal border. The tip of this cusp generally lies about half way along the mesiodistal (projected) length of P_3. We may conclude therefore that the projected length of P_3 parallel to the long axis of the cheek teeth would have been between 14 mm and 18 mm and its maximum length perhaps between 16 mm and 20 mm.

A groove runs superiorly, between the two contact facets described, along the middle of the mesial face of P^3. There is a slight cingulum on the mesial half of the labial border running obliquely inferiorly and distally.

The paracone is moderately worn, a small area of dentine being exposed. The distolingual surface of the paracone shows wear facets from articulation with the protoconid of P_4.

The crown of the right P^3 is intact, the paracone is larger and higher than the protocone; paracone height above cervix, *11.5 mm, and protocone height above cervix, *8.0 mm. Both cusps show moderate wear, dentine being exposed on the paracone tip.

A high crest runs between the cusps and is itself traversed by a mesiodistal sulcus running from the small pit which represents the anterior fovea to the talon basin. A small groove, almost obliterated by wear, runs across the tooth parallel to the distal border. The distal border is convex and has a wide (*4.0 mm long) contact facet with P^4. The buccal and lingual surfaces of the crown slope relatively sharply towards the occlusal surface. The buccal surface in particular is less vertically oriented than the normal condition in gorillas and chimpanzees. Measurements are given in Table 7.

Metrically UMP 62–11 is closest to *Gorilla gorilla*; in maximum length and buccolingual breadth the fossil is just a little short of the means for female gorillas. However, the mesiodistal length of the crown measured in the midline of the tooth is 2 mm shorter than the female means and is outside the 95 per cent confidence interval for females. The shape of the crown is more triangular in the fossil than in gorillas (and chimpanzees), the mesiobuccal corner of the crown projecting some way mesial to the rest of the mesial border, particularly at the level of the cervix. If the fossil is to be regarded as ancestral to living gorillas, then the following changes have occurred in P^3 structure since the Miocene. The tooth has become larger, the tips of the cusps farther apart, and the buccal and lingual surfaces more vertical. The shape of the paracone in

Table 7 P^3 measurements of UMP 62-11, Gorilla and Pan

	UMP 62-11			G. g. gorilla		P. troglodytes	
	L	R		males (n=20)	females (n=20)	males	females
MDi L	8.0	8.2	$\bar{X}$	10.9	10.2	7.3 (n=14)	7.0 (n=12)
			95%CL	9.4-12.4	9.0-11.4	6.2- 8.3	6.2- 7.9
Max L	10.6	10.7	$\bar{X}$	12.3	11.0	8.1 (n=14)	7.9 (n=12)
			95%CL	10.8-13.8	9.5-12.4	6.8- 9.3	7.0- 8.9
BuLi B	-	14.6	$\bar{X}$	15.6	14.8	10.5 (n=13)	10.5 (n=11)
			95%CL	13.4-17.8	12.8-16.8	9.3-11.6	9.2-11.9

particular has changed so that the mesial border no longer slopes backwards but has become more nearly vertical. The cusps have become higher and more pointed, the crests sharper and more clearly defined.

SECOND PREMOLARS

Each P^4 is a very broad tooth with strongly sloping buccal surfaces like P^3. The paracone is somewhat higher than the protocone. Roots are a little smaller than in P^3, the buccal root being approximately 12 mm long. There is a small cingulum at the mesiolingual corner and the rest of the lingual surface is etched with vertical grooves. On the buccal surface there are two vertical grooves, one on the mesial moiety, the other on the distal. Such features are seen occasionally in gorillas.

The paracone and protocone are united by a low crest. There is a small anterior fovea which is displaced towards the buccal side of the crown. The talon is similar to that of P^3 and bulges distally, there being a rather long area of contact with M^1 (5 mm) which has worn a concave facet on the mesial border of M^1.

The crown is moderately worn with dentine exposed on the protocone. Mesial to the paracone-protocone crest there are wear facets for the distal surfaces of the protoconid and metaconid of P_4, and distal to the crest wear facets for the mesial cusps of M_1. Measurements are given in Table 8.

In breadth UMP 62–11 falls within the gorilla range, in length between gorillas and chimpanzees. Like the lateral incisor, canine, and first premolar,

Table 8 P^4 measurements of UMP 62-11, Gorilla and Pan

	UMP 62-11			G. g. gorilla		P. troglodytes	
	L	R		males	females	males	females
MDi L	7.9	8.0	$\bar{X}$	11.1 (n=20)	10.6 (n=20)	7.0 (n=14)	7.0 (n=12)
			95%CL	9.9-12.2	9.1-12.0	6.4- 7.7	6.4- 7.6
BuLi B	14.8	14.7	$\bar{X}$	15.3 (n=20)	14.4 (n=19)	10.2 (n=13)	10.2 (n=11)
			95%CL	13.7-16.8	12.5-16.4	8.4-10.9	9.6-10.8

this tooth is relatively short mesiodistally. The cusps are lower and the crests less sharp than is the case in living gorillas.

The antemolar teeth as a whole are rather broad when compared to the molars. Thus the range of the ratio (BLi B M^1/BLi B P^4) × 100 in gorillas is as follows: for 20 males, the mean is 97.5 and the range is 89.4–108.3; for 19 females the mean is 97.8 and the range 92.7–110.7.

The value of this ratio for the left P^4 and M^1 of UMP 62–11 is 116.5, the P^4 breadth being relatively greater than in any of 39 gorillas. An explanation is difficult to find. Perhaps the broadening of P^4 is associated with the breadth of the anterior dentition and alveolar region in general. The great cervical breadth of P^4 and the closeness of the tips of the paracone and protocone result in the markedly sloping buccal surface, such a slope being absent in living gorillas where the surface is more nearly vertical.

Once again, if the specimen is regarded as a proto-gorilla, phylogenetic trends have been towards increase in cusp size and height; changes in shape are also involved, (e.g., slope of buccal and lingual surfaces becoming steeper correlated with a relative widening of the intercuspal occlusal area).

FIRST MOLARS

The left tooth is rhomboidal, with a marked distal convex bulge. Paracone, metacone, and hypocone are subequal; the protocone is the largest cusp. The fine features of occlusal morphology have been largely obliterated by wear. Small patches of dentine are exposed on the paracone and metacone. A somewhat larger area on the hypocone is 2.5 mm in diameter, and the largest area occurs on the protocone, where it is 4.5 mm in diameter. The distal bulge has worn a wear facet on the mesial face of M^2, the area of contact being 4.5 mm long.

The groove between paracone and metacone is still patent. There is a marked buccal cingulum between the two buccal cusps and a slight cingulum at the buccodistal corner. The cingulum runs onto the distal surface. In lateral view the buccal cingulum gives the appearance of a row of inferiorly projecting, isolated spurs. The lingual cingulum has been largely obliterated by wear except for a fine groove running parallel to the mesial margin of the protocone and 1 mm internal to it. This cingulum probably ran only as far as the mesial margin of the hypocone and not around the hypocone.

All the roots are present. The lingual root diverges lingually at an angle of 30 degrees to the buccal roots and has a vertical groove on its lingual aspect. The lingual root is 9.4 mm thick mesiodistally just above the cervix and has a vertical length of about 15 mm. The buccal roots are rather more delicate and perhaps not much more than 12–13 mm in vertical length.

The right M^1 is essentially similar to the left, although the area of dentine exposed on the hypocone is somewhat larger on the right. Measurements are given in Table 9. In size, the first molars of UMP 62–11 fall between those of chimpanzees and gorillas. Length/breadth indices are a little lower than those of gorillas and rather higher than those in chimpanzees. Like the other teeth, this tooth is relatively small mesiodistally when compared to those of gorillas. Few details of the occlusal surface can be determined, although the unworn crowns were probably similar to UMP 66–41 from Napak IV and UMP 62–07

Table 9 M^1 measurements of UMP 62-11, *Gorilla* and *Pan*

	UMP 62-11			*G. g. gorilla*		*P. troglodytes*	
	L	R		males (n=20)	females (n=20)	males	females
MDi L	*11.7	*11.6	$\bar{X}$	14.8	14.1	9.9 (n=14)	9.8 (n=12)
			95%CL	13.0- 16.6	12.5- 16.6	8.8-11.0	8.7-11.0
BuLi B	12.7	12.6	$\bar{X}$	15.6	14.8	11.2 (n=12)	11.2 (n=11)
			95%CL	13.7- 17.5	13.2- 16.6	10.1-12.2	9.9-12.5
Index L/B x 100	92.1	92.1	$\bar{X}$	94.7	95.2	89.2 (n=12)	88.1 (n=11)
			OR	84.0-105.0	85.8-105.1	82.6-94.5	79.5-95.5

from Napak V. In all three lingual cingula are present and the unworn molars show some resemblances to those of *Gorilla gorilla.* These resemblances are discussed in the following chapter.

The degree of development of the roots of M^1 in UMP 62–11 is midway between that seen in gorillas and that of chimpanzees and appears to be correlated, at least to some extent, with tooth crown size. Measurements of UMP 62–11, a female gorilla, and a male chimpanzee first molars, selected at random, are listed in Table 10.

SECOND MOLARS

As in the first molar the protocone is the largest cusp, the paracone, metacone, and hypocone being smaller and subequal in area. The lingual and buccal sides converge very slightly from front to back. There is a distal bulge, as in P^3, P^4, and M^1, and since the lingual side is longer than the buccal, the bulge appears to be more prominent in the lingual half of the distal border.

The crown shows some wear, not as much as M^1, but enough to expose dentine in a small area on the protocone. The crests between paracone and protocone, and metacone and hypocone, have been worn so that the occlusal surface now shows very little relief. A trace of the anterior fovea is present, closed lingually by the protoconule.

Table 10 Crown and root dimensions in UMP 62-11, *Gorilla* and *Pan*

	Gorilla female DPr52.0.4	UMP 62-11	Chimpanzee female DPr53.0.9
MDi L	*13.9	*11.7	*10.2
BuLi B	15.5	12.7	*11.2
Crown area	*201.55	*148.59	*114.24
Vertical L lingual root	*18.0	*15.0	*13.5
MDi T lingual root	11.1	9.3	7.7
Vertical L buccal roots (max)	*15.0	*13.0	*12.0

The buccal cingulum is similar to that of M^1, appearing as a series of spurs. It is most prominent between the two main cusps and on the buccodistal corner. A sulcus runs parallel to the distal border in its buccal half and separates the metacone-hypocone crest from the flattened most distal part of the crown. The lingual cingulum runs from the midpoint of the mesial surface of the protocone, around the mesiolingual corner, along the lingual border, and around the hypocone onto the distal border. The cingulum is beaded and the lingual slopes of protocone and hypocone are etched with vertical grooves which merge into the beading.

The roots are less widely splayed than is the case for M^1. The buccal roots have a maximum vertical length of 13.0 mm and the lingual root a length of about 16–17 mm. The latter has a mesiodistal thickness of 11.5 mm just above the cervix.

The mesiolingual corner of the right M^2 is missing. Apart from this, the features of crown and roots are the same as for the left side. Measurements for M^2 are given in Table 11. UMP 62–11 falls within the 95 per cent confidence limits for female gorillas and is a relatively small tooth when compared to those of male gorillas. The cusps are relatively lower and their sides less steeply sloping than in gorillas. In general, though, the Uganda fossil is reminiscent of gorillas in molar morphology.

Table 11 M^2 measurements of UMP 62-11, *Gorilla* and *Pan*

	UMP 62-11			*G. g. gorilla*		*P. troglodytes*	
	L	R		males (n=20)	females (n=20)	males	females
MDi L	*13.1	*13.1	$\bar{X}$	16.0	14.8	10.2 (n=14)	10.0 (n=12)
			95%CL	13.9- 18.1	12.8- 16.8	8.8-16.8	8.7-11.3
BuLi B	14.0	14.1	$\bar{X}$	16.7	15.6	11.7 (n=13)	11.4 (n=11)
			95%CL	14.7- 18.5	13.7- 17.5	10.6-12.8	10.0-12.9
Index L/B x 100	93.5	92.9	$\bar{X}$	96.2	94.7	87.4 (n=13)	86.7 (n=11)
			OR	91.1-106.2	87.4-104.5	80.2-94.0	77.4-95.1

THIRD MOLARS

The crowns are less worn than in the other molars and the trigon crests are still well marked. The protocone is the largest cusp. Buccal and lingual cingula are well developed as in M^2, the lingual cingulum being especially prominent around the protocone, thus giving the mesial moiety of the tooth a greater breadth than the distal. The contact facet with M^2 is a little over 3 mm long.

Measurements are given in Table 12. Although relatively broader than M^3 of female gorillas, the lengths and breadths of M^3 fall within the 95 per cent confidence limits. As a general feature of this dentition, mesiodistal lengths are reduced when compared to gorillas, particularly male gorillas. The increased

Table 12 M^3 measurements of UMP 62-11 *Gorilla* and *Pan*

	UMP 62-11 L	UMP 62-11 R		*G. g. gorilla* males (n=20)	*G. g. gorilla* females (n=20)	*P. troglodytes* males (n=11)	*P. troglodytes* females
MDi L	12.8	12.7	$\bar{X}$	15.0	13.7	9.2	9.0 (n=10)
			95%CL	13.0- 17.1	11.6- 15.8	7.9-10.5	7.7-10.3
BuLi B	14.4	14.3	$\bar{X}$	15.7	14.8	11.0	10.9 (n=9)
			95%CL	13.6- 17.8	12.4- 17.2	9.8-12.2	9.5-12.2
Index L/B x 100	88.9	88.8	$\bar{X}$	95.8	92.7	84.0	83.0 (n=9)
			OR	87.8-111.5	82.1-103.8	76.2-97.7	75.0-89.6

lengths in male gorillas are probably associated with a general increase in head length, as pointed out by Gregory (1916, p. 276).

THE UPPER DENTITION AS A WHOLE

Table 13 sets out a number of measurements for the upper dentition as a whole. The length of the cheek tooth row—from P^3 to M^3—is 54.4 mm. This falls towards the lower part of the 95 per cent confidence interval for female gorillas. This measurement reflects the relatively short mesiodistal lengths of the cheek teeth when compared to those of gorillas.

The tooth row is a little compressed—the combined mesiodistal lengths of cheek teeth are 56.1 mm, 1.7 mm greater than P^3–M^3 length. The crowding is best described as moderate when compared to the condition in the living great apes (see Appendix 1).

The other measurements listed in Table 13 are taken across the tooth rows and are maximum external measurements. The narrowing from canine, to second premolar, to third molar is a reflection of the relatively great breadth of the canine region. The proportions are similar to those seen in male gorillas (see Appendix 1). (In overall size the specimen is closest to female gorillas.) The

Table 13 Measurements on the upper dentition of UMP 62-11, *Gorilla* and *Pan*

	UMP 62-11		*G. g. gorilla* males (n=20)	*G. g. gorilla* females (n=20)	*P. troglodytes* males (n=14)	*P. troglodytes* females (n=12)
P^3 -M^3 L	54.4	$\bar{X}$	67.6	61.6	43.6	43.6
		95%CL	61.3-73.9	52.0-71.2	39.8-47.4	40.1-47.1
C^1 B	*69.1	$\bar{X}$	75.0	58.2	58.3	54.6
		95%CL	65.7-84.4	45.0-71.4	54.1-62.5	48.7-60.6
P^4 B	64.8	$\bar{X}$	71.3	62.0	57.6	57.5
		95%CL	63.8-78.7	52.5-71.6	52.5-62.8	52.3-62.8
M^3 B	60.5	$\bar{X}$	71.4	63.9	55.7	56.8
		95%CL	64.3-78.4	56.8-71.1	49.9-61.5	50.8-62.9

tooth row is therefore convergent posteriorly, yet there are clearly a number of points which need to be made about this statement. The measurements listed are external breadths. Because of the relatively great breadth of P^4, the breadth at P^4 is much greater than the breadth at M^3, or indeed at M^1. Yet another estimate of divergence could be the minimum internal breadths between homologous teeth, measured at the cervix. Thus for UMP 62–11 the values are: between C^1, *38.5 mm, between P^4, 35.7 mm, and between M^3, 32.3 mm.

The internal narrowing between C^1 and M^3 is 6.2 mm, in contrast to an external narrowing of 8.6 mm, and is a reflection of the fact that C^1 and P^4 are broader teeth than M^3.

However, this still does not satisfactorily answer our problem. Since the function of the cusps and basins of the cheek teeth are occlusion, the best index of convergence—the best way of comparing the relevant parts of the upper tooth row and the relevant parts of the lower—is to utilize distances between cusps and basins. Accordingly, the distances between the tips of the protocones of the homologous pairs of cheek teeth have been measured. When we come to discuss the type of lower dentition with which UMP 62–11 would have occluded, we shall then know the absolute (and relative) positions of the central basins of P_4–M_3. The interprotocone breadths for UMP 62–11 have to be estimated because of occlusal wear. They are : at P^4, *41.8 mm, at M^1, **41.2 mm, at M^2, *40.0 mm, and at M^3, *40.4 mm. Values for hypocones show a similar trend.

Thus there is a gradual convergence from front to back, although M^3 is rotated a little so that the protocone has swung distobuccally. When we come to discuss the mandible of *Dryopithecus (Proconsul) major* from Songhor (NMK 190,1), we shall be able to examine the breadths between the basins of the lower teeth with which the protocones occlude, and thus to compare these mandibular and maxillary tooth rows. It seems that this is the most satisfactory functional measure of tooth row convergence and divergence.

Discussion of the Maxilla

UMP 62–11 was adult; the third molars had been in occlusion, but not for very long. The specimen is fairly clearly a male, at least unless this Miocene species exhibited no (appreciable) sexual dimorphism. This is unlikely, for even in those hominoid species which exhibit little size dimorphism, the canines and associated structures are larger in males than in females. The only clear exceptions are species of *Hylobates* and *Symphalangus.*

The canines are as large as those of male gorillas and clearly do not resemble the canines of female gorillas or chimpanzees. Associated with these large canines is the broad anterior palatal and alveolar region. The shape of the alveolar region and palate and the morphology of the paranasal areas are typical of male gorillas. The height of the face from nasion to nasospinale is also absolutely large and falls within the range for male gorillas. However, although the proportions are different, in overall size UMP 62–11 is closest to the female gorilla. The facial breadth measurements show that the specimen was relatively narrow faced, even considering the small size of the fossil. In fact, indications are that the fossil was narrower faced and of more delicate upper facial build even than many chimpanzees.

Thus we have an individual with a high, rather narrow face, a face which is at least as prognathous as those of female gorillas. From what is known of the lateral orbital and malar regions, and from what can be deduced about the masticatory musculature from the size of the cheek teeth, the fossil had an upper face similar again to that of a female gorilla; a supraorbital torus was probably present.

Since we can make but a poor estimate of the size of the masticatory muscles, and since we have no idea at all as to brain size, it is difficult to say whether or not the specimen possessed a sagittal crest. Crests occur in gorillas only when the dentition is proportionately very large; it is possible that UMP 62–11 had a sagittal crest.

Incisor tooth wear is perhaps slightly heavy when compared to premolar and molar wear, but it should be remembered that the single central incisor bore the brunt of the anterior chewing stresses. The postcanine dentition is relatively small compared with that of gorillas, most of the dimensions falling within the range of female gorillas. The mesiodistal lengths tend to be relatively smaller than buccolingual breadths and length/breadth indices are accordingly low. Thus, the mesiodistal lengths of P^3, P^4, and M^1 fall below the lower 95 per cent confidence limit for female gorillas. M^1 is the only tooth in which both dimensions fall outside at least the female confidence intervals.

The morphology of the dentition is gorilla- rather than chimpanzee-like. This applies particularly to the anterior dentition. The cheek teeth show some similarities, but the cusps are not as high, conical, steep-sided, and sharp as in *G. gorilla*. However, it is probable that UMP 62–11 is sampled from a species which is ancestral to, or close to the ancestry of, *G. gorilla*. The living gorilla is predominantly a shoot- and leaf-eater rather than frugivorous like the chimpanzee (Schaller, 1963, 1965). This is at least a partial explanation for its lophodont cheek teeth with high, steep-sided cusps, and sharp intercuspal crests. UMP 62–11, together with other material from Napak, discussed below, show that the probable Miocene forerunners of *G. gorilla* also had somewhat lophodont teeth, although this trait was not as well developed as in the living form.

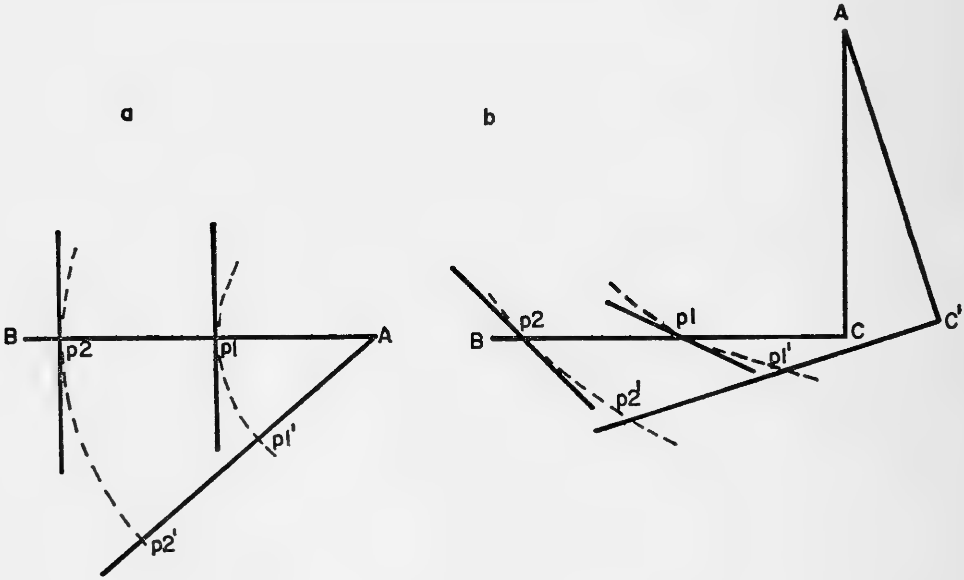
Two further points remain to be discussed: the depth of the palate and the degree of pneumatization of the maxilla.

It is perhaps a little misleading functionally to speak of palatal depth. What is really meant is alveolar height—the projection inferiorly of the alveolar tooth-bearing processes. The height of the process is correlated first with the size of the tooth roots; as roots get longer and more robust, the alveolar processes project more, and the palate gets deeper. However, this is not the whole story. Considering M^1, we have noted that the crown- and root-size of UMP 62–11 are intermediate between those of a female gorilla and a male chimpanzee. The palatal depth of the female gorilla (Duckworth Pr 52.0.4) at M^1 is about 20 mm, and of the male chimpanzee (Duckworth Pr 53.0.9) about 10 mm. However, palatal depth in the fossil is only some 6 mm. Also, the vertical lengths of the lingual roots of premolars and molars are fairly constant in UMP 62–11, although the palate deepens somewhat from front to back. Palatal depth between C^1 and P^3 is about 4 mm and at M^2 about 7.5 mm. Clearly, some factor other than root size is involved.

Davis (1964) has recently discussed the mechanics of chewing in the case of the herbivorous carnivore, *Ailuropoda,* the Giant Panda. Figure 2 (a), which is adapted from Davis, represents the situation in which the point of mandibular articulation is at the level of the plane of the cheek teeth. Such a system is seen among the Carnivora with the clear exception of *Ailuropoda.* It is also found in the Prosimii. A point p_1 on the lower dentition travels along the arc $p_1^1 - p_1$ during centric occlusion. A tangent to the arc drawn at p_1 is perpendicular to the tooth row—this is also the case for p_2 and for any other point along the tooth row. During occlusion there is little or no mesiodistal movement.

Figure 2 (b) represents a mandible with the point of articulation raised above the tooth row. The tangent at p_1 to the arc $p_1 - p_1^1$ crosses the tooth row obliquely and the obliquity of the tangent increases from front to back, from B to C. Thus, from front to back there is an increasing component of horizontal, mesiodistal, movement as the teeth occlude. Even without anteroposterior or rotatory movements at the temporomandibular joint (and these would certainly have occurred), any food material placed between the upper and lower teeth will be subject to horizontal as well as vertical chewing movements. "In *Ailuropoda* . . . an anteroposterior grinding action is achieved by elevating the articulation" (Davis, 1964, p. 69). Similarly in the herbivorous great apes, the distance between the mandibular articulation and the plane of the cheek teeth is relatively great.

FIGURE 2. Representation of occlusal relationships when the point of mandibular articulation is (a) at the level of, and (b) above, the plane of the tooth row (from Davis, 1964; 71, fig. 32).



There are two ways of increasing this distance: by raising the plane of the temporomandibular joint, and by lowering the tooth row. The tooth row is lowered by increasing the inferior projection of the alveolar processes, carrying the cheek teeth further inferiorly, which results in a deepening of the palate.

If this line of argument is correct, Miocene forms show evidence of being less well adapted than modern gorillas to chewing tough vegetable material. As we have seen, the morphology of the cheek teeth and of the roots also suggest this.

Davis (1964, p. 69) has also pointed out that increasing the depth of the skull increases the volume of the temporal fossa thus providing greater space for masticatory muscles, improves the muscular efficiency for producing pressure at the occlusal surfaces, and increases the magnitude of the vertical stresses that the skull can withstand.

As was noted above, the presence of marked wear facets on the upper lateral incisors suggests a less tight interlocking of the upper and lower canines than in *G. gorilla*. The "anchoring" of the anterior dentition in the living species may be associated with an increase in the grinding efficiency of the cheek teeth. (The development of overbite in post-Neolithic human populations is said to serve a similar function.)

As the alveolar processes lengthen and carry the dentition inferior to the plane of the palate, the palatal processes can become pneumatized by extensions of the maxillary sinuses. As the bony parts of the face become more extensive, pneumatization will spread, too, in order to lighten the face. The maxillary sinuses of UMP 62–11 are probably as extensive superiorly (as far as the orbits) and laterally (into the zygomatic processes) as in living gorillas. However, inferiorly—into the palate and between the tooth roots—the sinuses are not as extensive in the fossil. Neither do they extend as far anteriorly, for in UMP 62–11 they stop at the level of the distal border of P^4. In living gorillas they spread much further forward. But this lack of pneumatization is no doubt also correlated with the brevity of the alveolar processes.

In conclusion, the specimen represents, with a high degree of probability, a male individual, which may well be sampled from a species ancestral to, or close to the ancestry of, the living gorilla. However, the Miocene form is smaller than its putative descendants, and less well adapted to a diet consisting almost exclusively of tough vegetable material.

UMP 62–10 and UMP 66–01

(FIG. 20)

The specimen consists of two fragments of the horizontal ramus of a large anthropoid. The portion of the right ramus, UMP 62–10, has been fully described by Allbrook and Bishop (1963) and figured in Bishop (1963b). This fragment contains the roots and extensively worn crown of M_1, the roots of M_2, and the mesial root of M_3. The fragment from the left side, UMP 66–01, added since Allbrook and Bishop's description, consists of several adjacent pieces of the ramus. These pieces have never been fully described before.

Opposite M_1 of UMP 62–10 the internal surface of the mandible slopes lingually at an angle of about 60 degrees to the occlusal plane. More distally, opposite M_2 and M_3, the internal border falls away more sharply. Externally, the buccinator crest is present opposite the mesial root of M_3 and the distal root of M_2 where it begins to merge into the horizontal ramus as the superior lateral torus.

No attempt has been made to estimate the crown size of M_2 and M_3; these teeth are present in more complete form in the left fragment, UMP 66–01. Part of the crown of right M_1 has been preserved at the distobuccal corner. Traces of a large wear facet are preserved on the hypoconid. Crown dimensions of M_1 have been estimated by measuring root dimensions at the cervical border and comparing these with the root dimensions of intact crowns of other molars from East African Miocene deposits. They are: MDi L, **11.8 mm, Tri B, *10.8 mm, and Tal B, *11.0 mm.

One piece of UMP 66–01* comes from immediately to the right of the symphysis and consists of the most anterior 20 mm of the planum alveolare. Anteriorly the most distal 15 mm or so of the roots of the incisors is preserved. These roots are very narrow mesiodistally and more elongate labiolingually. It is impossible to estimate dimensions since the roots are broken some distance below the alveolar margin and obliquely to their longitudinal axes. The medial border of the fragments forms the right side of the symphyseal joint. An approximate estimate of the bilateral distance between the distal borders of lateral incisors is not more than 23 mm. Posteriorly on the distal margin of the fragment, a small portion of the canine alveolus is preserved. Although there is some difficulty in orienting the fragment accurately, it is probable that the anterior 20 mm of the planum alveolare sloped gently posteriorly and inferiorly at an angle of approximately 30 degrees to the occlusal plane.

The remaining piece of the left side of this mandible is reconstructed from several fragments, also from the UMP 66–01 lot. Crowns or roots of the tooth row from canine to last molar are present, together with the adjacent parts of the horizontal ramus and two small pieces of the ascending ramus.

One piece of the ascending ramus represents what is probably the most superior portion of the anterior border. The crista endocoronoidea and the anterior portion of the crista endocondyloidea are present on the internal surface and these circumscribe the inferior corner of a planum triangulare. Where the cristae join, the ramus is 11 mm thick.

Laterally, the horizontal ramus runs from canine to last molar. The buccinator crest is preserved opposite M_3. The ramus is 24.5 mm thick at the level of the mesial moiety of M_3. Anteriorly the crest merges into the superior lateral torus which finally disappears at the level of M_1. Between M_1 and the canine and premolar juga the lateral face of the mandible is slightly concave. The root of the canine and the mesial root of P_3 have associated with them prominent alveolar juga which fuse inferiorly. At the level of the canine the broken mandible is approximately 30 mm deep. Parts of the mental canal are exposed in various places on the inferior portion of the fragment. The position of the mental foramen is indicated by the presence of lipping anteriorly and by the most distal part of the canal posteriorly. The foramen was probably single and is situated below the midpoint of P_3 approximately 29 mm below the cervical border.

Internally, the ramus is preserved between the distal border of the canine and the back of the trigonum postmolare. Posteriorly, the most inferior 13 mm of the crista pharyngea merges into the superior alveolar margin. The most superior 15 mm or so of this margin is moderately well preserved. Opposite M_3

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* I should like to thank Prof. P. V. Tobias for help with the interpretation of this fragment.

the medial border falls abruptly away from the tooth, while opposite M_1 the slope is approximately 60 degrees to the occlusal plane. The slope becomes shallower anteriorly. Opposite P_3 the most superior 25 mm of the margin is preserved and the morphology indicates that anteriorly a long and gently sloping planum alveolare was present, sloping backwards to the superior transverse torus.

The most distal 24 mm of the canine root is preserved. The root is massive and is responsible for the lateral convexity at this part of the mandibular ramus. Length and breadth measurements of the crown would have been approximately 16 mm and 12 mm. The root curves medially at an angle of between 70 and 80 degrees to the occlusal plane. This angle increases proximally, suggesting that the longitudinal axis of the crown would have been at 80 or more degrees to that plane. The mesial root and the alveolus for the distal root of P_3 are preserved. The most mesial point on the root is level with the most distal part of the canine root. The tooth is massive and large, the long axis being set at about 40 degrees to the axis of the other cheek teeth. Length and breadth of the crown have been estimated at about 16 mm and 9.5 mm. From the roots of P_4 very approximate estimates of crown length and breadth can be made. These are 9.5 mm and 10.0 mm. No estimate was possible for M_1; dimensions of M_1 were estimated from the opposite side of the jaw (UMP 62–10). The crown of M_2 has been broken off inferiorly and distally from the mesial border of the occlusal surface to the distal cervical margin. Fragments of weathered enamel remain on the mesial border, on the buccal border of the protoconid, and on the lingual border of the metaconid. Dentine remains exposed on the protoconid wear facet. This facet was some 3 mm in diameter, a little smaller than the wear facet on right M_1. Since the mesial border of both M_2 and M_3 are present, the length of M_2 can be obtained. Buccolingual crown diameters have been estimated from root dimensions and are therefore less reliable. The measurements are; MDi L, *13.0 mm, Tri B, **12.2 mm, and Tal B, **12.0 mm.

M_3 is the best preserved tooth crown. Enamel is absent from all but the most mesial and distal parts of the lingual border, and from the protoconid. An area of dentine barely 2 mm in diameter is preserved on the protoconid. Wear facets of similar size are also present on hypoconid and hypoconulid. The tooth narrows distally and is triangular in occlusal view. The dimensions are: MDi L, 15.0 mm, Tri B, 12.5 mm, and Tal B, *10.4 mm. The total length of the cheek tooth row is approximately 63 mm.

UMP 67–28

Remains of several large chimpanzee-sized vertebrae from Moroto II have been described and figured by Walker and Rose (1968). They most probably come from the same specimen as the maxillary and mandibular specimens UMP 62–11, UMP 62–10, and UMP 66–01. Particularly well-preserved is a middle lumbar vertebra, UMP 67–28. Morphologically the vertebra is like that of living hominoids rather than cercopithecoids. Walker and Rose note that the vertebra resembles those of *Pan* and *Gorilla,* with a few hominid features. Resemblances to *Pan* and *Homo* may well be primitive characters, or those associated with body size, while those to *Gorilla* could indicate that this Miocene pongid is ancestral to the living ape. Walker and Rose (1968, p. 981) conclude that there are "quite eclectic resemblances to modern hominoid vertebrae to be seen in the Moroto vertebra, but none of them would necessarily preclude *Dryopithecus* (*Proconsul*) *major* from being a direct ancestor of the genus *Gorilla*."

DISCUSSION OF THE MOROTO II PONGID

UMP 62–10 and 66–01 with a high degree of probability represent the same individual. The relationship between the maxilla (UMP 62–11) and these mandibular parts remains to be discussed. Both represent a species of large Miocene pongid. Although little of tooth crown morphology (particularly mandibular) can be seen, from what is known of other Miocene pongid species and of living *Pan troglodytes* and *Gorilla gorilla,* the two sets of material can plausibly be referred to the same species. In 1963, Allbrook and Bishop assigned UMP 62–10 tentatively to *Proconsul major* [*Dryopithecus* (*Proconsul*) *major* according to Simons and myself].

The presumed morphology of the horizontal and ascending rami would have resembled broadly those of moderately robust female gorillas, although canine size suggests that the individual was male. Unfortunately, the inferior portion of the symphysis is not preserved, and it is not possible to tell whether or not the inferior margin projected posteriorly as a simian shelf.

Can the maxillary and mandibular material (UMP 62–11, 62–10, and 66–01) be referred to a single individual? One way to answer this is to consider the probable dimensions of the mandibular teeth which would be associated with UMP 62–11. Very approximate lower cheek teeth lengths can be gauged by measuring between the hypocone tips of adjacent upper cheek teeth. Thus, the distance between the hypocones of P^4 and M^1 is approximately equal to the length of M_1, and so on. The length of M_3 can be estimated by measuring from the hypocone of M^2 to the distal border of M^3. Estimated lengths from UMP 62–11: P_4, 9.0 mm; M_1, 12.0 mm; M_2, 13.0 mm; and M_3, 15.0 mm. Measured lengths of UMP 62–10 and 66–01: P_4, **9.5 mm; M_1, **11.8 mm; M_2, 13.0 mm; and M_3, 15.0 mm.

The correspondence between estimated and measured lengths is good. As is the case for UMP 62–11, the lower teeth are closer in size to those of gorillas than to those of chimpanzees. If the fossil lower tooth measurements are compared to those of female gorillas, it will be noted that the fossil breadths lie close to or within the confidence interval of the living pongids, while the lengths of all but M_3 lie generally below the lower confidence limit.

There is a contrast in the state of preservation of the maxilla and the mandibular fragments, this could be due to earlier weathering out of the latter. Although the two sets of material were found separated by some distance on opposite sides of an erosion gully, there is no geological reason why they should not represent the same individual. However, at least one further individual of the same species is represented at Moroto by UMP 62–12. Accordingly, the allocation of UMP 62–11, 62–10, 66–01, (and 67–28) to the same individual should be regarded as tentative.

Using casts of mandibular remains of *D.* (*P.*) *major* from Songhor, a mandible has been constructed to occlude with UMP 62–11. This mandible is discussed in more detail in a later chapter. From this reconstructed mandible, estimates of various mandibular dimensions have been made. Although the Moroto maxillary and mandibular remains may not belong to the same individual, the overall mandibular dimensions inferred from the reconstructed mandible of the undistorted maxilla have been used for estimates of the dimensions of the fossil mandible from Moroto II. These dimensions are listed in Appendix 2.

Represented at Moroto, therefore, is at least one individual of a species of large pongid, morphologically and metrically suitable for consideration as an ancestor of *Gorilla gorilla.* The species represented is most probably *D. (P.) major,* as Allbrook and Bishop (1963) suggested. However, Leakey (1963, p. 32) disagrees with this allocation and states that, "in my opinion it is not . . . [*Dryopithecus major*] at all. It is pongid, possibly ancestral to Gorilla." The taxonomic position of these specimens will be discussed in detail in subsequent chapters.

UMP 62–12

This tooth, a left upper canine described by Allbrook and Bishop (1963), demonstrates the existence of at least a second individual of *D. (P.) major* at Moroto II. It is similar to Napak canines UMP 62–03, 62–04, and 62–05 in all features of both crown and roots. Measurements are given in Table 14, p. 47, and show the metrical similarities within this sample of canines. There is very little size difference between the various specimens, and, except for the length of UMP 62–12, all measurements fall within the 95 per cent confidence intervals for a small sample of male gorillas and outside those for females.

CHAPTER V. *DRYOPITHECUS (PROCONSUL) MAJOR* FROM NAPAK, UGANDA

HISTORY OF DISCOVERY

Primate material from Napak in Uganda was first described in 1958 by Leakey (*in* Bishop, 1958). Further material from Napak was discovered and described in subsequent years. For the purpose of this study, the three primate-yielding sites Napak I, Napak IV, and Napak V are regarded as stratigraphically contemporaneous. The pongid material recovered from these sites belongs, in all probability, to a single species, *D. (P.) major.* It will be discussed tooth by tooth, rather than site by site.

SPECIMENS

UPPER DENTITION

INCISORS

UMP 66–03. A right upper lateral incisor from Napak V, the specimen was mentioned by Bishop (1964, p. 1329). The tip of the root is missing, together with most of the crown, except for the proximal portion of the lingual face. The cervical border extends farther towards the occlusal surface on the mesial and distal faces than on the lingual. There is a slight lingual cingulum, but this merges into the wrinkled lingual face of the crown. On the mesiolingual corner there is an oval wear facet approximately 7 mm by 4 mm, worn by the lower canine. The measurements are: MDi L, *8.2 mm, and BuLi L, *10.1 mm.

In the limited parts preserved, UMP 66–03 resembles very closely indeed the homologous tooth of UMP 62–11 (p. 29). Wear facets of similar size and shape are found in both specimens.

CANINES

UMP 62–03. A right upper canine from Napak I, the specimen was described by Leakey *in* Bishop (1962, p. 8) as a left upper canine. "The specimen, including the enamel structure, is so typical [of *Dryopithecus major*] that I have no hesitation in my identification." Allbrook and Bishop (1963, p. 1190) described it as a right upper canine. It was figured by Bishop (1963b).

Measurements are given in Table 14. The tooth is similar in overall morphology to others of this sample from Uganda, although the root is somewhat more slender than those of UMP 62–04 and 62–05 from Napak V. The crown tapers fairly rapidly to a point, more so than in many *G. gorilla.* The buccal border is increasingly convex towards the tip; the lingual border is decreasingly concave towards the tip. Metrically, like UMP 62–11 and 62–12, 62–03 falls within the 95 per cent confidence limits for male gorillas. Morphologically UMP 62–03 is very similar indeed to the Moroto specimen. The tip of the crown was broken prior

Table 14 Comparative measurements of C^1 in D. (P.) major specimens

	UMP 62-11	UMP 62-03	UMP 62-12	UMP 62-04	UMP 62-05
Max L	*18.6	*18.7	17.6	19.3	18.8
Trans B	*15.7	*15.7	16.1	16.0	16.1
Labial H	*27.6	*25.0	*22.0	*22.0	*22.5
Index L/B x 100	118.4	119.1	109.2	120.6	116.8

to fossilization and the dentine is exposed. Enamel has been chipped from various parts of the crown, particularly mesiobucally. Mesially a groove runs from the cervix towards the tip of the crown. Lingual to the groove there is a broad (approximately 3.0 mm) wear facet worn from contact with the lower canine. Damage to the tip prevents the estimation of total facet length.

The buccal border at the cervix is mostly concave, although distally it is flat; the lingual border is similar. There is a slight lingual cingulum. Buccal and lingual surfaces meet at the distal border to form a distinct ridge, at least in the superior half of the crown, and on this ridge, beginning some 6 mm below the cervix, is a 2 mm broad facet worn by P_3.

The root has been damaged after fossilization, the enamel being chipped away lingually in the proximal half. A marked groove runs along the mesial aspect, just lingual to the mesial border. There is a slight depression running from root tip to cervix just buccal to the distal border.

UMP 62–04 and UMP 62–05. The specimens are a right upper canine and a left upper canine respectively. They are both from Napak V and have been described by Allbrook and Bishop (1963) and figured by Bishop (1963b).

These two canines probably come from the same individual. Morphologically and metrically they are almost identical and they exhibit similar degrees of wear. In both cases the crown tips have been broken subsequent to fossilization. There are barely discernable wear facets mesially and distally. The crowns and roots are larger in length and breadth dimensions than is the case for other canines in this sample (see Table 14). The crown height however is relatively small, giving them a "stubby" appearance. The length and breadth measurements suggest that the specimens are from a male individual—certainly there must be few, if any, present day female gorilla canines with dimensions as large as those of UMP 62–04 and 62–05—yet it would be difficult to find male gorillas with canine crowns as low as these.

FIRST MOLARS

UMP 62–07 (Fig. 21). A right upper first molar from Napak V, the specimen was described by Allbrook and Bishop (1963) and figured by Bishop (1963b). The buccal roots have been broken subsequent to fossilization. The mesiobuccal corner of the crown has also been broken off. This has been restored, although a small segment of the buccal surface and part of the paracone are missing. The occlusal surface is rhomboidal in outline, paracone and metacone being relatively mesial to protocone and hypocone. There is a marked distal bulge. The protocone is the largest cusp, the hypocone, metacone, and paracone being subequal and smaller. The mesial moiety is also somewhat broader buccolingually than the distal. The cusps tend to be pyramidal rather than rounded, particularly the relatively unworn buccal cusps. Crests are similarly rather sharply defined. Moderate wear facets are present on the occlusal surface and a tiny area of dentine is exposed on the tip of the protocone.

A protoconule is developed just lingual to the midpoint of the mesial border and is lingual to the sulcus separating paracone from protocone. There is no marked crest between paracone and protocone. The protoconule is worn and merges into the protocone, although a small furrow remains between them on the lingual side. The metacone-protocone crest is crossed by a sulcus separating metacone from protocone. A small cuspule lies between metacone and hypocone. There is also an accessory cuspule distal to the hypocone.

The lingual cingulum runs lingually from the protoconule round the protocone and hypocone to the accessory distal cuspule. It is much less prominent on the hypocone than on the protocone. It is beaded, particularly between protocone and hypocone, and the beading is carried onto the lingual surfaces of these cusps as vertical wrinkles which have been variably worn. A distal ridge or cingulum surrounds the posterior fovea distally. The buccal cingulum is represented by a distinct spur-like mesostyle between paracone and metacone and by slight lipping at the mesiobuccal corner of the paracone.

There is a mesial wear facet some 3 mm long, worn from contact with P^4, and a distal facet approximately 4 mm long. The lingual root diverges lingually at an angle of about 60 degrees to the occlusal plane (approximately 30 degrees to the buccal roots) as in UMP 62–11. It is characterized by a lingual longitudinal groove. Crown and root measurements are included in Table 15. Allbrook and Bishop assigned this tooth tentatively to *D. (P.) major.*

UMP 66–41 (Fig. 21). The specimen is a right upper first molar from Napak IV and is mentioned by Bishop (1964, p. 1329). The crown and lingual root are perfectly preserved. The buccal roots are broken 8 mm (mesial root) and 4 mm (distal) below the cervical border. The lingual root is splayed lingually as in UMP 62–07 and 62–11. Crown features are essentially similar to those of UMP 62–07, although the cusps are somewhat more pyramidal and the crests more sharply defined. The metacone is relatively better developed than in UMP 62–07. There is some occlusal wear, and a small area of dentine is exposed on the protocone tip. The smaller cuspules—protoconule and accessory hypocone cusp—are present, although both are rather less distinct than in UMP 62–07. The paracone-

Table 15 Comparative measurements of M^1 in <u>D.</u> (<u>P.</u>) <u>major</u> specimens

	UMP 62–11 Left	UMP 62–07	UMP 66–41
MDi L	*11.7	*11.4	12.0
BuLi B	12.7	*13.9	14.0
Index L/B x 100	92.1	82.0	85.7
Crown area	*148.59	*158.46	168.0
Vertical L Ling. root	*15.0	*15.0	*15.0
MDi T Ling. root, maximum	9.3	8.3	9.5

protocone crest is better developed than in UMP 62–07 and the two cusps are not separated by a sulcus. The crest merges with the protocone just lingual to the tip of that cusp and is joined at the point of merging by a small distal extension of the protoconule. The lingual cingulum is better developed than in UMP 62–07 and is clearly demarcated around the hypocone as far as the accessory distal cuspule. Although reduced by wear, the beading of the cingulum and the vertical wrinkling of the lingual faces of protocone and hypocone are still clearly visible. The distal cingulum reaches the distobuccal corner and is extended onto the buccal border mainly as heaping of the enamel rather than as a distinct ledge. The mesostyle is poorly developed. Measurements are given in Table 15.

Although the crown features of UMP 62–11 right M^1 from Moroto II have been largely obliterated by wear, the essential similarities to these other right upper first molars, UMP 62–07 and 66–41, are immediately obvious (Figs. 18 and 21) and all can be treated as one species. All are rhomboidal in crown outline, with a marked distal bulge. Mesiodistal lengths are similar, ranging only from 11.4 to 12.0 mm. The buccolingual breadth varies rather more, from 12.7 mm to 14.0 mm. The differences in shape are shown by the crown indices, varying 10.1 units from 82.0 to 92.1. Such a range is certainly not greater than those found within species (see Table 9, p. 35). The details of cuspal and sulcal morphology are very similar, as far as can be ascertained within this small sample. The lingual cingulum is best developed in UMP 66–41, where it is as well marked on the hypocone as it is on the protocone. In UMP 62–07 it is less well developed on the hypocone and in UMP 62–11 the hypoconal cingulum is probably less developed than in UMP 62–07. In contrast the mesostyles of UMP 62–11 and 62–07 are more prominent than those of UMP 66–41. The morphology and placement of the roots are similar in all three teeth. There is no reason to place these teeth in more than a single species.

All four main cusps are well-developed, prominent, and rather pyramidal in form. The intercuspal crests are also well developed. The tendency towards hypsodonty and lophodonty is not as marked as in *Gorilla gorilla* and the tooth crowns are not so large. The paracone-protocone and metacone-hypocone crests are generally better developed in living gorillas. The possible functional explanations for such changes have been noted in the preceding chapter. The cingulum is generally quite well developed in gorilla upper molars (Korenhof, 1960; Frisch, 1965; Remane, 1960). It is rarely as clearly marked as in these Miocene specimens, although the overall morphology—the beading and vertical wrinkling—is otherwise very similar. In *G. gorilla,* the buccal cusps, especially the metacone, are well developed and the distance between the tips of paracone and metacone is generally very similar to that between protocone and hypocone. In the Miocene species the distance between the lingual pair is generally greater, making the distal bulge more pronounced on the lingual side of the crown.

These specimens from Uganda make reasonable morphological precursors for living gorillas. If they are indeed ancestral, the main trends since the Miocene would have been towards increase in crown size producing cusps of subequal volume, increased hypsodonty and lophodonty, and some cingular reduction.

SECOND MOLARS

UMP 62–08 (Fig. 21). A left upper second molar from Napak V, the specimen has been described by Allbrook and Bishop (1963, p. 1190) and figured by Bishop (1963b). The roots have been broken off since fossilization, exposing an extensive pulp cavity. The cavity extends furthest occlusally below paracone and metacone. The crown is rhomboidal, the lingual border being longer than the buccal. The four main cusps are subequal in size, the greater length of the lingual moiety being accounted for by accessory cuspules and mesial and distal cingula. Although moderately worn, the cusps, particularly the buccal, still retain their distinct pyramidal form. The metacone-protocone crest is well developed. Paracone and protocone are separated by a sulcus, as are metacone and hypocone. There is a prominent protoconule on the mesial border, from which two small crests run buccally to the paracone and one distolingually to the protocone. The lingual cingulum is well developed, beginning at the lingual border of the protoconule, and running around the protocone and hypocone to a distal accessory cusp, distal to the hypocone. It is beaded and the lingual surfaces of protocone and hypocone are vertically wrinkled. Around the hypocone beading and wrinkling merge and the cingulum is not as clearly demarcated as it is on the protocone. The vertical wrinkling is continued on the buccal border. A small mesostyle is present. A distal cingulum or marginal ridge runs from the distal accessory cusp to the distobuccal border. A small posterior fovea separates this from the metacone-hypocone crest. The fovea sides are also wrinkled. Contact facets 4 mm long are present on the mesial and distal borders. Measurements are given in Table 16.

UMP 62–09. A left upper second molar from Napak I, the tooth has been described by Allbrook and Bishop (1963, p. 1190). The specimen is part of an unerupted molar crown. The crown is broken and only the buccal three-fifths or so has been preserved. The paracone, metacone, and half of the hypocone are present, together with the metacone-protocone crest, and a pair of lingual crests from the paracone. Comparison with UMP 62–08 indicates that this is, with a high degree of probability, a second molar. The occlusal surface is covered with wrinkles, varying from relatively fine in the trigon fossa to relatively coarse in the posterior fovea. Measurements are given in Table 16.

UMP 62–11 and 62–08 are very similar (Figs. 18 and 21) and can be regarded as representatives of a single species. Allbrook and Bishop placed them provisionally in *D.* (*P.*) *major.* Apart from the stronger mesostyle of UMP 62–11 (mesostyles are well developed on all three molars of the individual from Moroto II), there is hardly a morphological feature present in one which is absent in the other. UMP 62–08 is considerably larger than the homologous tooth of UMP 61–11. The size and shape range for male gorilla M^2, shown in Table 11, p. 36, is great and there is no reason to doubt that UMP 62–11 and 62–08 are to be placed in one species only. UMP 62–11 is almost certainly a male and, because of size, UMP 62–08 probably is, too, indicating that in this species there were individuals with larger teeth than UMP 62–11 and quite possibly larger maxillae and faces.

Like M^1 the second molars show resemblances to those of living gorillas. There are also a number of differences, but none of the differences rules out the

Table 16 Comparative measurements of M^3 in: (a) *D. (P.) major*, (b) *G. gorilla*

(a)	UMP 62-11 Left	UMP 62-08	NMK 102, CMH35	NMK 405, 381	NMK 101, CMH34	UMP 62-09
MDi L	*13.1	15.1	12.7	14.4	12.0	15.2
BuLi B	14.0	17.3	15.3	16.3	13.6	-
Index L/B x 100	93.5	87.3	83.0	88.3	88.2	-

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)
MDi L	$\bar{X}$	16.0	14.8
	95%CL	13.9-18.1	12.8-16.8
BuLi B	$\bar{X}$	16.7	15.6
	95%CL	14.8-18.5	13.7-17.5
Index L/B x 100	$\bar{X}$	96.2	94.7
	OR	91.1-106.2	87.4-104.5

probability that the fossil species represented is close to the ancestry of *G. gorilla*.

Lower Dentition and Mandibles

UMP 62–06 (Fig. 22). The specimen, from Napak V, has been described by Allbrook and Bishop (1963, p. 1190) and figured by Bishop (1963b). It consists of the anterior portion of the left mandibular horizontal ramus of an infant. It was tentatively assigned to *D. (P.) major* by Allbrook and Bishop (1963, p. 1190). The anterior surface of the mandible and the alveolar margin have been eroded, exposing the crown of an unerupted incisor, the alveolus of the deciduous canine and the alveolus for the mesial root of the deciduous anterior premolar. The distal root of dP_3 and mesial root of dP_4 are preserved in the jaw; dP_3 was elongated mesiodistally. The unerupted crown of P_4 (not M_1 as Allbrook and Bishop tentatively suggested) was exposed on the lateral surface of the ramus and this was carefully removed for study. Openings to gubernacular canals are present lingual to the incisor and canine. The specimen is broken mostly lateral to the symphysis, although the actual symphysis is represented in the inferior and posterior parts of the region, there being some local excavation suggesting incomplete fusion.

The posterior symphyseal surface slopes gently inferiorly to the superior transverse torus, forming a planum alveolare, the most posterior point of which is opposite the distal root of dP_3. The posterior symphyseal surface then slopes slightly anteriorly and inferiorly to the inferior transverse torus. Thus the most posterior point of the inferior transverse torus is just anterior to that of the superior torus. Between the tori is a small genial pit. Although a simian shelf or basal plate is absent inferiorly, the symphyseal structure of UMP 62–06 is very similar to that of infant *Gorilla gorilla,* where a gently sloping planum is generally present, in contrast to the usual condition in *Pan troglodytes* where the planum normally slopes more abruptly. (It was inferred in Chapter IV that a long, gently sloping planum would have been present in UMP 66–01/62–10 from Moroto II.) At the level of dC_1, the horizontal ramus is about 28 mm deep. The body shallows posteriorly.

Some very approximate measurements are possible for the tooth sockets and roots. The depth of the canine alveolus from the interdental septum is approximately 20.0 mm; and the buccolingual breadth of the distal root of dP_3 is about 5.0 mm and that of the mesial root of dP_4 about 5.5 mm.

The incisor was identified by Allbrook and Bishop as a lateral incisor. Morphologically, however, the crown resembles those of pongid central incisors. Careful inspection reveals two gubernacular openings distal to the exposed incisor and mesial to dP_3 (for C_1 and I_2). It is unlikely, too, that there would be sufficient space between the mesial border of the incisor and the midline to accommodate another permanent tooth. The tooth is therefore regarded here as a central incisor. In sagittal section the crown is elongate and triangular, the labial surface being gently convex and the lingual more strongly concave. The labial surface is symmetrical, mesial and distal labial margins being of equal length in contrast to the condition found in pongid lateral incisors where the distal border is shorter. Lingually, too, the crown is symmetrical. There are slight marginal ridges and a hint of central thickening in the proximal two-thirds of the crown. The crown narrows towards the cervix more markedly on the lingual surface. The crown is broken lingually just above the cervix. The measurements are: MDi L, 6.4 mm, LaLi B, *8.0 mm, La H, *14.0 mm, and Li H, *13.0 mm.

In overall shape the tooth resembles those of gorillas rather than chimpanzees, the crown being relatively narrow mesiodistally, high, and symmetrical. The mesiodistal diameter at the lowest level of the cervical margin is 4.4 mm. The measurements of I_1 roots of the *D. (P.) major* mandible from Songhor described by Clark and Leakey (1951, p. 59) are MDi, 4.0 mm, and LaLi, 7.2 mm.

These measurements are taken on roots below the cervix and will be somewhat smaller than the dimensions at the cervical level. Metrically, therefore, the Napak and Songhor specimens are very similar.

The P_4 was removed from its crypt. In position the most superficial part of the tooth would have been at least 8.0 mm below the alveolar margin. Resorption of dP_4 roots had probably not begun. The crown is relatively more molariform than in other posterior lower premolars in this sample (Fig. 22). The crown is clearly not fully formed, the buccal surface in particular being less fully convex than in adult specimens. There is a good deal of relief on this surface too. The protoconid and metaconid are subequal in height, the protoconid being marginally greater in area. The two cusps are joined by a crest, itself crossed by a mesiodistal sulcus. Mesial to the crest is an anterior fovea, surrounded in front and to the sides by a mesial cingulum or marginal ridge. The mesial portion of the tooth is well developed relative to others in this sample. Small buccal and lingual cusps are present on this ridge just mesial to protoconid and metaconid. Distal to the protoconid, and separated from it by a sulcus, is a small hypoconid. From the hypoconid a ridge surrounding the posterior fovea runs distally and then lingually to the metaconid. The ridge is beaded. The sulcus between protoconid and hypoconid is continued down the buccal surface as a prominent groove.

An unerupted P_4 at an approximately similar stage of development to UMP 62–06 was dissected from an infant gorilla (Duckworth Pr 52.0.5). In this gorilla the main cusps are relatively more massive, and the main crest and the mesial and distal marginal ridges less well developed—possibly due to the greater immaturity of this specimen. In general features, however, the two teeth are similar.

The only reliable measurements possible are those of length. The mesiodistal length would probably not have exceeded 10.3 mm. The trigonid length was about 6.9 mm and the talonid length 3.4 mm, giving a talonid/trigonid length index of 49.3. In full development the buccolingual breadth would have been at least 10.0 mm and possibly several tenths of a millimeter more.

UMP 62–13 (Fig. 22). The specimen from Napak I, figured in Bishop (1963b), consists of the anterior part of the right horizontal ramus from an infant mandible. Apart from a small portion of the symphysis, only the superior parts of the ramus are preserved. The roots of dC_1, dP_3, and dP_4 are preserved, the crowns being broken off at the junction of crown and root. The fragment is broken mainly lateral to the symphysis, except inferiorly, and the unerupted and broken crown of I_2 is exposed. The first permanent molar had erupted through the gum; wear facets show that the tooth had come into occlusion, although eruption was probably not complete. Openings to the gubernacular canals are present lingual to dC_1 and dP_3.

The symphyseal morphology is similar to that of UMP 62–06. A gently sloping planum alveolare was present, leading backwards to a superior transverse torus situated opposite the distal root of dP_3. Inferior to this torus is a shallow area of excavation, the genial pit. There was apparently no posteriorly projecting simian shelf, although the superior transverse torus projects only slightly posterior to the inferior transverse torus.

A few measurements are comparable with UMP 62–06. The depth of the ramus opposite dC_1 is approximately 26 mm, some allowance being made for superior and inferior breakage. The buccolingual diameter of the distal root of dP_3 is 4.6 mm and of the mesial root of dP_4 6.5 mm. UMP 62–13 is a little smaller and more gracile than UMP 62–06, but the differences are no more than individual or possibly sexual, and the two specimens are assignable to a single species.

Crown dimensions have been estimated from the roots of the deciduous teeth. They are: dC_1, Max L, *7.5 mm, Trans B, *5.0 mm; dP_3, MDi L, *8.5 mm; and dP_4, MDi L, *9.8 mm, BuLi B, *7.8 mm.

The unerupted posterior premolar was carefully removed from its crypt by drilling. The most superficial part of the crown was some 4.0 mm from the alveolar margin. The crown may not be fully formed, although it is certainly more developed than UMP 62–06 and the dimensions are probably close to what they would have been in the erupted condition. The buccal surface is fuller and more rounded than in UMP 62–06 and is less vertical than the lingual surface, thus the cusps appear to be situated more towards the lingual edge of the occlusal surface. The anterior fovea is less well developed than in UMP 62–06; protoconid, metaconid, and hypoconid are similar to those of UMP 62–06. There is a slight buccal groove running from the protoconid-hypoconid sulcus. The enamel extends farthest inferiorly on the buccal side. The lingual part of the distal border projects farthest distally. The measurements (also included in Table 19, p. 61) are: MDi L, 8.6 mm, BuLi B, 9.1 mm, Index L/B × 100, 93.5, Tri L, 5.9 mm, Tal L, 2.7 mm, and Index Tal L/Tri L × 100, 45.8.

The first molar is slightly worn. There is no distal wear facet. Morphologically this tooth is very similar to others in this sample. The metaconid, entoconid, and hypoconid are subequal in size, the protoconid somewhat smaller, and the hypoconulid smallest. The metaconid is slightly distal to the protoconid and the hypoconulid is shifted a little buccal to the midline. Metaconid and hypoconid are in contact for about 2 mm, and hence the "*Dryopithecus* Y" pattern is clearly developed. The tail of the Y is only slightly mesial to the tip of the hypoconid, and the two arms diverge at approximately equal angles from the tail. The buccal cingulum is present between protoconid and hypoconid, closing buccally the groove between these two cusps. This part of the cingulum is faintly beaded. There is a pit at the mesiobuccal corner and a buccal extension and deepening of the sulcus between hypoconid and hypoconulid, representing the mesial and distal limits of the buccal cingulum. Mesial and distal marginal ridges enclose the anterior and posterior fovea. Crests unite adjacent cusps around the margin of the occlusal surface and are particularly well developed between metaconid and protoconid, and entoconid and hypoconulid.

The cusps are well defined and pyramidal. There is a tiny protoconulid mesial to the protoconid. Grooves on the distal faces of metaconid and protoconid and on the mesial face of metaconid demarcate tiny cuspules, too small to warrant naming. The measurements (also included in Table 20, p. 62) are: MDi L, 10.8 mm, Tri B, 9.0 mm, Tal B, 9.2 mm, Index L/B × 100, 117.4, and Index Tal B/Tri B × 100, 102.1.

UMP 62–14 (Fig. 22). This lower first molar from Napak I was described by Leakey (*in* Bishop, 1958, p. 1481) as representing a "quite typical lower right second molar" of *Dryopithecus (Proconsul) nyanzae.* It was figured by Bishop (1958, 1963b). The specimen consists of the very well-preserved crown of what is probably a first molar (rather than a second molar). The roots are broken some 5 mm below the cervical border. There is a mesial wear facet from contact with dP_4 or P_4; a small distal area of wear on the hypoconulid suggests that M_2 had just erupted. Occlusal wear has not proceeded very far although farther than in UMP 62–13; a tiny patch of dentine has just appeared on the tip of the protoconid.

Although described as a M_2 by Leakey, comparisons with other *D. (P.) major* M_1's from Uganda (Fig. 22) and from Songhor in Kenya show that this is a first molar. Morphologically it is very similar to UMP 62–13 and others in this series. However, isolated first and second molars of *Dryopithecus (Proconsul)* species are often difficult to tell apart on morphology alone. Size is not a uniformly helpful criterion either. It is possible, within single sex gorilla series, to find with some frequency M_1 and M_2 of similar size and shape, and this tendency is accentuated when pooled male and female series are used (see Appendix 1).

The largest cusps are metaconid and hypoconid, with hypoconulid the smallest. The hypoconulid is just buccal to the midline and the metaconid just distal to the protoconid. The Y pattern is again well developed. In all these features

UMP 62–14 resembles UMP 62–13. The cingulum is prominent and quite strongly beaded, the beading running onto the protoconid and hypoconid as vertical wrinkling. The buccal cingulum is almost continuous from the mesiobuccal corner to the hypoconulid, although it is interrupted for a short distance on the protoconid; the pit at the mesiobuccal corner is very similar to the condition noted in UMP 62–13.

In almost all features of morphology, extending even to the most trivial of occlusal wrinkles and accessory cuspules, the crowns of UMP 62–13 and 62–14 are very similar. The measurements (also included in Table 20, p. 62) are: MDi L, 12.0 mm, Tri B, 10.2 mm, Tal B, 10.5 mm, Index L/B × 100, 114.2, and Index Tal B/Tri B × 100, 103.0.

UMP 62–15 (Fig. 22). The specimen, a left lower first molar from Napak I, was figured by Bishop (1963b). This tooth had apparently only just erupted. There are a few traces of wear on the mesial moiety of the crown and what is possibly a tiny mesial facet. The roots have been broken off at the cervical border. The occlusal surface has the rather coarse wrinkles characteristic of unerupted or unworn teeth. The metaconid is more markedly distal to protoconid and the hypoconulid more centrally placed, than on either UMP 62–13 or 62–14. Both features point to this tooth being M_1 rather than M_2 (Frisch, 1965, p. 79–94). Unlike UMP 62–13 and 62–14, the buccal cingulum is continuous from the mesiobuccal corner to the hypoconid. It is represented by vertical wrinkling on the more distal and buccal parts of the hypoconid and by the distobuccal deepening of the intercuspal sulcus between the hypoconid and hypoconulid. The measurements (also included in Table 20, p. 62) are: MDi L, 12.7 mm, Tri B, 10.6 mm, Tal B, 10.9 mm, Index L/B × 100, 116.5, and Index Tri B/Tal B × 100, 102.8.

UMP 62–16 (Fig. 22). This specimen, from Napak I and described by Leakey (*in* Bishop, 1962, p. 8), consists of the left lower last premolar and first molar, joined by adherent alveolar bone. The buccal root of P_4 has been broken off subsequent to fossilization and the crown rotated slightly in a distobuccal direction. The crown of M_1 has a small crack running lingually from the hypoconid to the lingual border. This has increased the trigonid diameter to 9.5 mm, although originally it was probably 9.3 mm or 9.4 mm. Both teeth are moderately worn, with dentine being exposed on the protoconid, metaconid, and hypoconid of M_1; the buccal wrinkling and cingulum beading are practically removed.

Leakey tentatively identified this specimen as *Sivapithecus africanus*? Clark and Leakey, though he has since transferred it to *Kenyapithecus* (1967). His description in Bishop (1962, p. 8) is here quoted almost in full:

> The measurement of the molar tooth is 11 × 9 mm, which is not nearly large enough for *Proconsul major.* Moreover the tooth in question does not look like that of a *Proconsul major.* On the other hand it is far too large for the first lower molar of *Proconsul nyanzae,* from which it also differs in the complete absence of a cingulum. The 4th premolar also does not seem to resemble that of *Proconsul nyanzae.* Unfortunately we know nothing definite about the lower dentition of *Sivapithecus africanus,* but if we tentatively place this specimen in this genus and species we shall not be far wrong.

The last premolar is similar in size and morphology to UMP 62–13, although it is not as long (Fig. 22). It also resembles BM(NH) M14086 from Koru, described by Clark and Leakey (1951) as *Proconsul nyanzae,* in size and shape (Fig. 23) and those specimens of *D.* (*Proconsul*) from Songhor figured by Clark and Leakey (1951, pl. 4, figs. 19 and 22; pl. 5, fig. 35). The anterior fovea and the morphology of the buccal surface, with mesial and distal vertical grooves, are also similar to other premolars in the Uganda and Kenya samples. The measurements (also included in Table 19, p. 61) are: MDi L, 7.9 mm, BuLi B, 9.0 mm, Index L/B × 100, 87.8, Tri L, 5.3 mm, Tal L, 2.6 mm, and Index Tal L/Tri L × 100, 49.0.

Although the M_1 of UMP 62–16 is more extensively worn than others in this sample, the occlusal morphology is again remarkably similar. The metaconid is slightly distal to the protoconid and the hypoconulid is just buccal to the midline. The accessory cuspules on protoconid and metaconid are identical to those on UMP 62–13 and 62–14 (Fig. 22).

A pit is present on the mesiobuccal corner, as in UMP 62–13 and 62–14. Leakey's statement that there is "complete absence of a cingulum" is rather puzzling. Although not as prominent as that of UMP 62–14, the cingulum between protoconid and hypoconid is nevertheless quite distinct. In recent Pongidae and those Dryopithecinae where cingula are reduced or lacking [many specimens of *Dryopithecus* (*Sivapithecus*) species for example], the sulcus between protoconid and hypoconid descends the buccal face uninterrupted, sometimes almost to the cervical border, before shallowing and merging with the enamel surface. In all the East African mid-Tertiary pongid material the sulcus is terminated buccally by this part of the buccal cingulum. Although reduced in height and smoothed out by wear in UMP 62–16, it is nevertheless clear that a buccal cingulum is present, and was as extensive as that on UMP 62–14 and 62–13. This also applies to the cingulum or marginal ridge between hypoconid and hypoconulid. The measurements (also included in Table 20, p. 62) are: MDi L, 10.7 mm, Tri B, *9.4 mm, Tal B, 9.4 mm, Index L/B × 100, *114.9, and Index Tal B/Tri B × 100, *100.0.

UMP 66–02 (Fig. 22). This specimen, a slightly worn and rootless crown of a right lower last premolar from Napak V, was mentioned by Bishop (1964, p. 1329). There are small mesial and distal contact facets. The distolingual corner projects a little distally. In this feature UMP 66–02 is intermediate in morphology between UMP 62–13 and 62–16. In other features of occlusal surface morphology UMP 66–02 resembles the P_4 of UMP 62–16 closely. The cervical border extends inferiorly at the mesiobuccal corner, as in all other premolars in this sample, and also those from Songhor and Koru (described in Chap. VI). The measurements (also included in Table 19, p. 61) are: MDi L, 7.8 mm, BuLi B, 9.0 mm, Index L/B × 100, 86.7, Tri L, 5.2 mm, Tal L, 2.6 mm, and Index Tal L/Tri L × 100, 50.0.

DISCUSSION OF THE LOWER DENTITION

The last premolars show some variation in size and morphology, but this is not as great as that seen within the presently living African pongid species (see Table 19). Similarly the first molars exhibit no more metrical and morphological variability than might be expected within a single species, particularly if that species exhibits some sexual dimorphism in size (see Table 20).

The cusps are pyramidal rather than rounded, particularly on the lower molars. Like the upper molars considered before, these lower molars are morphologically acceptable as ancestral to *G. gorilla*. In the living form, the homologous teeth are very much larger and the cusps are often more projecting. In terms of overall tooth size the cusps on these fossil teeth are no lower than those of most gorillas. However, the relief of the gorilla molar is much more striking. The sulcus between metaconid (generally the highest cusp) and entoconid, for example, usually approaches the cervical margin much more closely in gorillas. The newly erupted M_1 crown from Napak I, UMP 62–15, was compared with an unerupted, although fully formed, M_1 of *G. gorilla* (Duckworth Pr 52.0.5), see Table 17.

Table 17 M_1 measurements of *D.* (*P.*) *major* and *G. gorilla*

	UMP 62-15	Pr52.0.5.
Tri B	10.6	12.2
Metaconid H	7.2	8.6
Index H/B x 100	67.9	70.5
Metaconid/Entocd. sulcus H	5.5	4.0
Index cusp H/ sulcus H x 100	130.9	215.0

Although protoconid height, measured from the cervical border, is relatively little greater in the gorilla, the cusp relief is more marked because the intercuspal sulci and basins are deeper. Both last premolars and first molars are more lophodont in gorillas than in the fossil species.

DISCUSSION OF THE UGANDAN PONGIDS

There is no reason to assume that the pongid material from Moroto II, Napak I, IV, and V described above should be referred to more than a single species, particularly if the individual, sexual, geographical, and temporal factors affecting variability within a single evolving lineage are considered. It has already been established, at least, that the upper and lower dentitions fall into single species groupings; can the two dentitions be associated?

Unfortunately, only one site, Moroto II, has yielded remains which might possibly include associated upper and lower dentitions. From Napak I we have only lower first molars, while uppers are known only at Napak IV and V. However, treating the Napak sites as a single assemblage and including Moroto II as well (although this site could prove to be geologically somewhat younger), we have for consideration the upper and lower dentitions of a large pongid. Cuspal and cingular morphology is very similar in the two sets of material. These maxillary and mandibular samples resemble each other as closely as do upper and lower dentitions of *P. troglodytes*, *G. gorilla*, *D.* (*P.*) *africanus*, or *D.* (*P.*) *nyanzae*. It has also proved possible to occlude UMP 66–41 from Napak IV

(M^1) with UMP 62–14 from Napak I (M_1), producing an extremely good fit (Fig. 24).

It is of interest to note here the functional role of some of the crown structures. With the upper molar stationary, when the lower molar moves buccally from centric occlusion the paracone and metacone tips occlude between the buccal cingulum and the buccal cusps of the lower molar. When the lower molar moves lingually, the lower molar lingual cusps occlude between the lingual cingulum and cusps of the upper molar. In both cases the cingula act as extra cusps. During side-to-side movements the protoconule, a prominent feature of the upper molars, occludes with the protoconid-metaconid crest.

The upper and lower dentitions from Uganda and the associated maxillary and mandibular material, are probably sampled therefore from a single species. The species includes those specimens described by Allbrook and Bishop (1963) as *Proconsul major,* by Leakey (*in* Bishop, 1958 and 1962) as *Proconsul nyanzae* and *Sivapithecus africanus,* and by Simons and me (1965) as *D. (P.) major.* Whether or not this assemblage does represent *D.* (*P.*) *major,* known before 1958 only from Kenya, will be considered in the following chapter.

CHAPTER VI. *DRYOPITHECUS (PROCONSUL) MAJOR* FROM KENYA

BACKGROUND OF THE MATERIAL

As noted in Chapter III, the collections from Songhor and Koru in Kenya may be considered as representing relatively short periods of time. Koru and Songhor are geographically close together and probably temporally close, too. The material from the two main sites can be considered here as forming a single assemblage. Napak, Moroto II, Songhor, and Koru represent stratigraphically a relatively uncomplicated set of sites, unlike the Rusinga series. This assemblage is probably broadly contemporaneous, although as noted Moroto II may be a little younger than the others. Quite possibly all these sites were deposited in similar environments.

The history of recovery of primate material from the East African Miocene sites has been discussed by Clark and Leakey (1951, p. 1–3). The first pongids to be described came from Koru (Hopwood, 1933 a and b). Specimens which concern us here are the maxilla which Hopwood made the holotype of a new genus and species, *Proconsul africanus* BM(NH) M14084 (see Fig. 25) and a mandible BM(NH) M14086 (see Fig. 23). In 1951 Clark and Leakey described two further species in this subgenus, *P. nyanzae* and *P. major,* and included the referred mandible in *P. nyanzae.* All but one of the specimens assigned by Clark and Leakey to *P. major* came from Songhor. This specimen, NMK 71, CMH 142*, from Rusinga has since been transferred by Leakey (1967) to his proposed species *Kenyapithecus africanus.* In 1952 Clark described further material from East Africa, including several more specimens of *P. major* from Songhor. Two also came from Rusinga, one a dP_4 (NMK 129,257). The other specimen was part of a right clavicle which came, according to Clark (1952, p. 280) from the surface, and according to the Museum catalogue from site R3a. This specimen is similar to the clavicle from Rusinga, site R106 (NMK 145,604) which Clark and Leakey suggested might belong to *P. major* (1951, p. 99). This clavicle from R106 has since been assigned tentatively by Leakey to his proposed species *Kenyapithecus africanus* (1967, p. 163). In 1965 Simons and I transferred all *Proconsul* species to *Dryopithecus.*

The dental and mandibular material from Kenya assigned with a reasonable degree of certainty to *D.* (*P.*) *major* therefore comes almost exclusively from Songhor. Most of the more complete remains have already been described in some detail in the literature. However, dimensions and certain further relevant observations are included below. Unless otherwise stated, specimens come from Songhor.

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* National Museum of Kenya primate specimen numbers consist of two sets of figures, separated here by commas. The first set lists the primates consecutively; the second set is apparently a field number and varies with locality and date of collection.

LARGE SPECIMENS

BM(NH) M16648 (Fig. 23). This specimen, the holotype of *D. (P.) major,* has been described and figured by Clark and Leakey (1951) and consists of part of a right mandibular horizontal ramus with the roots only of P_3 and the roots and crowns of P_4 through M_3. The second molar is damaged distally and in the distobuccal quarter of the crown. In the mandibular parts preserved, BM(NH) M16648 is very similar to UMP 66–01 from Moroto II. The roots of P_3 show that the long axis of this tooth was set at an angle of about 40 degrees to the axis of the distal tooth row. The crown size of P_3 has been estimated from the roots.

The large size of BM(NH) M16648 suggests that this is probably a male specimen. Compared with individuals of *G. gorilla* (see Appendices), this *D. (P.) major* has relatively small P_3, P_4, and M_1, and a relatively large M_3. The combined specimen from Moroto II (UMP 62–10 and 66–01) probably has a rather larger P_3 and a somewhat smaller M_3. Could these variations in size and proportions occur within a single species?

In a sample of 20 male lowland *Gorilla gorilla* (subspecies *G. g. gorilla*), the ratio (MDi L P_3/MDi L M_1) × 100 varied over 26 units from 99.4 to 125.8 with a mean of 111.8. This is one method, albeit unsatisfactory, of measuring the relative proportions of P_3, M_1 being chosen as standard. The ratio for BM(NH) M16648 is 115.7 (14.0/12.1 × 100), just a little above the gorilla mean. In the Moroto II mandible the ratio is 135.6 (16.0/11.8 × 100), 20 units higher. It should be noted, however, that there is evidence from Songhor (see below) of lower first premolars at least as long as those from Moroto II and no evidence of substantially larger mandibles (with larger M_1's) in which these P_3's could have been set. Considering the morphological features of similarity, it is unlikely that this difference in ratio between UMP 62–10 and 66–01, and BM(NH) M16648 is to be regarded as significant.

A number of authors (e.g., Clark and Leakey, 1951, p. 37, 56, 57, 62) have used the ratio (MDi L M_2/MDi L M_3) × 100 to measure the relative lengths of the last two lower molars. In the sample of male gorillas, this ratio varies from 86.6 to 109.9, a typically large range of variation. The value of the ratio in BM(NH) M16648 is 82.2 (14.8/18.0 × 100) and in UMP 66–01, 86.7 (13.0/15.0 × 100), only 4.7 units difference. The actual length of M_3 in BM(NH) M16648 is 18.0 mm and in UMP 66–01 15.0 mm. In the gorilla sample the mean value of this character is 17.6 mm and the 95 per cent confidence limits are 15.5 mm and 19.7 mm. Once again, considering both relative and absolute lengths of M_3, there is no reason to assign these two specimens to more than a single species.

Although the crowns of P_4 and M_1 are rather worn in BM(NH) M16648, enough detail is preserved to show that the dental material from Napak is very similar morphologically and metrically to that from Napak. Measurements are set out in Tables 18–22 which follow.

NMK 190,1 (Figs. 24 and 26). This specimen, described by Clark and Leakey (1951) and figured in Clark and Leakey (1951) and Leakey (1967), is the main portion of a right canine crown, found in 1932. The symphyseal region,

Table 18 Comparative measurements of P_3 in: (a) *D. (P.) major*, (b) *G. gorilla*

(a)	UMP 66-01	NMK 190,1	BM(NH) M16648	NMK 382,3 Left	NMK 383,4 Right	NMK 604,69	BM(NH) M14086
Max L	**16.0	**13.0	**14.0	*16.0	16.0	14.4	12.7
Trans B	**9.5	**8.2	**9.0	*9.0	9.0	9.8	7.2

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)
Max L	$\bar{X}$	17.5	14.9
	95%CL	15.4-19.6	13.1-16.7
Trans B	$\bar{X}$	12.1	10.4
	95%CL	9.7-14.4	8.4-12.3

Table 19 Comparative measurements of P_4 in: (a) *D. (P.) major*, (b) *G. gorilla* and *P. troglodytes*

(a)	UMP 62-06	UMP 62-13	UMP 66-01	UMP 62-16	UMP 66-02	BM(NH) M16648	NMK 190,1	NMK 272,56	BM(NH) M14086
MDi L	*10.3	8.6	**9.5	7.9	7.8	9.2	9.0	9.0	7.8
BuLi B	-	9.1	**10.0	9.0	9.0	9.7	9.7	10.6	9.0
Index L/B x 100	-	93.5	95.0	87.8	86.7	94.8	92.8	84.9	86.7
Tri L	*6.9	5.9	-	5.3	5.2	6.9	6.3	-	-
Tal L	*3.4	2.7	-	2.6	2.6	2.3	2.7	-	-
Index Tal L/ Tri L x 100	*49.3	45.8	-	49.0	50.0	33.3	42.8	-	-

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)	*P. troglodytes* (n=20)
MDi L	$\bar{X}$	11.7	10.8	-
	95%CL	10.2-13.2	9.6-11.9	-
BuLi B	$\bar{X}$	13.4	12.5	-
	95%CL	12.0-14.7	10.3-14.7	-
Index L/B x 100	$\bar{X}$	87.2	86.6	-
	OR	79.7-94.8	70.8-100.9	-
Index Tal L/Tri L x 100	$\bar{X}$	-	-	37.4
	OR	-	-	29.3-49.0

Table 20 Comparative measurements of M_1 in (a) *D. (P.) major*, (b) *G. gorilla*

(a)	UMP 62-13	UMP 62-14	UMP 62-10	UMP 62-15	UMP 62-16	BM(NH) M16648	NMK 190.1	BM(NH) M14086
MDi L	10.8	12.0	**11.8	12.7	10.7	12.1	11.8	*10.9
Tri B	9.0	10.2	*10.8	10.6	*9.4	10.2	10.9	9.3
Tal B	9.2	10.5	*11.0	10.9	9.4	10.7	10.8	9.5
Index L/B x 100	117.4	114.2	107.2	116.5	*114.9	113.0	108.2	114.8
Index Tal B/ Tri B x 100	102.1	103.0	101.9	102.8	*100.0	104.9	99.1	102.2

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)
MDi L	$\bar{X}$	15.7	14.9
	95%CL	14.4- 17.0	13.6- 16.2
Tri B	$\bar{X}$	13.4	12.6
	95%CL	12.3- 14.6	11.0- 14.3
Tal B	$\bar{X}$	13.4	12.7
	95%CL	12.6- 14.2	11.2- 14.2
Index L/B x 100	$\bar{X}$	116.3	116.7
	OR	110.0-122.4	108.1-124.0
Index Tal B/ Tri B x 100	$\bar{X}$	99.5	100.3
	OR	95.1-102.3	95.3-108.1

Table 21 Comparative measurements of M_2 in: (a) *D. (P.) major*, (b) *G. gorilla*

(a)	NMK 190,1	UMP 66-01	BM(NH) M16648	NMK 271,55	BM(NH) M14086
MDi L	13.9	*13.0	14.8	15.6	*12.6
Tri B	13.1	*12.2	12.8	14.1	10.8
Tal B	12.5	*11.9	*12.8	13.5	10.2
Index L/B x 100	106.1	106.5	115.5	110.6	116.7
Index Tal B/Tri B x 100	95.5	97.5	*100.0	95.7	94.5

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)
MDi L	$\bar{X}$	17.3	16.2
	95%CL	15.1- 19.5	14.5- 17.9
Tri B	$\bar{X}$	15.4	14.4
	95%CL	14.0- 17.0	12.0- 16.8
Tal B	$\bar{X}$	15.0	14.0
	95%CL	13.5- 16.6	11.8- 16.1
Index L/B x 100	$\bar{X}$	112.2	112.5
	OR	104.8-119.8	103.0-125.4
Index Tal B/Tri B x 100	$\bar{X}$	97.6	97.8
	OR	92.3-111.0	89.6-103.3

Table 22 Comparative measurements of M_3 in: (a) *D. (P.) major*, (b) *G. gorilla*

	BM(NH) M16648	NMK 190,1	UMP 66-01	BM(NH) M14086
MDi L	18.0	17.3	15.0	*13.5
Tri B	13.4	14.2	12.5	*10.5
Tal B	12.0	12.0	*10.4	-
Index L/B x 100	134.3	121.9	120.0	128.6
Index Tal B/Tri B x 100	89.5	84.5	86.7	-

(b)		*G. gorilla* males (n=20)	*G. gorilla* females (n=20)
MDi L	X̄	17.6	16.0
	95%CL	15.5- 19.7	13.7- 18.4
Tri B	X̄	15.3	14.2
	95%CL	13.6- 17.1	11.9- 16.5
Tal B	X̄	13.6	12.7
	95%CL	12.0- 15.2	10.1- 15.3
Index L/B x 100	X̄	114.1	112.9
	OR	108.0-122.8	105.8-123.3
Index Tal B/Tri B x 100	X̄	89.0	89.2
	OR	79.8- 99.3	82.5- 95.7

with the roots of the left canine, incisors, right premolars, and first molar, to which this canine crown belonged, was recovered in 1947 and the tip of the right canine in 1948. The specimen was first described by Clark and Leakey in 1951 (p. 59–60). In 1962 the horizontal ramus from the left side of the mandible was recovered and fitted onto the earlier symphyseal piece. The more complete specimen is figured in Leakey (1967, fig. 4e). The left dentition from P_4 to M_3 is very well preserved and is almost unworn. Comparison with the type of *D.* (*P.*) *major* shows that this is also a member of that species. The size of the dentition, particularly of the canine, indicates that NMK 190,1 is most probably a male. Morphologically the canine crown resembles male *G. gorilla,* although its long axis is more vertical than in the living ape.

Estimates of tooth size have, where necessary, been made from the roots preserved. The first premolar was probably a little smaller than that of the type specimen. Measurements are included in Table 18. The second premolar is also similar to that of the type (measurements in Table 19). Measurements for M_1, M_2, and M_3 are given in Tables 20, 21, 22, and 23. Metrically as well as morphologically, there is no reason to assume that the specimens listed in these tables form more than a single species.

The overall proportions of the mandible have been estimated by reconstructing both tooth rows. A cast of BM(NH) M16648 was used to build up the right mandibular ramus and teeth. Great care was taken to make the rami and tooth rows symmetrical. Measurements are given in Table 24.

Considering external measurements, the mandibular tooth row does diverge posteriorly, as it does in male gorillas. The specimen from Songhor is very similar

Table 23 Comparative measurements of C_1 in *D. (P.) major* and *Gorilla*

	NMK 190.1	UMP 66-01		*G. gorilla* male (n=20)	*G. gorilla* female (n=18)
Max L	15.1	**16.0	$\bar{X}$	18.1	13.0
			95%CL	15.2-21.0	11.1-14.9
Trans B	12.5	**12.0	$\bar{X}$	14.1	10.3
			95%CL	12.2-16.0	8.9-11.7

Table 24 Measurements of *D. (P.) major* and *G. gorilla* mandibular dentitions

	NMK 190,1	UMP 62-10/66-01		*G. gorilla* males (n=20)
I_1 B	**21.2	**23.0	$\bar{X}$	28.4
			95%CL	24.8-32.1
C_1 B	**46.0	**49.5	$\bar{X}$	56.3
			95%CL	47.4-65.2
P_4 B	**51.0	**54.5	$\bar{X}$	61.1
			95%CL	56.6-66.6
M_3 B	**58.5	**60.5	$\bar{X}$	67.1
			95%CL	59.4-75.8

in these dimensions to the reconstructed mandible from Moroto II (mentioned in Chap. IV, p. 45). The general size and proportions of the Moroto mandible were determined as follows. A reconstructed mandible of combining BM(NH) M16648 and NMK 190,1 was sawn in half at the symphysis and the half mandibles were oriented beneath the maxilla from Moroto II (UMP 62–11) until their correct relative occlusal positions were obtained. The small gap which separated the two rami at the symphysis was then filled with plaster and a new mandible cast. This new reconstruction provides estimates of the overall dimensions of the mandible associated with UMP 62–11. As can be seen from Table 24, in these dimensions the Moroto mandible is broader by 3.5 mm to 4.0 mm than the combined one from Songhor. Compared with the sort of size variation found in the sample of living male gorillas, the differences are relatively unimportant.

Although the tooth rows of the reconstructed mandible NMK 190,1 diverge posteriorly when external dimensions are considered, this is not the case for internal dimension. Internal measurements are: inside P_4, **32.0 mm, inside M_1, **32.0 mm, inside M_2, **31.0 mm, and inside M_3, **31.0 mm.

In Chapter IV, page 45, the problem of divergence and convergence of tooth rows was discussed and it was concluded that the most meaningful way of approaching the problem was from a functional point of view. Protocones of the upper premolars and molars occlude with talonid basins in the lower premolars and molars. The distance between the tips of M_1 protocones is therefore equal to the distance between the talonid basins of the M_1's.

The distances between the talonid basins of pairs of cheek teeth of NMK 190,1 were estimated first from the composite mandible and second from photographs. A photograph of NMK 190,1 was taken and a reversed print of the mandibular tooth row prepared. This reversed print was then oriented on the original in the following way to produce, by way of a mirror image, a composite photograph. A tangent AB was drawn to the most distal points of the two canines. This line was normal to the anteroposterior midline axis of the symphysis. A further tangent CD was drawn to the most lingual points of left P_4 and left M_3. The angle between AB and CD was measured. The right tooth row could then be oriented so that the tangent C′D′, drawn to the most lingual points of right P_4 and right M_3, subtended the same angle with AB. Distances between basins were then measured from the photograph. Measurements between the talonid basins of NMK 190,1 were obtained and are shown compared to the interprotocone dimensions of the Moroto palate, UMP 62–11, in Table 25.

Table 25 Measurements on upper and lower dentitions of D. (P.) major

	NMK 190,1 Photograph	NMK 190,1 Cast	UMP 62-11 (interprotocones)
Across P_4	**40.9	**39.3	*41.9
Across M_1	**40.3	**38.7	**41.2
Across M_2	**39.6	**38.0	*40.0
Across M_3	**39.6	**38.0	*40.4

There is a slight convergence posteriorly in both upper and lower dentitions. Although the Moroto II specimen is 2 mm or so larger in each measurement, the relative proportions of the two are remarkably similar. (These characters, like many others, show a wide range of variation in living gorillas.) Once again we have confirmatory evidence that we are dealing with individuals sampled from a single species, *D. (P.) major.*

Leakey has stated that he does not regard the specimen from Moroto II (UMP 62–11) as *D.* (*P.*) *major.* His views are summarized as follows. First, "in not just one but many specimens of four species, *Proconsul* has a relatively small canine with a molar-premolar series converging forward, as opposed to the backward convergence in pongids, including Bill Bishop's . . . fossil pongid from Moroto —a contemporary of *Proconsul*" (Leakey, 1965, p. 13–14). In addition, it has been "claimed that it should be possible to fit together a *Proconsul major* mandible with the maxilla found by Bill Bishop and attributed to *Proconsul major.* I have tried it with this backward converging maxilla, and I simply do not see how they could be made to articulate normally and with proper tooth contact" (Leakey, 1965, p. 106).

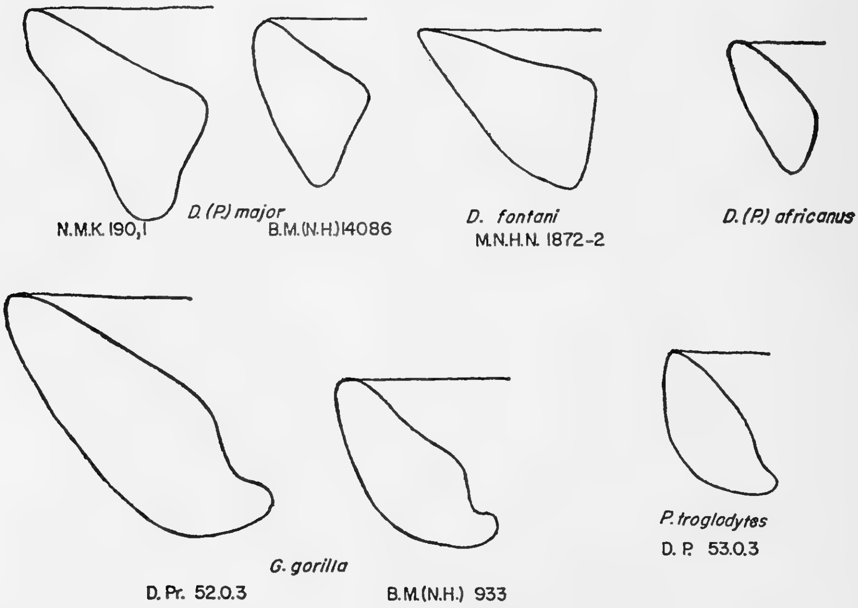
The mandibular specimen of *D. (P.) major* to which Leakey refers is NMK 190,1. As noted above, the tooth rows do diverge posteriorly if the *external* dimensions are used, and this is also the case for male gorillas (and for other living pongids—see Appendix 1). This is not the case, however, for internal dimensions, nor for the interbasin measurements. The internal contours of the mandible converge anteriorly, as do the external contours, and a superficial examination of the mandibular rami certainly makes it seem as though the mandible is convergent anteriorly. This feature is also to be seen in male gorillas. It seems clear, however, that Leakey is talking not about mandibular rami but about tooth rows. The tooth rows of NMK 190,1 and UMP 62–11 are very slightly convergent posteriorly using the interprotocone and intertalonid basin criteria.

They will not articulate with each other because the bicanine diameter of NMK 190,1 is a little too small to encompass the lateral incisors of UMP 62–11. This is hardly surprising since they come from different individuals from sites separated geographically and possibly temporally, too. What is perhaps more surprising is their similarity.

The mandibular symphysis of NMK 190,1 is of some interest. This was described by Clark and Leakey (1951, p. 60) and figured by them (p. 59). A longitudinal cross section of this symphysis is figured in Leakey (1967, p. 160, fig. 5a) and is also shown in Figure 3. The symphysis is approximately triangular in cross section, with a long planum alveolare gently sloping to the superior transverse torus, the most posterior point of which is opposite P_4. The internal contour then slopes inferiorly and anteriorly to the inferior transverse torus. The anterior border of the symphysis is rather straight. The length of this anterior border from infradentale to gnathion is approximately 52 mm and the symphyseal thickness normal to this dimension approximately 28 mm. It should be emphasized that this is the only complete symphysis of a male *D. (P.) major* known. The other less complete mandibular remains referred to this species share certain features with this specimen. Thus UMP 62–10/66–01 and BM(NH) M16648 show the thickening of the internal aspect of the mandible anteriorly and the gradual shallowing of the superior internal slope; in addition they have long, gently sloping plana. The infant mandibles from Napak also have these features and show that inferiorly the internal contour of the mandible slopes anteriorly and does not project backwards to form a simian shelf.

This symphyseal morphology contrasts with that seen in another African species of *Dryopithecus, D. (P.) africanus* (Fig. 3). Here the planum slopes

Fig. 3 Mid-symphyseal sections of living and fossil Pongidae (not to scale)



more steeply to the superior transverse torus. Although there is no posterior projection in the inferior symphyseal region, the inferior border is in some cases barely anterior to the superior transverse torus. The absence of a long, sloping planum is coupled with a relatively gracile internal mandibular contour, without marked lingual thickening. The two species are similar in having no simian shelf, and therefore a roughly triangular symphyseal cross section; they differ in the relative proportions of the triangle (this is shown clearly in Leakey, 1967, figs. 5a, 5b).

If we consider the superior two-thirds of the symphyseal area of *D.* (*P.*) *major,* it is of some interest that the contour of this region is very similar to that of many *G. gorilla.* It should be emphasized here that, as in all other features, gorillas are variable in symphyseal structure (Vogel, 1961; Schultz, 1963). In gorillas, there is generally a long planum alveolare, sloping gently to a superior transverse torus, the most posterior part of which is opposite P_4. The similarities of this and the anterior symphyseal contour to *D.* (*P.*) *major* are striking. Inferiorly, however, the gorilla mandible usually projects posteriorly as a simian shelf or basal plate, although this feature is quite variable in expression (Vogel, 1961; Schultz, 1963). The development of a simian shelf in *G. gorilla* has also produced the inferior rounding of the anterior symphyseal contour. Both anterior rounding and shelf are absent in *D. (P.) major.* It has been suggested by a number of workers that the simian shelf acts as a buttress to strengthen the anterior mandibular region, particularly in recent pongids where the anterior dentition is relatively broad (see, for example, Scott, 1963).

Table 26 contains values of the ratio, (I_1 B/P_3–M_3 L) × 100 for living chimpanzees and gorillas. This ratio has been calculated in an attempt to relate the breadth of the incisor region to the size of the cheek teeth and hence to chewing stresses. In gorillas the ratio is low mainly perhaps because the length of the tooth row is relatively great. In chimpanzees with a much shorter tooth row, the incisor region is as broad as in gorillas (see Table 27). Presumably the incisors are of similar importance in the two species, or perhaps of greater importance to the frugivorous chimpanzees; grinding and crushing are more important to the herbivorous gorilla, hence the great size of the cheek teeth. The value of this ratio in *D.* (*P.*) *major* is: UMP 62–10/66–01, 35.9, and NMK 190,1, 33.6.

Table 26 Ratio (BI_1/LP_3-M_3) x 100 in G. gorilla and P. troglodytes

	G. gorilla		P. troglodytes	
	Males (n=20)	Females (n=20)	Males (n=14)	Females (n=12)
$\bar{X}$	36.8	37.2	57.8	58.1
OR	34.6-40.8	33.0-42.0	53.4-61.8	54.0-62.3

The incisor region is, relatively speaking, no smaller than in gorillas. If the simian shelf in gorillas is a phylogenetic response to anterior chewing stresses, presumably these stresses act as selection pressures producing simian shelves only when the absolute values of the dimensions reach certain critical thresholds. The gorilla symphysis is buttressed not only by the simian shelf, but also by the superior transverse torus (which is very much smaller in chimpanzees).

The symphysis of the type observed in *D. (P.) major* could plausibly have

Table 27 Measurements of mandibular tooth rows of *G. gorilla* and *P. troglodytes*

		G. gorilla males (n=20)	*G. gorilla* females	*P. troglodytes* males (n=14)	*P. troglodytes* females (n=12)
I_1 B	$\bar{x}$	28.4	26.4 (n=20)	29.0	28.9
	95%CL	24.8-32.1	22.5-30.3	26.3-31.8	25.7-32.1
C_1 B	$\bar{x}$	56.3	44.7 (n=20)	47.6	45.1
	95%CL	47.4-65.2	37.9-51.5	43.1-52.0	39.6-50.5
P_4 B	$\bar{x}$	61.1	52.2 (n=19)	51.4	50.9
	95%CL	56.6-66.6	42.2-62.2	45.9-56.9	44.6-57.2
M_3 B	$\bar{x}$	67.1	62.0 (n=19)	54.6	55.1
	95%CL	59.4-75.8	54.5-68.5	49.3-60.0	50.0-60.3
P_3 -M_3 L	$\bar{x}$	77.4	71.0 (n=20)	50.3	49.7
	95%CL	70.1-84.7	64.0-78.0	44.5-56.1	47.0-52.5

evolved into the gorilla type of symphyseal morphology. Until we understand fully the functional anatomy of the symphysis it may well be impossible to evaluate the importance of the simian shelf. It has probably evolved separately in all three living pongids, presumably as some sort of phylogenetic response to chewing stresses. Too great an emphasis should not be placed on its degree of development, particularly in phylogenetic and taxonomic studies.

Table 28 shows a further ratio calculated in an attempt to interrelate jaw size, via cheek tooth length, to mandibular breadth; the ratio is (C_1 B/P_3–M_3 L) × 100. Once again, the relatively short cheek tooth length in chimpanzees is to be noted. Male gorillas have relatively broader bicanine breadths than females and therefore have somewhat higher ratios. The values of this ratio for *D. (P.) major* are: UMP 62–10/66–01, 77.3, and NMK 190,1, 73.0.

Enough is preserved of the horizontal ramus from Moroto II for comparison with NMK 190,1 to be useful. The external surface of the ramus is virtually identical in size and morphology in the two individuals. Canine and premolar juga are present in both, making the anterior part of the body convex. Posterior to this is a concave region below P_4 and M_1, before the body becomes thick and convex again opposite M_2 and M_3.

Table 28 Ratio (BC_1/L P_3—M_3) x 100 in *G. gorilla* and *P. troglodytes*

	G. gorilla		*P. troglodytes*	
	Males (n=20)	Females (n=18)	Males (n=13)	Females (n=12)
$\bar{x}$	70.7	62.5	93.6	90.6
OR	64.6-77.8	57.3-68.5	85.0-100.8	83.6-98.2

In summary, as far as dental and mandibular morphology, dimensions, and proportions of these relatively complete *D. (P.) major* mandibles from Uganda and Kenya are concerned, all three fall within a range of variation to be expected in a sample drawn from a single species. It is probable, too, that all three specimens are male. It is particularly important to note that the palate from Moroto II and the most complete mandible from Songhor (NMK 190,1) do fall in all probability within the same species.

Further specimens of *D. (P.) major* from Songhor were described by Clark and Leakey (1951, p. 60–61) and Clark (1952, p. 279–281). As noted, some of these have been removed by Leakey (1967). Those that are, in my opinion, definitely *D. (P.) major* are briefly noted here and their measurements given.

NMK 271,55. The specimen is a left lower second molar, described and figured by Clark and Leakey (1951). They noted that this tooth, an unerupted, weathered crown, was morphologically similar to the M_2's of *D. (P.) nyanzae,* although they recognized it as a *D. (P.) major.* It is very similar to the M_2's of *D. (P.) major* specimens BM(NH) M16648 and NMK 190,1, although it is a little larger. Measurements are included in Table 21.

NMK 272,56. The specimen is a left lower second premolar, described and figured by Clark and Leakey (1951). Morphologically this tooth is similar to the others from Songhor and Napak. Measurements are included in Table 19.

NMK 382,3 and 383,4. The specimens are a left and a right first lower premolar, described and figured (NMK 383,4) in Clark (1952). They are the crowns and roots of two first premolars, probably from the same individual. The left tooth is broken mesially. The right crown is well preserved. Morphologically, the crowns are similar to those of *G. gorilla.* Although said to contrast morphologically with the P_3's of *D. (P.) nyanzae,* these teeth are similar to the *D. (P.) nyanzae* from Koru [BM(NH) M14086] described below. Measurements are given in Table 18.

NMK 604,69. The specimen is the weathered and worn crown of a *D. (P.) major* first premolar. Measurements are included in Table 18.

NMK 102, CMH35. The specimen is a right upper second molar, described and figured by Clark and Leakey (1951). This tooth, tentatively identified as a second molar, was only provisionally assigned by Clark and Leakey to *D. (P.) major* because of its large size and its similarity to teeth of other species of that subgenus. Measurements of this specimen are included in Table 16, p. 51. The crown morphology is similar to molars of *D. (P.) africanus* and *nyanzae* in having a well-developed cingulum. This cingulum is beaded and the lingual surfaces of protocone and hypocone are wrinkled. A distinct protoconule is also present mesial and buccal to the protocone. In all these features, NMK 102, CMH35 resembles the upper molars from Moroto II and Napak referred here to *D. (P.) major.*

NMK 405,381 (Fig. 21). The specimen is a left upper second molar, described and figured in Clark (1952). The morphology of the crown is very similar indeed to that of UMP 62–08 from Napak (see Fig. 21). There can be little doubt that this is a second molar of the species to which UMP 62–08 and 62–11 belong. Measurements are included in Table 16, p. 51.

Clark and Leakey (1951) and Clark (1952) had at their disposal only two upper teeth which might possibly be referred to *D. (P.) major.* Since these molars resembled the mandibular teeth of *D. (P.) major* in much the same ways that the upper molars of *D. (P.) nyanzae* and *D. (P.) africanus* resembled their respective mandibular teeth, a tentative assignment to *D. (P.) major* was made. At Moroto II, Napak and Songhor, upper molars of this type are found with mandibles referable to *D. (P.) major.* As noted already, the Moroto II maxilla has the dental morphology and proportions to be expected of a *D. (P.) major* palate. The M^2 from Napak V, UMP 62–08, occludes well with NMK 190,1 from Songhor (see Fig. 24). It is perhaps a little too big and would probably occlude best with the slightly larger BM(NH) M16648. However, it is not possible to test this as UMP 62–08 is from the left side and BM(NH) M16648 from the right. Therefore, unless we are dealing, at three separate localities, with the upper dentition of one large pongid and the lower dentition of another large pongid, both species having similar proportions and morphologies, it seems best to assume that we are dealing with a single, variable species. As Bishop has pointed out (1964, p. 1331), it would be illogical to do otherwise, particularly since the new evidence accumulated since 1952 strengthens rather than weakens the hypothesis that only one species is involved.

So far in this review, no mention has been made of unequivocal *D. (P.) major* material from the deposits at Rusinga. In 1952, Clark described the only well-identified specimen, NMK 129,257, from site R3 on Rusinga Island.

NMK 129,257. The specimen, a left deciduous second premolar from Rusinga R3, lower Hiwegi Series, was described by Clark (1952). Clark assigned this tooth to *D. (P.) major* because it was clearly that of a pongid, and because of its large size. Measurements are given in Table 29. It was said by Clark (1952, p. 280) to be "intermediate in general dimensions between chimpanzee and the gorilla." This statement is not correct, Table 29 shows the specimen falling within

Table 29 Comparative measurements of dP_4 in: (a) *D. (P.) major,* (b) *G. gorilla* and *P. troglodytes*

(a)	NMK 129,257	NMK 277 58'48(S)	UMP (62-13) (Napak)
MDi L	10.3	9.7	*9.8
Max B	8.1	7.8	*7.8

(b)		*G. gorilla* (n=12)	*P. troglodytes* (n=17)
MDi L[1]	$\bar{X}$	13.6	9.0
	95%CL	11.4-15.8	7.3-10.7
Max B[1]	$\bar{X}$	10.3	7.6
	95%CL	7.9-12.7	6.0- 9.2

[1] Comparative data from Ashton and Zuckerman (1950)

the chimpanzee confidence limits. The estimated crown dimensions of dP_4 of UMP 62–13 from Napak are only a little smaller than those of the Rusinga specimen.

Discussion of the Large Specimens

The material from Songhor and Moroto II, and presumably some from Napak, probably represents male specimens—the large size of the canines, for example, suggests this. It also seems a reasonable hypothesis that *D. (P.) major* is ancestral to or close to the ancestry of the living species *G. gorilla.* It is well known that this living species shows considerable sexual dimorphism in dental and mandibular size, particularly canine size (see Appendix 1 and Figs. 4–6). This is in contrast to *Pan troglodytes* where, in the dental and mandibular dimensions that we have been discussing, there is little size dimorphism. One is tempted, therefore, to ask where the females of *D. (P.) major* are, for one should expect to find them; one would expect them to be morphologically similar to, though smaller than, the males of *D. (P.) major.* Some of the smaller specimens from Napak are probably females. (It should be cautioned here, however, that smallness is not invariably to be equated with "femaleness," as a glance through Appendix 1 clearly shows.)

Clark and Leakey published the diagnosis of *D. (P.) major* in 1950. The diagnosis included the following sentence (1950, p. 261). "The lower teeth resemble those of *P. nyanzae* in their relative proportions and cusp pattern, but are of a much larger size." As noted above, large upper teeth were assigned to this taxon because they also resembled morphologically those of *D. (P.) nyanzae.* The specimens assigned to *D. (P.) major* in 1951 and 1952 are therefore probably almost entirely those of males. It has been suggested already that female *D. (P.) major* are present at Napak. To discuss other probable females we must return to the two Kenya sites, Koru and Songhor.

SMALL SPECIMENS

BM(NH) M14086 (Fig. 23). The specimen, from Koru, has been described and figured by Hopwood (1933b). It consists of right and left mandibular rami, broken at the symphysis on the right and just lateral to it on the left. The left side contains the root of C_1 and crowns of P_3 to M_2. The roots of M_3 are preserved. The mandible has been dissected internally to expose the tooth roots. On the right side the same root and crowns are preserved, together with the buccal three-fourths of the mesial moiety of the M_3 crown.

This individual was referred originally by Hopwood to the species *Proconsul africanus* and later transferred to *Proconsul nyanzae* [*D. (P.) nyanzae*] by Clark and Leakey (1951, p. 39). The mandible and dentition were described in detail by Hopwood (1933b) and only a few details will be noted here.

The symphysis is thick, with a triangular cross section and a long, gently sloping planum alveolare. The ramus thickens anteriorly, so that the internal contours converge. In all features preserved, the rami and symphyses of BM(NH) M14086 and NMK 190,1 are identical (see Fig. 3). Comparative measurements are given in Table 30.

Table 30 Measurements of *D.* (*P.*) *major* mandibles

	NMK 190,1	BM(NH) M14086	NMK 198,28
Symphyseal H from infradentale to gnathion	*52.0	*42.0	*41.0
Symphyseal T	*28.0	*23.0	23.5
Rameal D at P_4	41.0	36.5	*33.0
Rameal T at P_4	21.0	17.0	-
Rameal D at M_3	34.5	*32.0	-
Rameal T at M_3	25.5	*20.0	20.5

If *D.* (*P.*) *major* is ancestral to *G. gorilla* and is assumed to be dimorphic like the gorilla, and if NMK 190,1 is accepted as a male, a reasonable hypothesis is that BM(NH) M14086 is a female of the same species. Measurements of the edentulous mandible NMK 198,28 from Songhor, described and figured by Clark and Leakey (1951, p. 48 and pl. IV, fig. 21) are also included in the above table. The symphysis has the same morphology as BM(NH) M14086. The size and proportions of the cheek teeth, as judged from their roots, were probably similar to those of BM(NH) M14086, and this specimen, too, can be regarded as a female *D.* (*P*) *major.* It is possible to estimate some measurements from the tooth rows of these three specimens (see Table 31). If reference is made to Table 27, it will be seen that these differences are no greater than might be expected within even a moderately dimorphic species.

The dentition of BM(NH) M14086 is not particularly well preserved. Both canines are broken at the alveolar margin. Their lengths and breadths are approximately 13.5 mm and 9.5 mm, expectable dimensions if this is a female. Both first premolar crowns are in good condition. The mesial border slopes straight back to the main cusp. There is a mesial wear facet worn by the upper canine and a groove lingual to this; the groove has a small cingulum at its mesial-lingual extremity. A moderate talonid is developed distally. The buccal surface is moderately convex in its upper third, then rather flattened. Morphologically, the P_3's are similar to NMK 382,3 and 383,4 from Songhor discussed above. Length and breadth are 12.7 mm and 7.5 mm. The rest of the dentition is worn and eroded and almost all occlusal details have been lost. It has been possible to estimate with some accuracy the lengths and breadths of right P_4 and M_2 and left M_1. Since these differ from the values given by Hopwood (1933b, p. 447), they are listed here: right P_4, MDi L, *7.8 mm, BuLi B, *9.0 mm; left M_1, MDi L, *10.9 mm, Tri B, 9.3 mm, Tal B, 9.5 mm; right M_2, MDi

Table 31 Measurements of *D.* (*P.*) *major* mandibular dentitions

	NMK 190,1	BM(NH) M14086	NMK 198,28
I_1 B	**21.2	**20.0	-
C_1 B	**46.0	**42.0	-
P_4 B	**51.0	**48.0	-
P_3-M_3 L	*63.0	*54.0	*52.0

L, *12.6 mm, Tri B, 10.8 mm, Tal B, 10.2 mm; and, left M_3, MDi L, *13.5 mm, Tri B, *10.5 mm.

The P_4 and M_1 of UMP 62–16, the fragment assigned originally to *Sivapithecus africanus* by Leakey (*in* Bishop, 1962), is very similar to BM(NH) M14086 in dimensions and, as far as can be seen in M14086, morphology (Appendix 2 and Fig. 23). It is probable that UMP 62–13, 62–16, and 66–02 from Napak in Uganda are also female specimens.

Three more small specimens are probably smaller individuals of *D.* (*P.*) *major.*

NMK 101, CMH34. A left upper second molar from Songhor, the specimen has been described by Clark and Leakey (1951). The crown is moderately worn. Morphologically, the occlusal surface resembles other M^2's in this species. Measurements are included in Table 15, p. 51. The metacone is somewhat reduced in size. The lingual cingulum runs from protoconule to the distal accessory cuspule and the buccal cingulum is rather rudimentary.

NMK 198,28. The specimen, from Songhor, has been described and figured by Clark and Leakey (1951). This edentulous left horizontal ramus has already been mentioned during the discussion of BM(NH) M14086 from Koru.

NMK 277,58. The specimen is a left deciduous lower second molar from Songhor. The morphology of this specimen is similar to that of NMK 129,257 from Rusinga, although the cusps are a little less massive and the length and breadth a little smaller. Measurements are included in Table 29.

It should be borne in mind, however, that future finds may reveal that some or all of these individuals belong in a taxon separate from *D.* (*P.*) *major.* The evidence at present available makes the hypothesis outlined here rather more likely. Since much of the medium-sized material from Songhor and Koru has either been transferred by Leakey (1967) out of *D.* (*Proconsul*) to his proposed species *Kenyapithecus africanus* (transfers with which I agree), or reassigned by me to *D. (P.) major,* there is a clearly marked metrical gap between *D.* (*P.*) *africanus* and *D.* (*P.*) *major* at Songhor and Koru (see Appendix 2, Figs. 4–6 and 14–17). Two lower molars from Songhor, NMK 389,11 and NMK 390,12, described by Clark (1952, p. 277) as second molars, apparently bridge this size gap (Table 32).

The difficulty of differentiating small M_2's and large M_1's has already been noted. There are several possible explanations for these two teeth. 1) They are both small M_2's of *D.* (*P.*) *major.* 2) They are M_1's of *D.* (*P.*) *major.* 3) They are

Table 32 Lower molars of uncertain status

	NMK 389,11	NMK 390,12
MDi L	10.8	11.7
Tri B	10.3	10.5
Tal B	10.2	10.7
Index L/B x 100	104.9	109.3
Index Tal/Tri x 100	99.0	101.9

M_2's of *D.* (*P.*) *nyanzae.* 4) They are lower molars of some other hominoid species. I hesitate to choose between these alternatives, although the last is perhaps least likely.

DISCUSSION OF THE *D.* (*P.*) *MAJOR* MATERIAL FROM EAST AFRICA

The methods involved in Principal Coordinates Analysis have already been outlined in Chapter II. Briefly, Principal Coordinates Analysis enables one to take a swarm of points in multidimensional space (each point representing p standardized measurements on an individual) and reduce the number of dimensions to a much smaller number, two or three, thus enabling the points to be visualized and plotted on one or two graphs. During the dimensional reduction, the interindividual distances in n–1 space are preserved with the minimum amount of distortion.

Analysis was performed first on material of known species and sex. Data on sets of male and female chimpanzees and gorillas were analyzed. Using 28 mandibular dimensions, the two species are clearly separated; so, too, are male and female gorillas, although male and female chimpanzees are not (Fig. 4). In these dimensions, therefore, gorillas show a great deal of sexual dimorphism while chimpanzees do not. When the most complete specimens of *D.* (*Proconsul*) from Moroto, Songhor, and Koru are analyzed with the chimpanzees and gorillas

Fig. 4 Principal Coordinates Analysis of *Pan troglodytes* and *Gorilla gorilla*

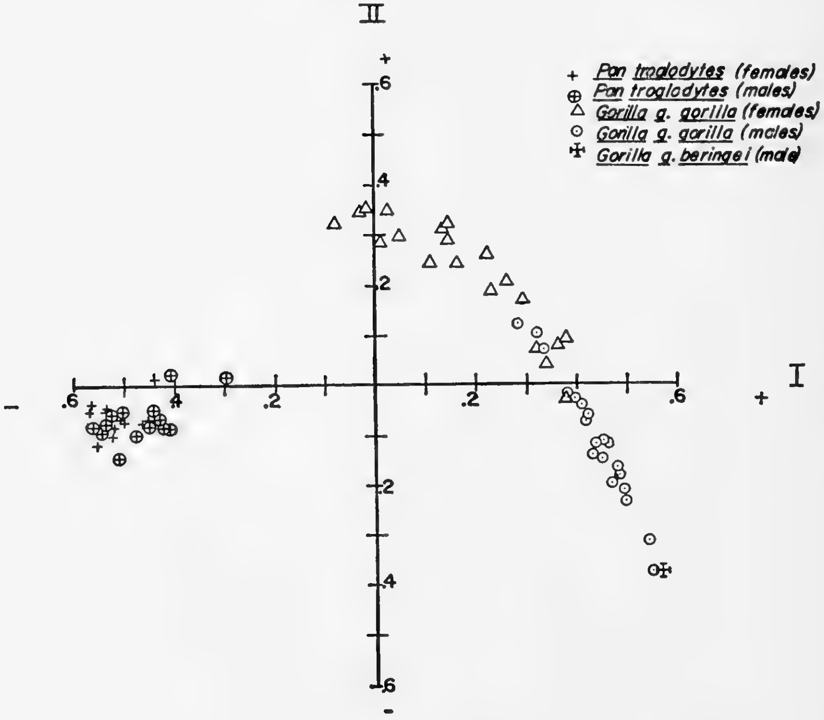
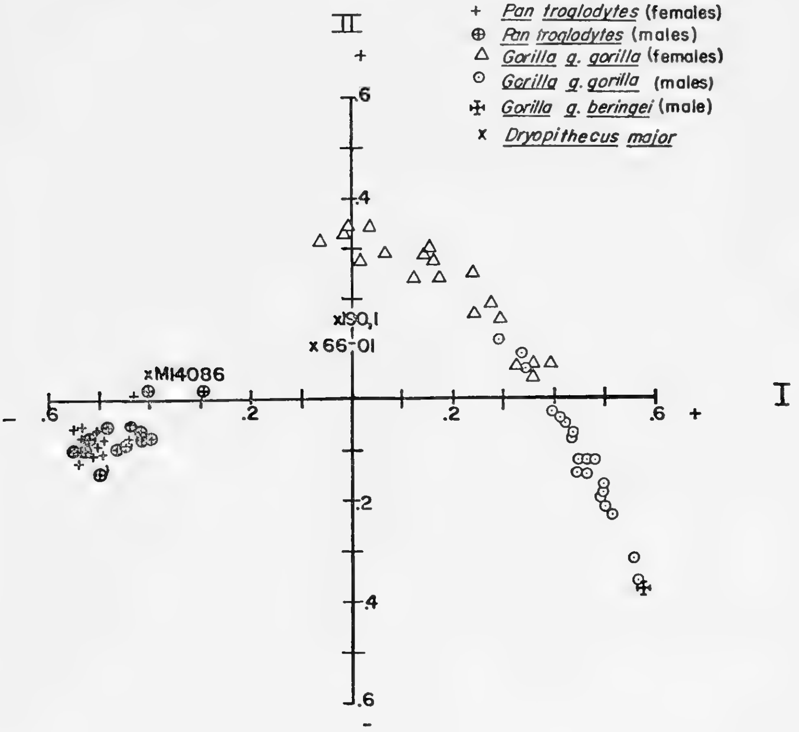


Fig. 5 Principal Coordinates Analysis of *Pan troglodytes*, *Gorilla gorilla*, and *Dryopithecus major*.

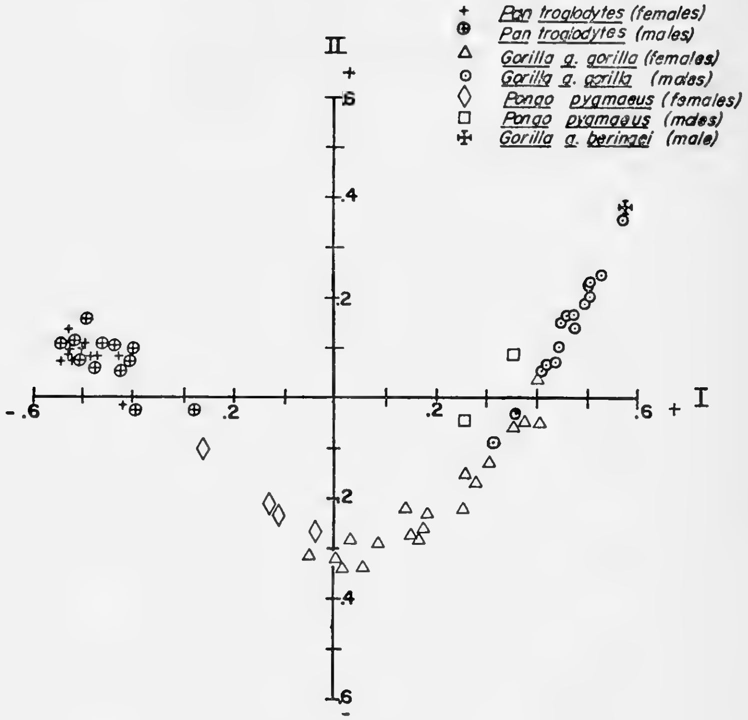


(Fig. 5), it can be seen that they lie between the two living species and are a little dispersed (see Figs. 14–17). They could, of course, represent two species, but since the larger specimens are probably males, it might be expected that the females of this species would fall on the graph approximately where the Koru specimen is plotted.

In order to test this hypothesis further it would clearly be desirable if another species of pongid, smaller than *G. gorilla* but also sexually dimorphic in these features, could be included in the analysis. *Pongo pygmaeus,* the orangutan, is a species which fulfills these requirements. A small sample is included in the analysis shown in Figure 6. The two sexes can clearly be separated. The material from Moroto, Napak, Songhor, and Koru assigned here to *D. (P.) major* could therefore belong to one species. As noted above, this conclusion is strengthened by the great morphological similarities within the sample of fossils.

Before fossil material can be classified in one species, two basic questions must be answered. First, can the individuals be regarded as drawn from a single, evolving lineage? Second, starting at the time level of the oldest known fossils, where in the evolving continuum should the (arbitrary) boundary between this species and the next youngest be drawn? The first question has been answered already, in that all the material discussed so far appears to be sampled from a single lineage. The possibility remains, however, that material

Fig. 6 Principal Coordinates Analysis of *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*.



from Moroto II may be younger than that from the other sites, and may show some evolutionary advances over that from Napak, Koru and Songhor. This possibility has been rendered considerably less likely, however, by the recent discovery at Napak of P_4 and M_1 of *D. (P.) major* (the specimens are as yet undescribed). Both specimens are almost identical to homologous teeth in the Moroto palate.

If this species is ancestral to the gorilla, the palate from Moroto II can give us information about the sorts of changes which have occurred in this lineage since the Miocene. If we then indulge in a little more speculation, it is possible to extrapolate back through time and make hypotheses about the as yet unknown and undiscovered parts of earlier individuals in this, and preceding, species. One might conclude that the anterior dentition and supporting structures of the face would be smaller in pre-Early Miocene forms. The absolute size of premolars, particularly upper ones, would have been less, and so too would the lengths of some of the posterior cheek teeth, particularly M_1 and M_2.

In conclusion, the material discussed in this and the preceding chapters can safely be assigned to a single species *D.* (*P.*) *major* which is probably ancestral to, or close to the ancestry of, the gorilla and which is probably, like the gorilla, sexually dimorphic as far as tooth and jaw size are concerned. This species is found at the Ugandan sites, and at Koru and Songhor in Kenya. Only one specimen of a tooth has been found at Rusinga, a left deciduous second premolar, NMK 129,257, from site R3. The majority of the dental remains therefore have been collected at deposits for which an elevated, forested environment has been inferred. If *D.* (*P.*) *major* is a species confined mainly to such a habitat, or even to lowland forest, this might account at least in part for its under-representation at Rusinga.

The presence at Rusinga, Songhor, and perhaps other sites, too, of another medium-sized species, called by Leakey (1967) *Kenyapithecus africanus,* demands that we exercise a certain amount of caution in the consideration of the postcranial material from these sites. However, some skeletal remains could represent *D.* (*P.*) *major.*

Walker (personal communication) reports that two distal femoral fragments from Napak probably belong in *D.* (*P.*) *major.* They are approximately chimpanzee-sized. No other species of large hominoids have been described from the Napak sites. These femoral specimens resemble one described by Clark and Leakey (1951, p. 97) from site R1 on Rusinga Island (NMK 89, R1932). These fragments, if they do indeed represent *D.* (*P.*) *major,* contrast with *Pan* and *Gorilla* in that they have shorter femoral necks than the living forms; this feature, together with the disposition of the trochanters, suggests perhaps some leaping locomotor behavior patterns.

A talus (NMK 111, CMH145) and associated calcaneum (NMK 112, CMH146) from Songhor, matching in size large adult male chimpanzees, probably represent *D.* (*P.*) *major,* too. The talus has been compared to living man on the one hand, and *Pan* and *Gorilla* on the other (Day, personal communication), using the multivariate statistical technique of Canonical Analysis. The Songhor talus matches that of the gorilla. Walker (personal communication) believes, however, that functionally this talus may also be similar to colobines, a conclusion which would tie in with the femoral evidence.

The Moroto vertebrae (p. 43) reinforce the dental, facial, and gnathic evidence indicating that we are dealing here with a probable gorilla ancestor, and the distribution of this species in sites which sample a forested upland habitat like that of the living mountain gorilla also supports this view. However, the total postcranial evidence indicates that *D. (P.) major* may well have been a more active and less terrestrial form than the living great ape. There is nothing to suggest that *D. (P.) major* was a "brachiating" animal, like *Pongo* for example. It might have been a knuckle-walker. However, arm-swinging quadrupedal behavior as in *Ateles* or *Lagothrix* is a distinct possibility.

CHAPTER VII. *DRYOPITHECUS (PROCONSUL) AFRICANUS* AND *DRYOPITHECUS (PROCONSUL) NYANZAE*

BACKGROUND OF THE MATERIAL

Hominoid fossils were first recovered from Rusinga Island and Songhor in 1931 and 1932 by L. S. B. Leakey and D. MacInnes. In 1933 Hopwood described a new ape, *Proconsul africanus,* from the Miocene of Koru. The mandible described by him has been transferred here to *D. (P.) major* (p. 71). Collecting has continued steadily since then, due principally to the magnificent efforts of Dr. and Mrs. Leakey, and now several hundred hominoid specimens are preserved in the National Museum Centre for Prehistory and Palaeontology in Nairobi. A large number of these are pongids. MacInnes (1943) described many of the Rusinga pongids as *Proconsul africanus.* In 1950 Clark and Leakey published diagnoses of two further species of this genus, *P. nyanzae* and *P. major,* together with a new species of *Sivapithecus, S. africanus.* This they followed in 1951 with a detailed monograph. Clark described additional specimens in 1952, and more recently Napier and Davis (1959) have discussed parts of the postcranial skeleton of *P. africanus.* Simons and I (1965) transferred the species of *Proconsul* to *Dryopithecus,* retaining them in a subgenus, (*Proconsul*).

No attempt will be made to describe in detail individual specimens of *D. (P.) africanus* and *D. (P.) nyanzae* in this chapter, since these have been covered adequately by Hopwood (1933b), MacInnes (1943), Clark and Leakey (1951), Clark (1952), and Napier and Davis (1959). However, the opportunity will be taken to compare the various species of the subgenus.

DRYOPITHECUS (PROCONSUL) AFRICANUS

D. (*P.*) *africanus* was first described by Hopwood in 1933 (a and b), the type specimen being BM(NH) M14084 from Koru, noted in the previous chapter. In these papers Hopwood made clear his view that *D.* (*P.*) *africanus* was ancestral to *Pan.* The specimen consists of part of a right maxilla with the upper dentition preserved from C^1 to M^3 (Fig. 25). Measurements are included in Appendix 2. The canine is relatively long, narrow, and high; its dimensions are given in Table 33 (comparative data from Ashton and Zuckerman, 1950).

The measurements fall squarely within the limits for the chimpanzee. The relatively great size of the canine, particularly its height, compared to the relatively small size of the cheek teeth, suggests that BM(NH) M14084 is a male.

The premolars are fairly simple bicuspid teeth with the paracone being higher than protocone, particularly in P^3. Both cusps are rather sharp. The buccal border of the tooth is longer than the lingual, due to the mesial

Table 33 C^1 measurements of *D. (P.) africanus*

	BM(NH) M14084		*P. troglodytes* males	*P. troglodytes* females
Max L	11.6	$\bar{X}$	13.6 (n=22)	11.3 (n=16)
		95%CL	9.5-17.7	8.0-14.6
Trans B	9.1	$\bar{X}$	10.9 (n=22)	9.0 (n=16)
		95%CL	7.4-14.4	6.9-11.1
La H	15.2	$\bar{X}$	20.1 (n=5)	14.7 (n=7)
		95%CL	8.5-30.7	9.8-19.6

projection of the mesiobuccal corner, and the enamel line is prolonged upwards in the mesial half of the buccal surface. The mesiobuccal edge of the paracone is straight and slopes downwards and distally from cervix to tip. There are faint buccal ridges mesially and distally. Mesial and distal marginal ridges are present, although not especially marked. The second premolar is similar, although there is not such a marked disparity in height between the cusps, nor is there a mesiobuccal extension.

The first two molars have well-marked trigons with low, moderately rounded, subequal cusps interconnected by rather rounded crests (Fig. 25). Mesial and distal ridges from the tips of the buccal cusps produce what is almost a continuous buccal crest. The hypocone is as large as the protocone and is shifted lingually. The trigon occupies a relatively small area of the occlusal surface, there being prominent mesial and distal marginal ridges and a lingually projecting shelf-like lingual cingulum which runs distally as far as the hypocone. On M^2, the largest of the three molars, this cingulum is faintly visible onto the hypocone. The buccal surface slopes strongly. There is a small buccal cingulum between paracone and metacone. The third molar is greatly reduced, particularly in the distal moiety. There is a decreasing development of the metacone from M^1 to M^3 and the protoconule is poorly developed on all three molars.

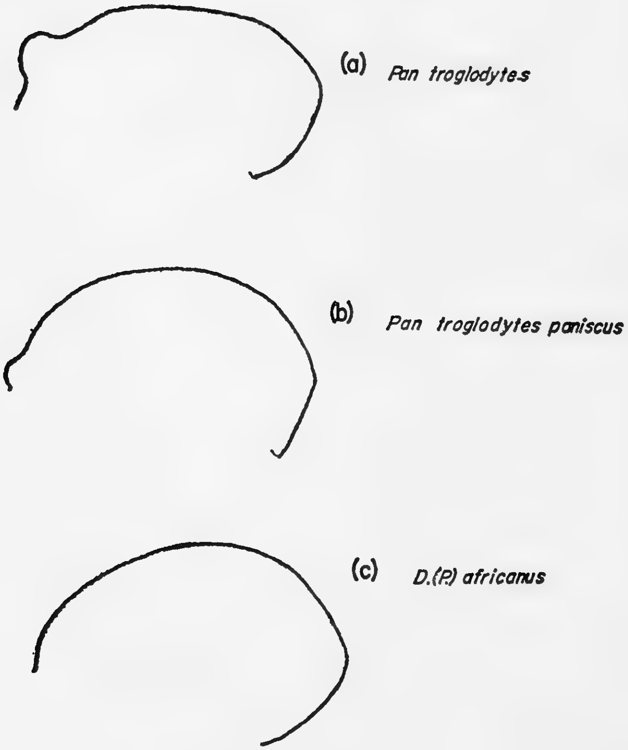
The zygomatic process begins to diverge 5 or 6 mm above the alveolar margin; it is set above the distal half of M^1. The maxilla is rather full above C^1 and P^3 due to the juga associated with the roots of these teeth. Above P^4 there is a slight concavity, indicating the presence of a small canine fossa.

A number of other maxillary specimens of this species are known from Songhor and Rusinga. In general details they are similar to the type, although the teeth are often smaller. One almost complete skull of *D.* (*P.*) *africanus* is preserved, NMK R1948,50 from site R106 on Rusinga. The dentition is very similar to that of the type, although the canine height is less. The incisor region is small and this, associated with the relatively small canines, means that the face is not particularly prognathous and that the tooth rows tend to diverge posteriorly. The skull is described fully by Clark and Leakey (1951, p. 16–28). It has been crushed and was restored by these workers. Robinson (1952) pointed out that the reconstruction was perhaps a little too prognathous.

The vault is thin, delicate and rounded, there being an almost total absence of cranial superstructures such as tori and ridges. This is presumably because the dentition and facial skeleton are delicately built, and therefore facial and cranial buttressing for powerful masticatory musculature are not required. A similar combination of factors is found in the pygmy chimpanzee, *Pan troglodytes paniscus,* although here the anterior dentition is larger than that of *D.* (*P.*) *africanus,* and the skull is somewhat larger and more robust. I (1965, p. 41) suggested that, "the fact that *africanus* is a small form like the pygmy chimpanzee accounts for the . . . rounded cranial vault, and the lack of brow ridges." Leakey replied to this (1965, p. 105), "if you enlarge photographs of the skulls of pygmy chimpanzees up to gorilla size, as I have done, you find that the pygmy chimpanzee has just as marked a torus relative to the size of the skull."

All illustrations and specimens of pygmy chimpanzees that I have located show clearly that the facial skeleton is relatively smaller than that in other "normal-sized" chimpanzees; the cranial vault is relatively larger. Correlated with these differences in proportions, the face in pygmy chimpanzees is less prognathous, the cranial vault more rounded, and the supraorbital tori less well developed. Figure 7, taken partly from Remane (1959) shows this clearly,

Fig.7 **Sagittal sections of *Pan troglodytes* and *D.(P.) africanus*.** (a) and (b) from Remane (1959); (c) modified from Clark and Leakey (1951).



as do the excellent illustrations in Weidenreich (1941, figs. 18–20). The important points are the relative proportions of face, torus, and vault; no amount of photographic enlargement will alter these proportions.

Certain features of the brain of *D. africanus* are primitive; for example, the relative underdevelopment of cerebral sulci, the small size of the frontal lobes, and the presence of a subarcuate fossa indicating a primitive cerebellar morphology. This combination of features has been described as cercopithecoid or hylobatid rather than pongid (Clark and Leakey, 1951), although these authors noted (p. 113) that these are best regarded as primitive catarrhine features which have been retained in some cercopithecoids and hylobatids, and lost (or rather overlayed) in the living pongids.

Mandibles and the mandibular dentition of *D.* (*P.*) *africanus* are fairly well represented in the collections. The morphology of the mandible is reminiscent of the chimpanzee, although the incisors and incisor region are smaller than in the living species. The bicanine breadth is also low, and hence the rami converge anteriorly. The rami are low (less than 27.0 mm deep at P^4), although relatively robust. The symphysis is primitive, the simian shelf being absent. The height of the symphysis from infradentale to gnathion is rarely more than 28 mm and symphyseal thickness rarely more than 12 mm. The anterior margin slopes backward and downward at an angle of about 60 degrees to the occlusal plane; the most inferior part of the anterior border curves gently until it is parallel to the alveolar plane as it merges into the posterior border. The posterior border slopes fairly steeply backward as a planum alveolare. The superior transverse torus is rather poorly developed and low down, only 8 or 9 mm above the inferior transverse torus, which projects posteriorly in the midline almost to the same level as the most posterior point on the superior torus. Apart from the absence of a simian shelf, the significance of which was discussed in the previous chapter, this symphyseal morphology is similar to that of the chimpanzee (see Fig. 3).

The postcranial skeleton of *D.* (*P.*) *africanus* is best known from the juvenile material recovered in 1951 by Dr. T. Whitworth at Gumba on Rusinga Island. This material is described in detail by Napier and Davis (1959); they described a representative set of bones from the forelimb, a few from the foot, the maxilla, mandible, and occipital bone of the same juvenile individual. Davis and Napier (1963) reconstructed the skull of this specimen and showed that the face was relatively orthognathous when compared to those of *D.* (*P.*) *major* and of the living pongids.

The forelimb skeleton of this *D.* (*P.*) *africanus* was discussed by Napier and Davis principally from the viewpoint of functional anatomy and locomotor behavior rather than of phylogenetic relationships. Their conclusions, together with some modifications suggested by Walker (personal communication), are briefly summarized here, bone by bone.

The proximal extremity of the humerus in general features is intermediate between those of the Old World arboreal quadrupeds like *Presbytis*, classified as quadrupedal semibrachiators (Napier, 1963a; Ashton, Healy, Oxnard, and Spence, 1965; Napier and Walker, 1967), and *Pan*. The distal extremity is very similar to that of *Pan*. In particular, the increased surface of origin for the brachialis muscle, the prominence of the keel, the absence of a sharp lateral border to the olecranon fossa, the high trochlear index, and the roundness and backward extension of the capitular surface, are all characteristic of the living chimpanzee. Presumably these features imply a forelimb that was mobile, that could be utilized to support the body's weight during locomotion, and an elbow joint providing freedom of movement and stability for pronation and supination during suspension.

The radius is basically that of an arboreal quadruped, although the lateral curvature of the shaft is reminiscent of that in *Pan.* Walker (personal communication) believes that some features of the radius suggest ground-living adaptations. The distal extremity of the ulna is not similar to that of *Pan,* but rather to those of New and Old World monkeys.

The brachial index (length of radius/length of humerus × 100) cannot be calculated exactly, but lies between 83 and 88. This specimen is juvenile and the adult brachial index would have been somewhat higher. The brachial index in *Papio* is 104, in *Cercopithecus* 96, in *Pan* 93, in *Lagothrix* 89, in *Gorilla* 80, and in *Homo sapiens* 75 (all sample mean values). In general, brachial indices of fossil primates, where known, tend to be lower than those of their putative descendants (Napier and Davis, 1959, p. 38). In this case *D.* (*P.*) *africanus* allies most closely with *Pan.*

Although the hand is relatively shorter than that of *Pan* when considered as a percentage of total forelimb length, the relative proportions of the different parts of the hand (carpus, metacarpus, and phalanges) are rather similar to those of *Pan.* It is tentatively concluded that the thumb of *D.* (*P.*) *africanus* was relatively longer than that of *Pan.*

There was a free *os centrale,* unlike *Pan.* The set of the trapezium resembles that of *Pan* and results in the presence of a deep carpal tunnel. This feature is associated with the well-developed flexor tendons of pongids (for example, *Pan*) and the most arboreal of the New World quadrupedal semibrachiators (for example, *Ateles*). According to Napier and Davis (1959, p. 60) the articular surface of the trapezium would not permit axial rotary movements of the first metacarpal (and hence true opposability). In general, the carpal bones resemble those of arboreal monkeys, although some features characteristic of *Pan* are present. Walker (personal communication) believes that some characters of *D.* (*P.*) *africanus* may indicate ground-living behavioral patterns. The metacarpals and phalanges resemble those of arboreal quadrupedal species.

The foot is represented by relatively few bones. The medial cuneiform, although morphologically reminiscent of *Cercopithecus,* is relatively short. Such shortening is connected by Napier and Davis with the general tarsal shortening thought to be associated with an arboreal way of life. On the other hand Walker sees the shortening of the anterior tarsal segment as a terrestrial specialization. The phalanges resemble those of *Pan.*

The morphology of the postcranial skeleton suggests an arboreal animal whose locomotor habits would have been similar to those of the New World forms like *Lagothrix* or *Ateles,* quadrupedal animals in which arm-swinging and body-suspension below flexible supports nevertheless play an important part in climbing and other locomotor activities. According to Walker (personal communication), *D.* (*P.*) *africanus* may also have been at least partially adapted to ground-living. Very tentatively, the evidence could be interpreted as indicating that *D.* (*P.*) *africanus* was a small, active "quadrupedal" form, armswing occasionally like some of the New World species. However, it may also have ventured to the ground. Ecologically, the species could have filled much the same sort of arboreal/terrestrial niche as *Cercopithecus aethiops.*

Special resemblances to living primates are almost exclusively to *Pan.* If *D.* (*P.*) *africanus* is the ancestor of the chimpanzee, or is similar to that ancestor, an increase in body size, more ground-living behavior, and the development of knuckle-walking adaptations (Tuttle, 1967), would convert the Miocene form into living *Pan.* In this way, we need not violate the actual fossil evidence, nor is there any necessity to postulate an improbable long-armed, gibbon-like, "brachiating" phase in chimpanzee ancestry.

THE AFFINITIES OF *D. (P.) AFRICANUS*

Dental and mandibular measurements of *D. (P.) africanus* are set out in Appendix 3, together with basic statistics for samples of more than eight individuals. There are no detectable differences between samples from Rusinga, Songhor, and Koru. Material from the three samples has been pooled in the calculation of statistics and all specimens can be regarded as being drawn from a single lineage. Leakey (personal communication) believes that some material previously assigned to *D. (P.) africanus* belongs to another, as yet unnamed, species of this subgenus. The specimen to be described as the holotype of this new species has not been included here. The possibility should be borne in mind that further material, at present classified in *D.* (*P.*) *africanus,* does not in fact belong there.

The general resemblances, particularly dental, between *D.* (*P.*) *africanus* and *D.* (*P.*) *major* are probably enough to warrant their retention in the same subgenus. In both species the upper molars and occasionally premolars have prominent cingula, particularly on the lingual side. The first molar is smaller than the second (see Table 34 for ratios of molar lengths). Cingula are also present on the lower molars although these are less marked. The lower molars

Table 34 Ratios of MDi lengths of D. (Proconsul) specimens, Gorilla and Pan

		D. (P.) africanus	D. (P.) nyanzae	D. (P.) major	G. gorilla	P. troglodytes
M^1/M^2 x 100	n	6	3	1	40	26
	$\bar{X}$	90.6	77.9	89.3	94.0	98.9
	OR	87.0- 97.4	72.3- 84.0	-	83.5-101.1	82.0-109.8
M^2/M^3 x 100	n	2	3	1	40	19
	$\bar{X}$	112.9	105.6	102.2	107.3	112.3
	OR	112.2-113.6	100.0-109.8	-	96.6-122.8	100.0-122.0
M_1/M_2 x 100	n	4	4	4	40	26
	$\bar{X}$	85.2	78.2	86.0	89.3	96.5
	OR	80.0- 89.9	75.4- 82.3	81.7- 90.8	85.3- 97.5	90.0-104.9
M_2/M_3 x 100	n	2	4	4	40	25
	$\bar{X}$	84.1	87.5	85.6	98.4	107.7
	OR	83.7- 84.5	83.2- 92.8	80.3- 93.3	86.5-106.9	96.5-122.1

increase in size from first to last. Simian shelves are lacking, and the most posterior part of the symphysis is the superior transverse torus. There are other less obvious similarities, for example, the mesial and distal grooves on the buccal surface of the upper premolars, the mesiobuccal extension of P^3, and the mesostyles of the upper molars. Many of these features are probably primitive and for that reason would not be of great significance.

The differences between the two species are also quite marked. Compared with *D. (P.) africanus,* the upper canines of *D. (P.) major* are relatively broader, and the upper premolars more massively built with lower cusps. It should be remembered however that only one individual of *D. (P.) major* is known which retains the upper premolars, and these should most certainly not be regarded as necessarily typical of that species through space and time. In the upper teeth the molar cingula of *D. (P.) major* are less shelf-like and projecting, although generally more extensive. The buccal surfaces of the cheek teeth are more vertical, the metacone is not as greatly reduced from first to last molar, and the hypocone does not project as far lingually. This means that, apart from the lingual cingulum, most of the molar occlusal surface is enclosed within the area circumscribed by the tips of the four main cusps. The cusps are less rounded and somewhat higher, and more pyramidal, while the intercuspal crests are rather sharper. The protoconule is better and more consistently developed.

The third molar of *D. (P.) major* is less reduced compared to the second than in *D. (P.) africanus* (see Table 34 for ratios of tooth lengths). In this characteristic and other features, *D. (P.) africanus* resembles *Pan troglodytes* while *D. (P.) major* resembles *Gorilla gorilla.* It has already been suggested that *D. (P.) major* is probably ancestral to *G. gorilla* (p. 76); there is a fairly good possibility that *D. (P.) africanus* is in or near the ancestry of *P. troglodytes.* Table 35 sets out for each dimension listed in Appendix 3 the position of the range in these Miocene species in relation to the ranges of the gorilla and chimpanzee samples included in the same appendix.

In 15 out of 24 dimensions, the range of *D. (P.) africanus* overlaps that of the chimpanzee; in the remaining nine the ranges fall below those of the chimpanzee. If Miocene protochimpanzees, like pregorillas, were generally smaller than their descendants, *D. (P.) africanus* is suitable metrically for consideration as the ancestor of *P. troglodytes.* It is of interest to note that in 13 dimensions the ranges of *D. (P.) major* overlap those of the gorilla, in seven

Table 35 Position of the range for 24 dental dimensions of D. (Proconsul) species

	Range overlaps G. gorilla range	Range intermediate between or overlaps both P. troglodytes and G. gorilla ranges	Range overlaps P. troglodytes range	Range below P. troglodytes range
D. (P.) africanus	-	-	15	9
D. (P.) nyanzae	2	5	17	-
D. (P.) major	13	9	2	-

they overlap both gorillas and chimpanzees, and in two they are intermediate between the ranges of the two living pongids.

The proportions of the molars of *D.* (*P.*) *africanus* (Table 34), particularly the reduced M^3, resemble those of the chimpanzee, as does their morphology. Loss of cingula seems to be a rather general trend in the Hominoidea (Frisch, 1965), and if it is assumed that protochimpanzees had cingula, then the low, rather rounded molars of *D.* (*P.*) *africanus* are what might be expected of such an ancestor. Clearly, however, many profound changes have occurred since the Miocene. All the teeth have increased in size, a change associated with increase in body size; the teeth anterior to M^2 have increased the most, the anterior parts of the dentition becoming greatly hypertrophied presumably in response to changes in feeding behavior or diet or both. This increase in the anterior dentition is also found in gorilla phylogeny (but to a lesser degree), and seems once again to be a trend found independently in all three living pongids.

The protoconule is less well developed in *P. troglodytes* then in *G. gorilla* and in this feature the fossil species parallel their possible descendants (Korenhof, 1960).

The maxillary sinus is preserved in only one specimen of *D.* (*P.*) *africanus,* the juvenile from Gumba (Napier and Davis, 1959, p. 13). It extends as far forward as the midpoint of P^4. The deepest part of the antrum is between M^1 and M^2. There is a trace of the lacrimal duct anteriorly opening into the inferior meatus; it would presumably have been tubular and rather short. In these features, *D.* (*P.*) *africanus* is very similar to *D.* (*P.*) *major* although built on a considerably smaller scale. The maxilla of *D.* (*P.*) *major* is, however, much more prognathous than those of *D. (P.) africanus.*

The mandible of *D. (P.) africanus* is similar to, though smaller than, that of *P. troglodytes.* In particular, the incisor region is very much smaller. (The distance between the distal borders of the lateral incisor alveoli is never more than 16 mm in *D. (P.) africanus.* In 26 individuals of *P. troglodytes* the value of this dimension does not fall below 26.4 mm.) Like the maxillary tooth rows, those of the mandible converge anteriorly because of the narrowness of the anterior part of the mandible.

The symphyseal cross section contrasts with that of *D. (P.) major* in that the slope of the anterior surface is shallower in *D. (P.) africanus* and the anterior and posterior surfaces do not meet sharply at an angle. In *D. (P.) africanus* the planum alveolare slopes more steeply than in *D. (P.) major.* As *D. (P.) major* resembles *G. gorilla* in symphyseal morphology, so too does *D. (P.) africanus* resemble *P. troglodytes* (Fig. 3).

The ascending ramus of the mandible is rather low relative to the horizontal ramus, in contrast to the condition seen in *Pan troglodytes, D. (P.) nyanzae* and, probably, *D. (P.) major.* This indicates that the face would have been less deep in *D. (P.) africanus,* indicating a system less adapted to transmitting chewing stresses. The significance of this feature was discussed in Chapter IV.

The mandibular dentitions of *D. (P.) africanus* and *D. (P.) major* are similar despite the great difference in size. The proportions of molar crown lengths in the two species are also generally similar (see Table 34, p. 83).

When the cranial, dental, and postcranial evidence is considered together, it seems likely that *D. (P.) africanus* may well be the early Miocene ancestor of *Pan,* albeit a much more primitive ancestor. Dentally and cranially the changes in this lineage are probably correlated mainly with changes in diet associated with increasing body size. However, until further work is available comparing the feeding behavior of the predominantly frugivorous chimpanzee with that of smaller cercopithecines with similar diets, little more can be said.

Postcranially, *D. (P.) africanus* was neither a knuckle walker like *P. troglodytes,* nor a brachiator like the gibbons (species of *Hylobates).* In terms of the rather inconvenient modern locomotor categories, it was probably a quadruped. However, *D. (P.) africanus* cannot be written off as a mere "monkey" because of this, at least not as a cercopithecoid-like monkey. The closest locomotor equivalent would probably have been the living New World quadrupedal semibrachiators or arm-swingers of subfamily Atelinae, perhaps with some ground-living features added. No gibbon-like "brachiator" phase need be posited for chimpanzee evolution. As noted before, similar conclusions concerning the relationship of *D. (P.) africanus* and *P. troglodytes* were drawn by Hopwood (1933 b).

The postcranial remains of *D. (P.) africanus* described above indicate that this species was a small, lightly-built, arboreal quadruped, yet a quadruped showing adaptations suggesting that arm-swinging was becoming a major component of its locomotor activities. Therefore, *D. (P.) africanus* and *D. (P.) major* contrast not only cranially but postcranially, too. However, the two species might well have shared a common ancestor in the earliest Miocene, an ancestor which possibly resembled *D. (P.) africanus.* For the moment they are best retained in the same subgenus.

DRYOPITHECUS (PROCONSUL) NYANZAE

As noted in Chapter VI the representation of *D. (P.) nyanzae* at Songhor and Koru is meager, and a number of specimens previously described as *D. (P.) nyanzae* have been transferred here to *D. (P.) major.* As far as Early Miocene deposits are concerned, the great majority of *D. (P.) nyanzae* specimens come from Rusinga Island. Measurements of specimens of this species are included in Appendix 2. There are no noticeable differences between the samples so far collected from the various time levels represented at Rusinga; sample sizes are too small for any trends to be detectable, and the levels appear to span only a short period of time. The samples have consequently been pooled for the calculation of the statistics included in Appendix 3.

Material assigned to *D. (P.) nyanzae* has been described fully by MacInnes (1943), Clark and Leakey (1951), and Clark (1952), and only brief points need to be made here. Dentally, facially, and gnathically, this species is generally larger than *D. (P.) africanus* and generally smaller than *D. (P.) major.* Bivariate plots for six upper and six lower teeth are included in Figures 8–13. Since the samples are so small, it is highly probable that the overlap between the three species would be increased were sample sizes also increased. (With such small samples, the effort involved in the construction of confidence limits or equiprobability ellipses would produce little worthwhile return.) Like the other two

Fig.8 Bivariate plots of C and P3 of *D. (Proconsul).*

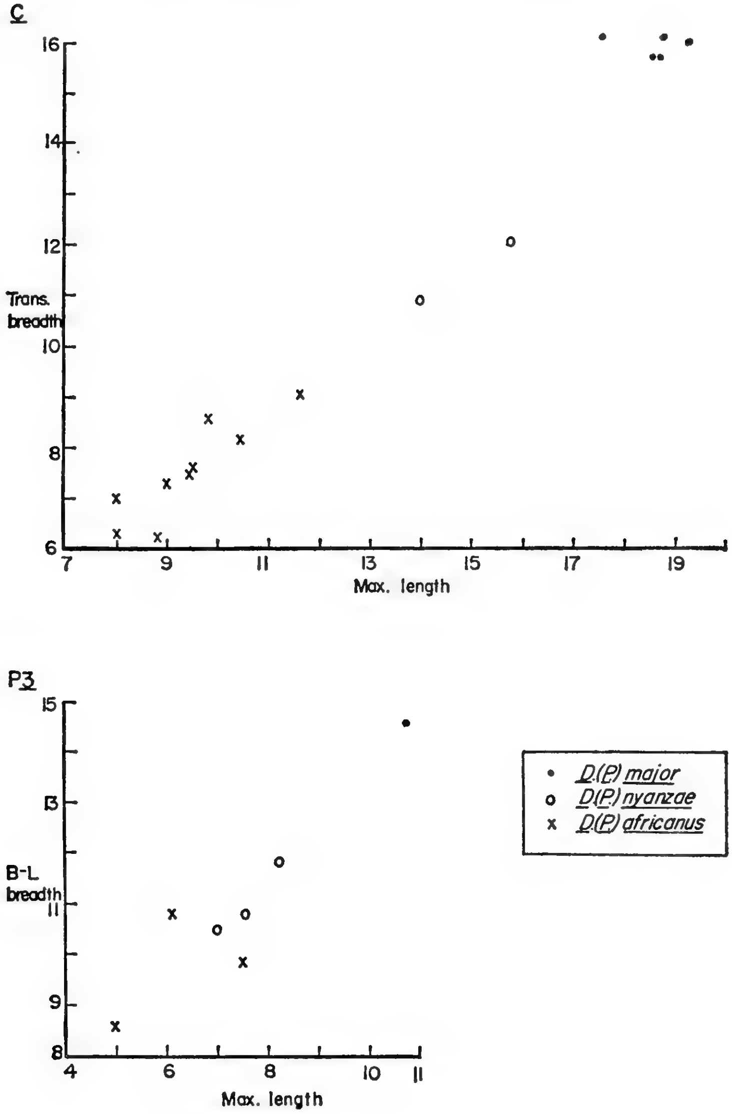


Fig. 9 Bivariate plots of P4 and M1 of *D. (Proconsul).*

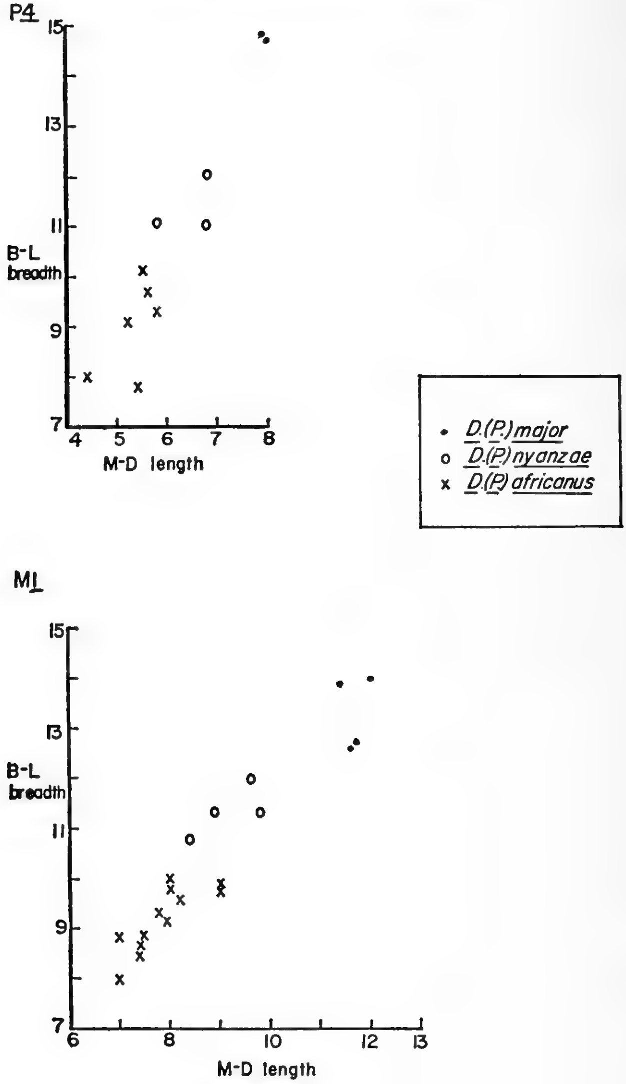


Fig. 10 Bivariate plots of M2 and M3 of *D. (Proconsul).*

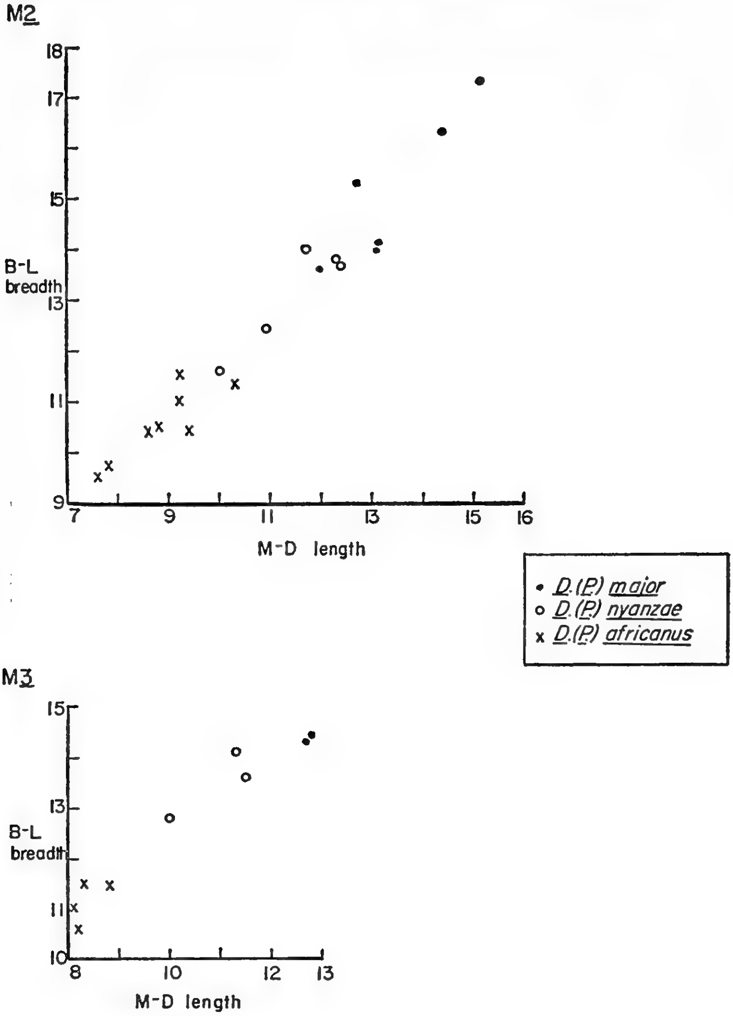


Fig. 11 Bivariate plots of $\bar{C}$ and $P\bar{3}$ of *D. (Proconsul)*.

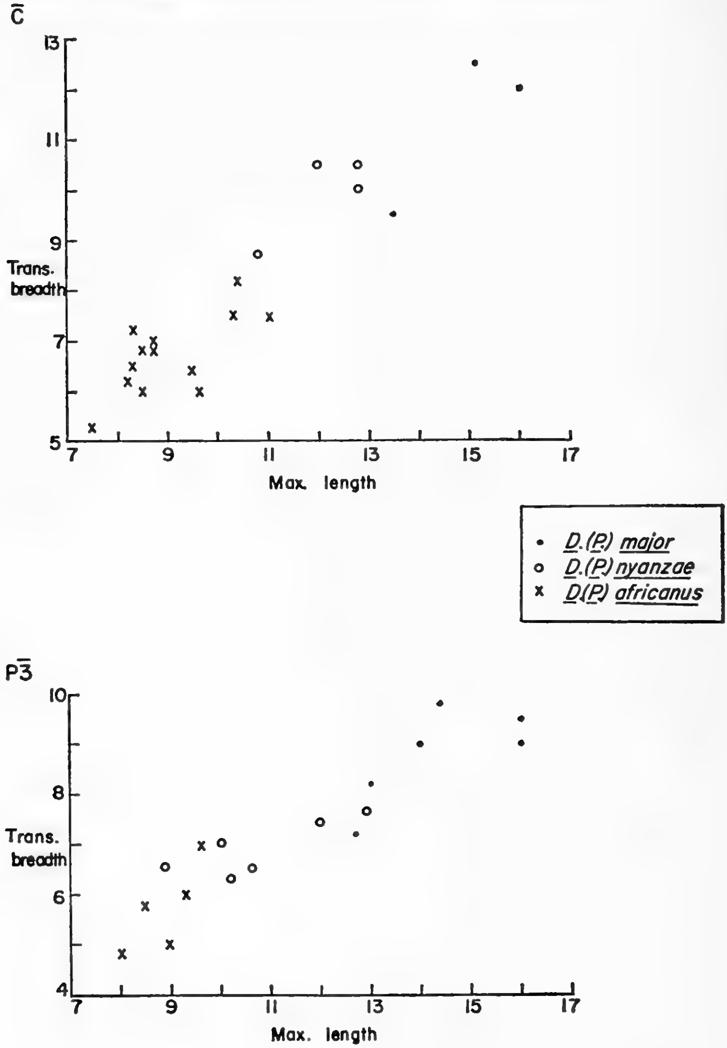


Fig. 12 Bivariate plots of P$\overline{4}$ and M$\overline{1}$ of *D. (Proconsul)*.

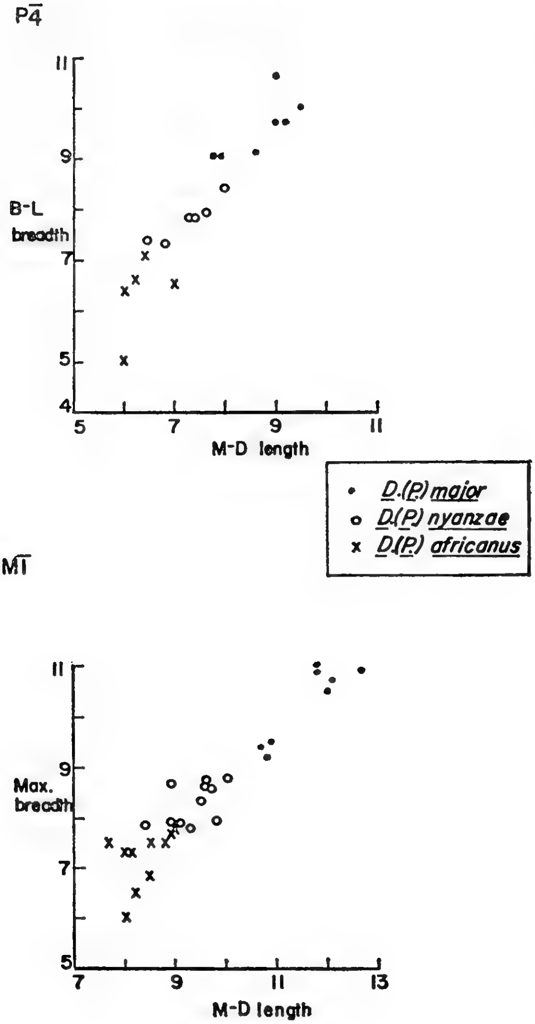
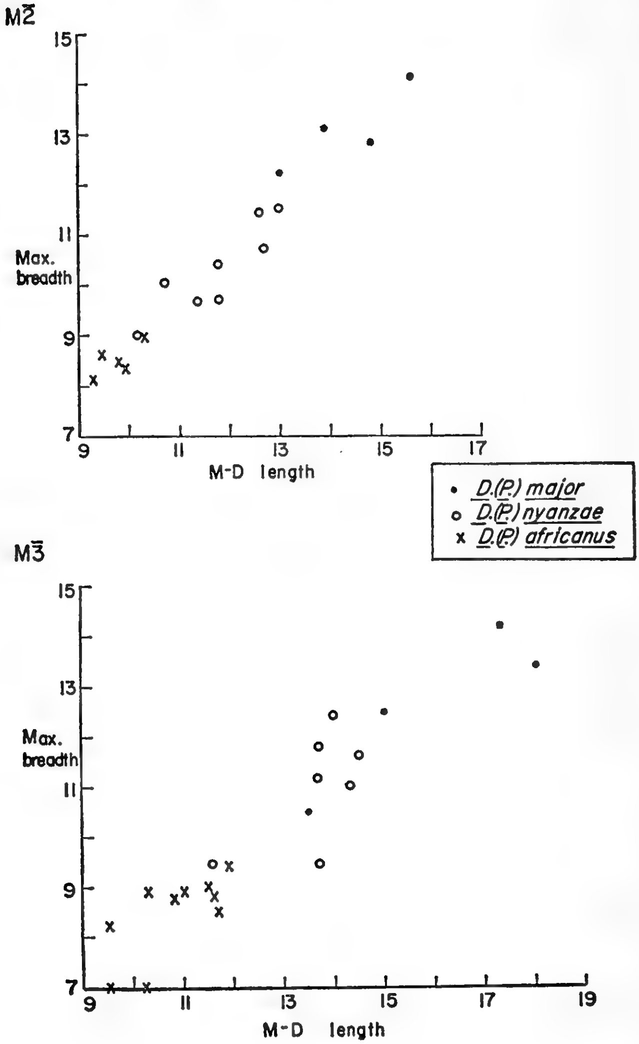


Fig. 13 Bivariate plots of M$\overline{2}$ and M$\overline{3}$ of *D. (Proconsul).*



species, *D. (P.) nyanzae* is variable and this variability is presumably due, at least in part, to sexual dimorphism.

Although *D. (P.) nyanzae* is in overall dimensions similar in size to the chimpanzee, the relative proportions of various parts of the dentition and facial skeleton are rather different. As in all early *Dryopithecus* the incisors are relatively small in the fossil form; consequently the premaxillary region is also small, and subnasal prognathism is not marked. The first molars are small compared with teeth distal to them (see Figs. 9 and 12). Table 34 includes ratios of molar lengths and shows that *D. (P.) nyanzae* has the lowest values of any *Dryopithecus (Proconsul)* species for the ratios $M^1/M^2 \times 100$ and $M_1/M_2 \times 100$. The value for *D. (P.) major* given in this table is from a single specimen and the value for this species should therefore be treated with caution.

Apart from these differences in proportions, the three species of *D. (Proconsul)* are probably similar enough to be classified in a single subgenus, although many of their similarities are primitive characters. Common features in the lower dentition of *D. (P.) africanus* and *D. (P.) major* have already been noted and *D. (P.) nyanzae* shares these similarities, too. The mandible of *D. (P.) nyanzae* is more similar in size and proportions to those of *D. (P.) major* than to *D. (P.) africanus* (see Clark and Leakey, 1951, p. 105), the horizontal and ascending rami being high. The symphysis lacks a simian shelf and is broadly similar to that of *D. (P.) major,* although it is less massive.

Even in the case of the "1942 mandible", NMK 1, CMH1 (Leakey, 1943; MacInnes, 1943, p. 171–174; Clark and Leakey, 1951, p. 45–47), the mandible is large, although the mandibular teeth are small, in size often overlapping *D. (P.) africanus* (see Appendix 2). This particular specimen is a little problematical; the dentition is crowded and the lower molars, particularly M_3, differ in some features from others of this species. The symphysis, although long from infradentale to gnathion, is not particularly thick. The ratio of symphyseal thickness to symphyseal length varies from 53.8 to 57.3 in three specimens of *D. (P.) major* (NMK 190,1; BM(NH) M14086; and NMK 198,28), and from 43 to 48 in three specimens of *D. (P.) africanus* (NMK 262,635; NMK R1948,50; NMK 640,417). The ratio in NMK 1, CMH1 is 43. Unfortunately data on other specimens of *D. (P.) nyanzae* are lacking. Specimen NMK 1, CMH1 has been treated here as a *D. (P.) nyanzae.*

Clark and Leakey (1951, p. 54–55) have summarized the main differences between *D. (P.) nyanzae* and *D. (P.) africanus* as follows:

> Apart from the absolute dimensions of the teeth of the premolar-molar series . . . other features of the dentition which distinguish *P. africanus* from *P. nyanzae* are as follows: the greater M^1/M^2 and M^2/M^3 ratios, the marked regression of M^3, the relatively smaller and more slender canines, the tendency to caniniform development of the buccal cusp of P^3, the relative height in the upper molars of the internal cingulum which tends to form a projecting shelf, the better definition of the trigon by clear-cut crests joining the protocone, paracone and metacone, the greater tendency for the hypocone to merge broadly with the internal cingulum (in M^1 and M^2), the relatively large size of the hypocone which in the first two

> molars approximates to that of the protocone, the weak development of the protoconule which forms little more than a slight thickening at the forward angulation of the ridge joining the protocone and metacone, the broader anterior cingulum, the weaker definition of the posterior cingulum, and the absence of the elaborate degree of coarse beading of the internal cingulum which appears to be so characteristic of *P. nyanzae.*

At the time of this description, *D. (P.) major,* particularly the upper dentition, was poorly known. Now that larger samples of this species are available it is clear that the upper teeth resemble those of *D. (P.) nyanzae* rather than *D. (P.) africanus,* for example, in the morphology of the trigon and cingulum, the relative proportions of the cusps, the slope of the buccal surface, and the well-developed protoconule. The upper molars, particularly M^2 and M^3, are very similar in *nyanzae* and *major.* One of the most complete specimens known of *D. (P.) nyanzae* is the holotype, BM(NH) M16647, first described by MacInnes (1943, p. 164–168) as *Proconsul africanus* (Fig. 27). It consists of much of the face and upper dentition of what is probably, from the evidence of the canines, a large adult male. The dimensions of the left canine are: Max L, 15.8 mm, Trans B, 12.0 mm, and La H, *21.5 mm. All these measurements fall outside the values of the 95 per cent confidence limits for female chimpanzees listed earlier in this chapter and close to the mean values for males.

The specimen was described further by Clark and Leakey (1951, p. 44–45) and figured by them (pl. IV, figs. 16 and 20). It is distorted and damaged. The incisors are missing and the premaxillary region between alveolare and nasospinale is almost entirely absent. The left tooth row from canine to first molar is preserved; the last two molars are intact, although displaced upwards. The right canine and first premolar crowns are damaged; the second premolar and first molar are intact and in position; the second molar is intact but displaced a little upwards and buccally; the third molar is broken in half mesiodistally, the buccal half facing almost sideways, the lingual half being pushed upwards.

The palate is intact to M^1 on the left and M^2 on the right. The suture between the palatine processes has been invaded by matrix, and this has forced the maxillae slightly apart. With respect to the right maxilla, the left has also shifted mesially. The separation of the palatine processes increases gradually from opposite the canines to the level of M^2, and thus the tooth rows appear to diverge, although in fact they probably may not have done so. The distance between the lingual surfaces of the P^4's is 32 mm; corrected for distortion the distance would be approximately 30 mm. The facial region is crushed and distorted, although well enough preserved on the right for some details and measurements to be determined.

This specimen, the holotype of *D. (P.) nyanzae,* will be compared very briefly here with the only complete maxillary specimen of *D. (P.) major,* UMP 62–11 from Moroto II. BM(NH) M16647 is built on a rather smaller scale than UMP 62–11, the alveolar breadths being at least 10 mm smaller. The alveolar juga associated with the canines are similar; there is no premolar jugum in BM(NH) M16647 since the buccal roots of P^3 are not as massive as in UMP 62–11. Posterior to the jugum is a concavity running upwards to the infraorbital foramen, the canine fossa. In BM(NH) M16647 the midpoint of this depression is 21.5 mm above the alveolar margin and is situated above the distal border of P^3. In UMP 62–11 the depression is similarly situated but is 25 mm above the alveolar margin.

The canine juga of BM(NH) M16647 surround the piriform aperture and gradually flatten superiorly to become long and narrow maxillary frontal processes. The nasal aperture was long and narrow; this much at least can be determined in spite of the fact that the right side is crushed inwards and the left side pushed forwards. The nasal bones were long and narrow and their curvature similar to those of UMP 62–11. The two specimens are very similar in the general architecture of the face and the internal parts of the nasal aperture, although BM(NH) M16647 is generally smaller. The zygomatic processes of both specimens are situated mainly above M^2. Some facial and other dimensions are included in Table 36 below. Many of the measurements of BM(NH) M16647 are approximations; distances between bilaterally symmetrical structures are generally measured from one side to the midline and doubled.

Table 36 Facial measurements of BM(NH) M16647 and UMP 62–11

		BM(NH) M16647	UMP 62–11
Nasal H		*75.0–*80.0	*98.5
Nasal B		*20.0	30.2
Nasals: L	Minimum	*45.0	60.0
Nasals: B at infraorbital foramina		*12.0	12.5
B across antr. lacrimal crests		*20.0	20.0
B across infraorbital foramina		*40.0	40.0
Infraorbital for. to antr. lacrimal crest		*29.0	*30.0
Palatal D: at C^1–P^3		*4.0	*4.0
at M^2		*7.0	*7.5

Measurements of the dentition and tooth rows of the two specimens are set out in Table 37. Length/breadth indices are also included. The diastema between lateral incisor and canine is 5.2 mm in UMP 62–11, 5.0 mm in BM(NH) M16647. The canine of BM(NH) M16647 is more slender than that of UMP 62–11 (L/B index 131.6 compared with 118.4). Other than this, the two teeth are morphologically similar. The premolars are more massively built in UMP 62–11. The paracone of P^3 in BM(NH) M16647 has been worn sharp on its mesial surface by attrition from P_3. The P^4's are similar, although those of BM(NH) M16647 are smaller. The buccal surfaces of P^3 and P^4 are similar in the two specimens, having mesial and distal vertical grooves. In UMP 62–11 the distal borders of P^3 and P^4 are convex distally; this bulging is absent in BM(NH) M16647, the distal borders being flatter, particularly in P^3. The first molars differ. The surface details of both have been largely obliterated by wear, although it is probable that the morphology of cusps, crests, cingula and so forth were broadly similar. The mesiodistal length of BM(NH) M16647 is

Table 37 Dental measurements of BM(NH) M16647 and UMP 62-11

		D. (P.)major UMP 62-11 (left, except for P^3)	D. (P.)nyanzae BM(NH)M16647
C^1	Max L	*18.6	15.8
	Trans B	*15.7	12.0
	LaHH	*27.0	*21.5
	Index L/B x 100	118.4	131.6
P^3	MDi L	8.2	7.0
	Max L	10.7	8.2
	BuLi B	14.6	11.8
	Max L/B x 100	73.3	69.5
P^4	MDi L	7.9	6.8
	BuLi B	14.8	12.0
	Index L/B x 100	53.4	56.6
M^1	MDi L	*11.7	9.6
	BuLi B	12.7	12.0
	Index L/B x 100	92.1	80.0
M^2	MDi L	*13.1	12.4
	BuLi B	14.0	13.7
	Index L/B x 100	93.5	90.5
M^3	MDi L	12.8	11.3
	BuLi B	14.4	14.1
	Index L/B x 100	88.9	80.1
P^3-M^3	L	54.4	*47.5
I^1	B	39.1	*30.0
C^1	B	*69.0	*55.0
P^4	B	64.8	*54.0

much less than that of UMP 62–11 and this is reflected in the crown index. The mesial and distal borders of BM(NH) M16647 M^1 are straight and parallel. The crowns of all the cheek teeth of UMP 62–11 are marked by their distal bulges; these bulges are absent in P^3, P^4, and M^1 of BM(NH) M16647, and these teeth are compressed mesiodistally. The last two molars, however, are very similar in UMP 62–11 and M16647, although the distal bulges are more marked in the former specimen. The protoconule is well marked on the right M^2 of BM(NH) M16647, and this is illustrated in Figure 27. The buccal cingulum of the molars forms a series of spurs in BM(NH) M16647, just as in UMP 62–11 (see Figs. 19 and 27).

The face of BM(NH) M16647 would have been narrower and less prognathous than UMP 62–11. The dentition anterior to M^2 is relatively smaller, less long mesiodistally, and more compressed in BM(NH) M16647. Nonetheless, the similarities between these two maxillae and upper dentitions are marked, and although they clearly are drawn from two different species, the smaller form could well represent a species morphologically—if not temporally—ancestral to *D. (P) major.*

D. (P.) nyanzae is more similar to *D. (P.) major* than to some of *D. (P.) africanus.* If *D. (P.) major* and *G. gorilla* are related, then some of the dental trends within this lineage are as follows: increase in size of the more anterior teeth, particularly P^3_3, P^4_4, and M^1_1, but including incisors and canines, too. If these trends are extrapolated back through time from *D. (P.) major*, the ancestor of *D. (P.) major* might well have resembled *D. (P.) nyanzae*. It is even possible that some of the oldest *D. (P.) nyanzae* could be ancestral to the larger species. A tentative hypothesis is that populations of *D. (P.) nyanzae* (or an immediately preceding species) became progressively isolated ecologically, perhaps in elevated and forested terrain, and evolved into *D. (P.) major*. More fossil material, with adequate stratigraphic control, good dating, and from a variety of sites representing a variety of environments, is necessary before this hypothesis can be any more, or less, than a possibility.

POSTCRANIAL REMAINS OF *D. (P.) NYANZAE*

The forelimb and foot skeleton of *D. (P.) africanus* from Gumba, Rusinga Island and the postcranial material of *D. (P.) major* from Uganda and Kenya have already been reviewed. The remainder of the material from the East African sites is listed below; much of it is *D. (P.) nyanzae,* although some could be Leakey's new species "Kenyapithecus africanus."

1) Left talus (NMK 74, CMH147) from Kalim, Rusinga, described by MacInnes (1943, p. 174–177) and Clark and Leakey (1951, p. 87–92).
2) Left talus (NMK 511,234) from Kulu Waregu, Rusinga, described by Clark (1952, p. 277).
3) Distal end of left tibia (NMK 553,924) from R2–4, described by Clark (1952, p. 278).
4) Most of right femur, proximal end of left femur, shaft of left humerus, and part of right clavicle, all associated (NMK 120, 1933), from Maboko Island, described by Clark and Leakey (1951, p. 93–98).
5) Fragment of lateral part of left clavicle (NMK 254,394) from R105–106, Rusinga, mentioned by Clark (1952, p. 278).
6) Fragment of lateral half of right clavicle (R313) from R3, Rusinga, described by Clark (1952, p. 278).

The two clavicular fragments are said by Clark (1952, p. 278) to be "very similar to (but slightly larger than) the clavicular specimen previously described from Maboko Island and provisionally referred to *P. nyanzae*. In general dimensions they are comparable to the clavicle of an adult male chimpanzee."

These postcranial specimens, if indeed they all belong to *D. (P.) nyanzae*, indicate that, like other species of this subgenus, *nyanzae* was a relatively lightly built, actively arboreal, quadrupedal form.

Leakey (1967) has suggested that some of the postcranial remains from East African Miocene sites may belong in "Kenyapithecus africanus." At present there is no way of proving this, although the material assigned to *D. (P.) africanus* and *D. (P.) major* seems to have been correctly classified.

CHAPTER VIII. THE EARLIEST HOMINIDS

In this chapter I shall be discussing the relationships between the late Miocene/early Pliocene hominid *Ramapithecus* from deposits in India and Kenya. Recently Leakey (1967) has suggested, among other things, that earlier hominids still have been found in East Africa. In order to discuss these matters in detail it is necessary to review some of the other species of *Dryopithecus*.

A large number of fossil apes have been recovered from the Siwalik Hills in India. Simons and I (1965) classified most of this material in *Dryopithecus (Sivapithecus)*. Within this subgenus were two species, *D. (S.) indicus* and the smaller *D. (S.) sivalensis,* the latter containing species described previously in the genus *Sugrivapithecus* by Lewis (1934, 1937a). My recent work (Pilbeam, in preparation) suggests that a majority of *D. (S.) indicus* and *D. (S.) sivalensis* are merely size variants within a single species *D. (S.) sivalensis.* Certainly the metrical and morphological variation among members of this proposed species would be less than that encountered within *Pongo pygmaeus,* the orangutan, to which the Tertiary form is possibly related.

A number of other workers (Gregory and Hellman, 1926; Lewis, 1937b; Simons, 1963) have suggested that some of the Siwalik pongids represent a species ancestral to the orangutan. Simons and I (1965) discussed the ancestry of *Pongo pygmaeus* and concluded then that its Tertiary ancestors were either unknown or unrecognized. It now seems rather more possible (see Pilbeam, 1966, 1967, and in preparation) that *D. (S.) sivalensis* could be ancestral to *P. pygmaeus;* the latter's occlusal specializations would then have been acquired mostly during the last 10 million years. *D. (S.) sivalensis* has been recovered from deposits of Miocene and Pliocene age in the Siwalik Hills (Chinji and Nagri zones), approximately equivalent in age to the period from European Sarmatian (or even Late Vindobonian) to Pontian (Simons and Pilbeam, 1965, p. 95–97). Absolute ages for these deposits are not available, although by analogy with European and African dated sites the ages of these beds would be between 14 or 15 million and 8 or 9 million years. If *Hipparion* evolved in North America about 12 million years ago, and if *Hipparion* is confined to the Nagri zone and is absent from the Chinji, then the Chinji-Nagri boundary would be drawn at around 12 million years.

The molars and premolars of *D. (Sivapithecus)* species differ from those of *D. (Proconsul)* in lacking buccal or complete lingual cingula, in having relatively rounded cusps in some specimens, and in exhibiting markedly sloping buccal and lingual surfaces. These and other diagnostic criteria, together with illustrations, are listed in Gregory and Hellman, 1926; Lewis, 1934, 1937a and b; and Gregory, Hellman and Lewis, 1938.

In 1943, MacInnes described a series of specimens collected in preceding years at Rusinga and Songhor. Among the specimens was a left maxillary fragment from R106, Rusinga Island containing P^3, P^4 and M^1 (1943, pl.

24, fig. 2), which was assigned by MacInnes to *Proconsul africanus.* In 1950 this specimen was made the type of a new species, *Sivapithecus africanus,* by Clark and Leakey (p. 261). It is at present in the British Museum (Natural History), number M16649. This specimen is illustrated in Figure 28. In 1951, Clark and Leakey described in detail this specimen, as well as two isolated upper molars (NMK 20, CMH27 and NMK 121, CMH26) assigned by them to the same species (Clark and Leakey, 1951, p. 62–67). Their conclusions were as follows (p. 67):

> In summary, the upper teeth of *S. africanus* differ from those of all the other large apes from the early Miocene deposits of East Africa in the absence of an elaborate internal cingulum and in the relative simplicity of the cusp pattern. They closely resemble the Asiatic species of *Sivapithecus* . . . in the large size of the upper premolars, the relative size of the main cusps of the upper molars, the limited extent and sharp definition of the trigon, the absence of coarse secondary foldings of the enamel, the absence of a large posterior fovea, and the clear separation of the hypocone from metacone and protocone. The specific separation of *S. africanus* from the Asiatic types may be justified by certain features such as the flatness of the palate . . . , the persistence of a trace of the antero-internal cingulum on the upper molars (which, however, is also indicated in an upper molar, D.176, of *S. indicus . . .),* the development of the internal cingulum on P^4, and the slightly smaller width of the first and second upper molars. Moreover, it is extremely improbable that representatives of an identical species would be found so widely separated in time and space.

They also stated (p. 110) that the East African species might be ancestral to *D. (S.) sivalensis.*

Although in 1951 he had agreed in the assignment of BM(NH) M16649 to a species of pongid, in 1953 (p. 178), Leakey wrote the following:

> The evidence of such teeth as we have, however, most strongly suggests that the Kenya *Sivapithecus* may prove a candidate for the role of a direct ancestor of man in the Lower Miocene. The genus *Proconsul,* and especially the species *nyanzae,* cannot be wholly ruled out of the picture, but the *Proconsuls* have, in particular, upper molar teeth which tend to suggest specialization away from the direction taken by man, whilst *Sivapithecus* has upper molars strongly suggestive of man himself.

It seems likely that it was the presence of molar cingula in *D. (Proconsul)* species which enabled Leakey to rule them out of the ancestry of man. The absence of cingula in BM(NH) M16649 does not mean, however, that it is necessarily related to Hominidae. Other undoubted pongids of genus *Dryopithecus* also lack cingula.

In 1962, Leakey described a primate from Late Miocene deposits at Fort Ternan, Kenya (see Chap. III) as *Kenyapithecus wickeri.* This specimen, he implied, might be a hominid, and it has since been accepted generally as such. Leakey, however, did not place it in any primate family, but wrote (1962, p. 696), "I strongly suggest that when the new genus is allocated to a family, *Sivapithecus africanus* will have to join it there and be removed from the Pongidae." In 1963 (p. 42) he wrote, "It now seems possible that *Sivapithecus africanus* should be treated as a species within the new genus *Kenyapithecus,* but one which is more primitive and perhaps ancestral to *wickeri.*"

In the same year, Simons suggested that "Kenyapithecus wickeri" was a junior synonym of a hominid described by Lewis in 1934, *Ramapithecus brevirostris.* In 1964, Simons described this and other material as *R. punjabicus.*

In 1965, Simons and I transferred BM(NH) M16649 from *Sivapithecus africanus* to *D. (S.) sivalensis.* Both reassignments have been strongly criticized recently in a paper by Leakey (1967), in which he maintains "Kenyapithecus wickeri" as a species distinct from *Ramapithecus,* and also transfers BM(NH) M16649 to *Kenyapithecus* to become *K. africanus,* ancestral to "K. wickeri". To this species he has also assigned a number of specimens, some newly recovered, from Rusinga and Songhor either previously undescribed or (mainly) classified as *D. (P.) nyanzae* or *africanus;* he regards "K. africanus" as the earliest hominid.

These taxonomic changes will be discussed in detail in the following pages, together with a certain amount of background material. For the remainder of this work the Fort Ternan hominid will be described either as "Kenyapithecus wickeri", without being italicised, or by its specimen numbers.

In 1934, G. E. Lewis described a new primate genus from the Siwaliks, *Ramapithecus.* When first described, this genus contained two species, *R. brevirostris* and *R. hariensis.* The latter came from Nagri beds of Late Miocene or Early Pliocene age (very approximate dates, from about 12 to 8 million years). The former was originally thought by Lewis to come from younger beds, but in 1937 (a and b) he corrected this and ascribed *R. brevirostris* instead to the Nagri zone (see discussion in Simons, 1964).

R. hariensis consisted of a distorted maxillary fragment with worn M^1 and fractured and broken M^2. In 1937 Lewis (1937a) transferred the specimen to *Sivapithecus sivalensis* (later regarded as *D. (S.) sivalensis* by Simons and myself, 1965). It is a fragmentary specimen and may in fact be a *Ramapithecus.* Its exact taxonomic position cannot at present be established.

R. brevirostris consisted of a right maxilla, YPM 13799, with P^3–M^2 preserved (Fig. 29). The canine alveolus, the root of the lateral incisor, and the lateral part of the central incisor alveolus are also present. In his first paper, Lewis (1934) gave a minute description of this specimen and concluded that it was either a manlike pongid, or a very primitive hominid. In his unpublished doctoral dissertation (1937b, p. 45–46) Lewis stated his view that *R. brevirostris* was ancestral to the Pleistocene genera *Australopithecus* and *Homo.* "The lack of diastemata; the relatively small incisors, canines, and premolars; the low relief and elliptical horizontal cross section of the upper premolars; and the bluntly rounded cusps and other morphologic features are common to *Ramapithecus, Australopithecus,* and *Homo.* It would seem therefore, that *Ramapithecus* is the structural, and possibly direct, ancestor of these two genera.

In the year following the original diagnosis of *Ramapithecus,* Hrdlicka (1935) published a highly critical note. His contribution is disappointingly subjective and should be ignored. Unfortunately, it seems to have had a considerable and stultifying influence upon paleoanthropological thinking. Until the 1960's, *Ramapithecus brevirostris* continued to be treated as the most manlike of the Middle Tertiary pongids, but no more than that. In a taxonomic revision of this and other Indian material Simons (1964) transferred it to *R. punjabicus.*

The premaxillary and anterior maxillary regions of YPM 13799 are relatively small and the juga associated with the tooth roots delicately built. Subnasal prognathism is not marked, and the distance between nasospinale and alveolare would have been little more than 10 mm. Fortunately, the maxilla forming the base of the lateral border of the nasal aperture and the lateral wall of the inferior meatus is preserved for 15 mm or so anteroposteriorly. The maxillary fragment and its mirror image can be mutually positioned using the planes of the lateral nasal walls and the orientation of the canine alveolus. The labiolingual axis of the canine alveolus is oriented at an angle of some 55 degrees to the long axis of the premolars and molars in both YPM 13799 and later hominids, suggesting that the dental arcade was parabolic.

The shape of the canine alveolus is oval, with the long axis labiolingual as in hominids, and not mesiodistal as in pongids. The alveolus measures 7.5 mm labiolingually (restored) by 6.5 mm mesiodistally. The canine root would have been some 15 mm long.

The zygomatic process is situated above M^1. Generally in living and fossil pongids the process is above M^2 or the distal root of M^1, although individual specimens, particularly of *Pongo pygmaeus,* may have processes situated further forward. Anterior to the process is a marked canine fossa, a tucking-in of the maxilla medial to the plane of the buccal tooth roots and posterior to the canine jugum.

Although each of these features may be found individually in living or fossil pongids, as a total morphological pattern they occur infrequently outside the Hominidae. The hominid characters are to be seen particularly in metrical features and proportions.

The morphology of the cheek teeth is of interest. The first premolar is roughly triangular in occlusal view. The buccal length is a little greater than the lingual, due to the mesial extension of the mesiobuccal corner. A distinct fovea is present at this corner and is circumscribed by the mesial marginal ridge and the more mesial of the two paracone-protocone crests. The mesiobuccal corner does not extend superiorly, as it does in Middle Tertiary pongids; for example *D. (P.) major* (see Chap. IV and Fig. 18), and *D. (S.) sivalensis* (Gregory, Hellman, and Lewis, 1938, pl. 1, fig. 2a; pl. 7, fig. 1). In these cases, also, the triangularity is more marked and the mesial border is concave mesially. In YPM 13799 the mesial border of P^3 is straight, any slight concavity being due to interproximal attrition with C^1 (Lewis, 1934, pl. 1, fig. 1a; Simons, 1961, fig. 1a; and Fig. 29).

Robinson has noted (1956, p. 56) similar features in *Australopithecus (Paranthropus) robustus.* "In occlusal view the crown is a little asymmetrical on account of the slight projection of the buccal half of the mesial face." For *Australopithecus africanus* he notes (1956, p. 58), "The mesiobuccal groove commonly is a definite groove which lies in a triangular-shaped depression which is wide at the occlusal margin. In some cases . . . this effect is so marked that there appear to be two mesiobuccal grooves converging as they pass upwards from the occlusal margin."

The relief of the little-worn cheek teeth is less marked than in *Dryopithecus.* The lingual surfaces of buccal cusps slope less steeply, and, particularly in contrast to *D. (S.) sivalensis,* the occlusal fovea occupies a relatively greater proportion of the total surface of the crown. In *D. (S.) sivalensis* the buccal and lingual surfaces of the cheek teeth slope gently and the minimum buccolingual breadth between the tips of paracone and protocone is often less than 50 per cent of the maximum across the same cusps (see Table 39, p. 107). The metacone-protocone crest is also more pronounced in *R. punjabicus* molars and is crossed by a less pronounced sulcus than in *D. (S.) sivalensis* (compare Simons, 1961, fig. 1A with Gregory, Hellman, and Lewis, 1938, pl. 7, fig. F; and Fig. 29 with Fig. 30). Morphologically, the molars and premolars of *Ramapithecus* differ from those of *Dryopithecus* in a number of features, and resemble *Australopithecus.*

The relative simplicity of the occlusal surface and the absence, or at best, poor development of lingual cingula gives *D. (S.) sivalensis* a superficial resemblance to *R. punjabicus.* This means that the allocation of isolated teeth or small fragments to one or the other sometimes becomes difficult. The two upper molars originally assigned by Lewis to *R. hariensis* are a case in point.

A number of authors have noted the essential basic similarity of the cheek teeth of all hominoid species (for example, Gregory and Hellman, 1926; Korenhof, 1960). Schuman and Brace (1954) remarked on the difficulty in discriminating isolated human and chimpanzee molars; this has also been the case with worn human and orangutan molars. Clearly, if the living forms are often difficult to tell apart, the problem is likely to be more acute in dealing with their Middle Tertiary ancestors. Figure 30 compares two molars of *D. (P.) major* and one of *D. (P.) sivalensis.* Apart from the variable development of the lingual cingulum, the three teeth are very similar and could easily have been sampled from a single variable primate species. It is to be expected therefore that certain of the cheek teeth of Miocene and Pliocene hominids and pongids will appear morphologically similar, particularly in the absence of obvious discriminating characters like large cingula.

In 1938, Gregory, Hellman, and Lewis described (p. 21–22) and figured (pl. 2, fig. 3) a right horizontal mandibular ramus (GSI D168). This specimen preserved crowns of P_3 to M_2 and the canine and incisor alveoli. They assigned it tentatively to *Ramapithecus* (in fact to *R.* cf. *brevirostris).* The mandible is gracile, with small cheek teeth worn flat; the P_3 is elongated and sectorial, and the inferior transverse torus is large and projects posteriorly as a simian shelf. This mandible is clearly not that of a hominid (Simons, 1961, 1964; Simons and Pilbeam, 1965) and is not to be associated with *Ramapithecus.* The tentative allocation of this specimen seems also to have confused later workers and hampered the correct interpretation of *Ramapithecus.*

In 1961, Simons wrote an important paper which began the long-delayed rehabilitation of *Ramapithecus* as the earliest known hominid. In this he discussed the dating of YPM 13799, the polemical nature of Hrdlicka's contribution, the misclassification of the mandible GSI D168 as well as a number of previously unmentioned morphologic and metric characters. For the first time in a published paper, a paleontologist noted the illogicality of regarding the maxilla as that of a manlike ape rather than as a hominid. In short, when they occur in *sufficient* numbers and in the right combination, similarities should be treated as homologies rather than parallelisms, unless or until such an interpretation can be disproved.

In 1962, Leakey described* a new primate from Fort Ternan in Kenya, from deposits approximately equivalent in age to the Chinji beds of the Siwaliks. They have been dated radiometrically to 14 million years (see Table 1, p. 17). The new find was composed of a left maxilla NMK FT 1272, with canine, roots of P^3, and crowns of P^4 to M^2; a right maxilla NMK FT 1271, with M^1, M^2, and roots of M^3; and a right M_2, and was made the type of a new genus and species, "Kenyapithecus wickeri" (Fig. 29). The new specimen showed many similarities to YPM 13799, as can be seen from a comparison of Leakey's paper with Lewis's original detailed description. Simons (1968) has recently reviewed this material in detail.

The canine crown and 10 mm of root are preserved intact in NMK FT 1272, and are set almost vertically in the maxilla; the canine jugum in YPM 13799 is set at a similar angle to the occlusal plane. The canine crown is small, as in hominids, although morphologically different from the earliest Pleistocene hominids. Both mesial and distal borders slope downwards towards the tip of the crown. In *Australopithecus* both borders are vertical for much of their length. Leakey (1962, p. 693) describes the canine as follows:

> It is a relatively compressed canine, bucco-lingually, and has a consequent slightly exaggerated anterior-posterior length, which is further stressed by a swelling on the lower anterior margin at the point where the internal cingulum ends. There is a shallow groove on the anterior face running from this swelling to the tip, much as may be seen in upper canines of the Proconsulidae and in some upper canines of the Asiatic *Sivapithecus,* but it is much less strongly developed. The lingual face of the canine is slightly convex but lacks the strong medium [*sic*-median?] ridge seen in the upper canines of the genus *Sivapithecus,* even in small females. On the posterior face there is a narrow area of wear extending longitudinally from the tip to a point just above where the cingulum ends posteriorly. This wear facet seems to postulate a lower third pre-molar of semi-sectorial type. The inner face of the crown of the canine is marked by a cingulum.

The canine is illustrated in the plate included in Leakey's paper. In this plate it is compared (fig. c) with "a cast of the smallest published *Sivapithecus* upper canine" (1962, p. 696). This is not the smallest published *D. (Sivapithecus)* C^1; that had been described (p. 12–13) and figured (pl. 1, fig. 1; pl. 2, figs. C, D, E; pl. 4, figs. A, B) by Gregory, Hellman, and Lewis (1938). This small canine is part of an upper dentition assigned by them to *D. (S.) sivalensis* and is numbered in the 1938 paper K29/466; it is now GSI D299/300. It is similar to the canine of NMK FT 1272 although 1 or 2 mm larger in each dimension. The mesial groove is shallow and there is no median lingual ridge, *contra* Leakey. The presence of a distolingual wear facet in the Kenya C^1

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* The description of this specimen was first published on 22nd May 1962, in Ser. 13, vol. iv, *Annals and Magazine of Natural History* for November, 1961.

implies that P_3 protoconid was prominent, not that it was necessarily sectorial or semi-sectorial, or that the canine projected more than in Leakey's reconstruction.

The dimensions of the canine of "K. wickeri" are, Max L, *10.0 mm, Trans B, *8.0 mm, and La H, *11.5 mm. The root is compressed, having the following cross-sectional dimensions at the (inferred) alveolar margin, Max L, *8.0 mm, and Trans B, *6.0 mm.

The canine crown of YPM 13799 is not preserved, although the alveolus is. The labial wall of this alveolus has been crushed lingually. The maximum diameter of the alveolus is a labiolingual one and is set at an angle of approximately 55 degrees to the mesiodistal line of the cheek teeth. The dimensions of the alveolus are, Max L, *7.5 mm, and Trans B, *6.5 mm.

If the long axis of the crown of the C^1 paralleled the mesiodistal line of the dentition from P^3 to M^3, the C^1 crown of YPM 13799 would have been set at approximately the same angle to the root as in NMK FT 1272, although the crown dimensions would presumably have been a millimeter or so smaller.

The crown of P^3 is missing in "K. wickeri". The tooth had three roots, the mesiobuccal being larger than the distobuccal, as in YPM 13799. The crown was evidently only slightly longer buccally than lingually and the mesial border was probably straight.

Another tooth, P^4, also from NMK FT 1272, is described thus by Leakey (1962, p. 693–694):

> This fourth upper pre-molar is specially interesting for a number of reasons: it differs markedly in its morphology from the corresponding tooth in *Sivapithecus africanus* described by Le Gros Clark & Leakey, and it is clearly of a different species. In the present specimen there is no cingulum at all, whereas in *Sivapithecus africanus* there is an anterior and a posterior cingulum with the latter extending to the lingual face.
>
> The crown of this fourth upper pre-molar of *Kenyapithecus wickeri* is very wide bucco-lingually . . . having almost the same diameter as the first upper molar; the surface of the crown is much more complex than in *Sivapithecus africanus.*
>
> In addition to the well defined anterior and posterior fovea, there is a mesial [*sic*] fovea formed as follows: a ridge runs from the tip of the lingual cusp towards the centre of the tooth and then divides into two parts which enclose the mesial fovea. This is a structure which I have not seen in any *Proconsul* or in any of the Asiatic *Sivapithecus, Ramapithecus,* or other Siwalik primates.
>
> A slightly similar structure is to be seen in some of the less worn upper pre-molars of Australopithecines.
>
> This fourth upper pre-molar is also very much lower crowned than in the Asiatic genus *Sivapithecus,* and is comparable, in this respect, to *Ramapithecus.* It is distinctly lower crowned than the corresponding tooth in *Sivapithecus africanus.*
>
> The contact facet between the fourth upper pre-molar and the third upper pre-molar is long, even though a part of it is missing on the chip at the external corner. This facet must have been at least 5 mm long when

> intact, a feature in which it resembles *Ramapithecus brevirostris,* and a character which is certainly connected with a shortening of the face and of the molar pre-molar series becoming compressed from end to end. This type of compression is not seen in *Sivapithecus africanus,* nor in any of the Indian species of *Sivapithecus* about which I can find record.

The "mesial" fovea should be termed "central", since a "mesial" fovea would be the anterior fovea. An exactly similar structure *is* formed in YPM 13799; apart from mesial and distal marginal ridges in YPM 13799, there are three further transverse ridges joining paracone and protocone, making five transverse ridges in all. The third and fourth (distalward) are crossed by a central mesiodistal sulcus. These features are described in detail by Lewis (1934, p. 165) and are very similar to those seen in "K. wickeri." Contact facets between adjacent cheek teeth are up to 5 mm long in "K. wickeri" and 6 mm or more in YPM 13799. As in the latter, the buccal and lingual surfaces of P^4 are much more vertical than in *D. (S.) sivalensis.*

The first molar in NMK FT 1271 and 1272 is low crowned, with enamel smoothed by wear. The occlusal fovea occupies most of the area of the crown and cingula are lacking, except for a mesiolingual cingular remnant. The metacone-protocone crest is prominent and is barely crossed by a faint sulcus which has been almost removed by wear. The lingual surfaces of the buccal cusps slope much more gently than in *D. (S.) sivalensis* or *D. (Proconsul)* and the cusps are less prominent.

The second molar is similar, though a little larger. The metacone and hypocone are relatively a little smaller than in M^1, and the buccolingual breadth across the distal moiety is accordingly smaller than that across the mesial.

In all these features, "K. wickeri" is closely similar to YPM 13799.

The third molar roots, preserved on the right maxilla, NMK FT 1271, indicate that this tooth was shorter than M^2. The zygomatic process of the maxilla is situated above the distal half of M^1, and there is a canine fossa, between the (presumed) canine jugum and the process, which is situated above the buccal roots of P^3 and P^4. The palate was arched much as in YPM 13799.

A right M_2 was also preserved (Leakey, 1962, plate, fig. d). There is a small cingulum between protoconid and hypoconid and the hypoconulid is situated in the midline. The tooth is low crowned and the cusp tips are situated close to the margins of the tooth. The buccal cusps are lower than the lingual.

Leakey concluded (1962, p. 695), "In all of these characters it ["K. wickeri"] shows a greater or lesser approach towards the structures we associate with the Hominidae. For this reason, I have purposely refrained from suggesting any family into which this new species should be placed." In subsequent publications (for example, Leakey, 1963, 1967) he has made it clear that he believes this specimen to be a hominid. In spite of Remane's recent comment that the canine is more like those of female pongids than of hominids (1965, p. 281), it is doubtful whether the combination of features seen in "K. wickeri" would occur outside the Hominidae.

From the published descriptions of Lewis (1934), Simons (1961) and

Leakey (1962), it is clear that YPM 13799 and "K. wickeri" are extraordinarily similar and that their similarities often extend to the most minute details (Simons, 1968). They are best classified in the same genus, probably in the same species (see Pilbeam, 1966, 1968). Any other classification would obscure the very great similarities between these specimens. It is difficult, indeed, to see which morphologic characters could be used to support species distinction. This point was made by Frisch (1962), and Simons (1963). However, the available material is not extensive and it might well prove that such limited remains simply do not permit identification at the species level. For example, similar fragments of two species of *Macaca* might well be difficult to tell apart. One solution to the problem would be to describe the Kenyan specimen as *R.* cf. *punjabicus.*

Simons also pointed out that specimen GSI D185, the right maxilla from the Siwaliks which Pilgrim (1915) had assigned to *Dryopithecus punjabicus*, was in fact a *Ramapithecus.* This specimen comes from the Nagri zone and has P^3–M^2 preserved and the distal part of the canine alveolus. The alveolus indicates that the permanent canine was small and vertically implanted. The premolar and molar occlusal morphology is very similar to YPM 13799. The zygomatic process is above M^1 and there is a canine fossa as in the other two specimens. The maxilla is described in detail by Pilgrim (1915, p. 16–22), and figured by him (pl. 3). Remane (1954, p. 124) has compared this specimen to the *Australopithecus africanus* maxillary fragment from Garusi in East Africa and has shown them to be very similar.

The dimensions of these three specimens are given in Table 38. The teeth of YPM 13799 in particular are mesiodistally shortened, and the mesiodistal lengths are accordingly estimates (see Chap. II). The L/B indices of YPM 13799 are also somewhat lower than those of the other specimens.

An attempt has been made to quantify one feature of occlusal morphology mentioned previously (see Table 39). The ratio of minimum to maximum buccolingual breadth across paracone and protocone has been calculated for

Table 38 Measurements of upper teeth of *Ramapithecus*

		YPM 13799	GSI D185 (from cast)	NMK FT1272
P^3	MDi L	7.0	5.9	
	Max L	7.5	6.6	
	BuLi B	10.5	9.0	
	Index Max L/B x 100	71.4	73.3	
P^4	MDi L	7.0	6.9	6.8
	BuLi B	10.0	9.2	10.1
	Index L/B x 100	70.0	75.0	67.3
M^1	MDi L	10.0	10.2	10.1
	BuLi B	10.9	10.3	10.4
	Index L/B x 100	91.7	99.0	97.1
M^2	MDi L	10.6	10.3	11.6
	BuLi B	11.7	10.8	11.6
	Index L/B x 100	89.8	95.3	100.0

Table 39 Ratios (Minimum BuLi B/ Maximum BuLi B) x 100 of Ramapithecus, D. (S.) sivalensis and BM(NH) M16649

	R. punjabicus (n=3)	D. (S.) sivalensis	BM(NH)M16649
P^4	62.0-66.4	46.0-50.0 (n=2)	43.9
M^1	67.0-68.5	48.8-57.0 (n=5)	46.6
M^2	66.6-69.7	46.4-61.3 (n=5)	-

P^4, M^1, and M^2, in *Ramapithecus* and in *D. (S.) sivalensis* (including BM(NH) M16649). A high ratio will reflect the fact that lingual and buccal surfaces are more vertical, a low ratio that they slope and that the occlusal fovea is relatively restricted.

The molars and second premolars are morphologically clearly distinguishable in the two species. The resemblances which they do have are due to their relatively simple cusp patterns and their lack of cingula. In 1963, Simons discussed briefly various synoptic views of higher primate classification. He comments (p. 888), "*Sivapithecus* . . . is not easily separated from *Ramapithecus.*" This presumably means that the two groups are superficially similar in some features, *not* that there is necessarily any special phylogenetic relationship between the two.

In 1964, Simons wrote another important paper on *Ramapithecus.* In this he re-emphasized the fact that the three maxillae discussed above are, on known parts, inseparable at the species level, and that the mandible GSI D168 was not a *Ramapithecus* at all. He also pointed out that mandibles of *R. punjabicus* were in fact probably already known.

In 1934, Lewis had described several species other than *R. brevirostris.* One of these was *Bramapithecus thorpei,* a species having as type specimen YPM 13814, a left horizontal ramus with M_3, M_2, roots of M_1, and the distal part of the distal alveolus of P_4. The specimen came from the Chinji zone, and thus is probably as old as the Fort Ternan material. The molars are short, broad, and closely approximated. The distal border of M_2 has worn a crescentic facet in the mesial border of M_3 and in turn has had worn in its mesial border a facet by M_1. The three molars are subequal in length. P_4 was also close to M_1. Clearly, the entire tooth row was compressed. The association of short teeth and a compressed tooth row has already been noted in YPM 13799.

The internal contour of the mandible also indicates that the tooth row and face were short anteroposteriorly. The ramus is shallow and thick at M_3, thinner at P_4. An arcuate tooth row and mandible is indicated. Lewis (1934, p. 174) noted that, "The sculpture of the crowns is highly suggestive of many human molars. . . . [This species] may very well lie near to the stem which led to the Hominidae proper."

The morphology of the molar crowns (see Lewis, 1934, pl. 1, fig. 4) contrasts with *D. (S.) sivalensis.* The cusp tips are relatively further apart and hence the occlusal fovea is wide. The crowns are low; the buccal cusps are lower than the lingual cusps. The hypoconulid is central on M_2 and M_3.

In combination these features make this mandible hominid-like and parallel many characters of the upper teeth of *R. punjabicus*. The M_2 of "K. wickeri" is similar to that of YPM 13814, although the tooth from East Africa is longer, just as the upper molars of NMK FT 1272 are longer than those of YPM 13799. There is a slight buccal cingulum between protoconid and hypoconid in both M_2's and in the M_3 of YPM 13814.

Lewis also described in 1934 a new species of *Dryopithecus, D. sivalensis,* having as type YPM 13806, a right mandibular ramus with M_2 and M_3 (p. 171–172, pl. 1, fig. 5). Lewis later transferred this species to *Bramapithecus* (1937a). The teeth are similar to those of YPM 13814 and specific distinction is not warranted (Simons, 1964; Simons and Pilbeam, 1965). These mandibles and dentitions are strongly reminiscent of shallow mandibles of Early Pleistocene hominids, for example, the *Australopithecus africanus* figured by Boné, 1955, and that formerly known as "Telanthropus capensis" (see Pilbeam, 1967; and Table 41).

The species *D. punjabicus* discussed above had been established in 1910 by Pilgrim, the types being GSI D118 and 119 consisting of a portion of right horizontal ramus with M_3 and a portion of the left with M_2. These were described comprehensively in 1915 by Pilgrim (p. 10–16). The tooth crowns are low, the occlusal fovea broad, and the hypoconulids central. In 1937a, Lewis transferred these mandibular fragments to *Bramapithecus*; they are also members of the same species as YPM 13814 and 13806.

Now, in 1963 Simons had referred the maxilla, GSI D185, to *R. brevirostris;* the mandibles GSI D118 and 119 were transferred by Lewis to *Bramapithecus.* It has already been shown that these mandibles are hominid-like, particularly in ways which parallel the hominid features of *R. punjabicus* maxillae. That these maxillae and mandibles belong in one and the same species seems most logical, for much the same reasons that the upper and lower dentitions of *D. (P.) major* (Chap. VI) and *D. (S.) sivalensis* (Gregory, Hellman, and Lewis, 1938) were associated. By extrapolating from living hominoid species it is possible to estimate which upper teeth are likely to go with which lowers; trial occlusions can raise the probability. When only one species of a given group is present (one species of hominid maxillae and one of mandibles) the probability is still further strengthened. The lack of associated material need not prevent the correct allocation of upper and lower dentitions of a species. In fact, associated dentitions are by no means common, at least as far as fossil primates are concerned.

The material described above has therefore been assigned to one species, the binomen of which is *Ramapithecus punjabicus.* The arguments outlined here are expanded in Simons (1964, 1965b, and 1968), Simons and Pilbeam (1965), and Pilbeam (1966). Dimensions of the mandibles and lower dentitions are given in Table 40.

R. punjabicus is known therefore from East Africa and India, from deposits of Late Miocene and Early Pliocene age. It is possible that other specimens should be assigned to this species (see Simons, 1964, p. 534; Simons and Pilbeam, 1965, p. 137).

A number of paleoanthropologists have accepted the synonymy of "K. wickeri" with *R. punjabicus,* among them Campbell (1966) and Clark (personal

Table 40 Measurements of lower teeth and mandibles of Ramapithecus

		YPM 13814	YPM 13806	GSI 118 & 119	"K. wickeri"
M_1	MDi L	*10.0			
M_2	MDi L	*11.1	11.1	11.8	11.0
	Tri B	10.4	9.6	10.1	9.0
	Tal B	10.1	9.7	9.5	8.9
	Index L/Tri B x 100	106.8	115.2	116.9	122.1
M_3	MDi L	*11.6	11.1	12.5	
	Tri B	10.8	8.9	10.6	
	Tal B	10.0	8.5	10.0	
P_4	D	*27.5			
	T	*12.5			
M_3	D	24.5	26.5	24.0	
	T	21.0	21.0	20.2	

communication and 1964). Leakey, however, has not agreed with this view. He wrote (1964, p. 49) in reply to a letter of Clark's in *Discovery* of London,

> So far as *Kenyapithecus* is concerned, Sir Wilfrid states—as though it was an established fact—'*Kenyapithecus* proves to be indistinguishable from *Ramapithecus*.' I challenge this *ex cathedra* statement. What I believe Sir Wilfrid means is that a young scientist at Yale has recently tentatively suggested that *Kenyapithecus* and *Ramapithecus* may belong to one and the same genus. This is a very different thing from 'proving that they are indistinguishable.' Moreover, in order to give a semblance of likelihood to this suggestion, the Yale scientist first had to claim that the lower jaw and dentition, which the original finder attributed to *Ramapithecus,* must be dissociated from the maxilla which constituted the type of that genus. Having done so, he then links some mandibles of another genus, *Bramapithecus,* with the *Ramapithecus* maxilla as representing its lower dentition.
>
> Such armchair juggling may, or, of course, may not, prove to be justified, in due course, when someone finds an associated upper and lower dentition of *Ramapithecus*. Meanwhile, since we have a lower molar of *Kenyapithecus,* and since it does not at all agree with the lower molars which Lewis described as those of *Ramapithecus,* the words 'proves to be indistinguishable' are, to say the least of it, inappropriate.
>
> I myself pointed out, in my original description, that there was some similarity between *Kenyapithecus* and *Ramapithecus* but there is no scientific evidence upon which to go further than that, at the moment.

"Armchair juggling", as we have noted, is a not unusual method of allocating isolated upper and lower dental material to one species. We have also noted the "Bramapithecus" mandibles are suitable for consideration as hominids, complementary to *Ramapithecus* maxillae, while GSI D168 (the mandible associated by Gregory, Hellman, and Lewis with *Ramapithecus)* is not a hominid.

Lewis has recently stated his belief that GSI D168 is a pongid (see Simons, 1964). Leakey's 1962 description in fact mentioned two points of similarity between *Ramapithecus* and "Kenyapithecus" and one point of difference which does not exist. There is a large amount of evidence indicating synonymy, at least at the generic level.

Finally, in 1967, Leakey produced a detailed statement of objections to Simons' (1964) and Simons' and my diagnosis (1965) of *Ramapithecus* and to our synonymy of the Indian and Kenyan specimens. In this paper he proposed that BM(NH) M16649 be transferred from *D. (S.) sivalensis (S. africanus* of Clark and Leakey, 1950 and 1951) to *Kenyapithecus,* this genus standing apart from *Ramapithecus.* His objections to the diagnosis given by Simons and me for *Ramapithecus* are as follows (1967, p. 156):

> a) It makes size a generic character in that it states 'slightly *smaller* overall size than *Dryopithecus* and *Australopithecus,*' but immediately refers to an exception. Moreover, should a larger species of the genus be discovered, it would automatically be excluded by this diagnosis. It must, therefore, be emphasized that size is never really valid as a generic character.
>
> b) It states that the mandible is 'shallower' than in *Australopithecus* and *Dryopithecus.* It does not say whether this is in relation to the overall size, or whether it is shallower only relative to the length of a tooth row. This feature again makes size, for example, 'shallower', a generic character, which is taxonomically unsatisfactory.

Several points need to be made here, the first of which is that *R. punjabicus* as defined in Simons (1964) and Simons and me (1965) is a monotypic genus. The diagnosis of the species therefore inevitably becomes the diagnosis of the genus, since, in the absence of other species in the genus, it cannot be known in advance which characters are "generic" and which "specific". This leads to another point which needs to be stressed. In the study of fossil forms (as in studies of the evolution, ecology, and population genetics of living populations) it is the species to which our attention is directed. We assign *individuals* to species and it is the species which is most important since it is the unit which evolves. Although formal species are often arbitrary (particularly in paleontology), nevertheless an approach to true species groupings can be made, particularly using multivariate statistical techniques. In addition, genera are arbitrary groupings of species, bracketed together because they are similar. Only when species have been grouped into genera can generic characters be listed.

Finally, Leakey objects to the use in diagnoses of characters to which exceptions can be found. It should be emphasized here that even with species, and particularly with genera, we are dealing with groupings or sets which are polythetic rather than monothetic (Sokal and Sneath, 1963). Polythetic sets are composed of individuals each of which possesses some, though not necessarily all, of a number of characters which define the set; one character is rarely possessed by all members. In contrast, to qualify for membership of a monothetic set each individual *must* possess a definite number of characters and all characters are found in all members of the set. It has for some time been realized that species, and other taxa in the hierarchy, are polythetic rather than monothetic sets, and therefore exceptions are bound to occur. To expect otherwise is to revert to typology.

To clarify one point, the known mandibles of *R. punjabicus* from the Late Miocene and Early Pliocene of India are absolutely shallower than most members of species of *Dryopithecus* except some *D. africanus* and *D. laietanus.* If width be taken into account, the mandibles are relatively shallower than all species of *Dryopithecus* (see Simons, 1964, fig. 1, and p. 531–532; and Table 41). The relative thickness has been calculated using mandibular thickness (M_3 T) and depth (M_3 D) measured at M_3.

Table 41 shows clearly that, out of 19 mandibular specimens of *Dryopithecus,* only one is more robust at the level of M_3 than the least robust of *R. punjabicus. R. punjabicus* is similar to Early Pleistocene *A. africanus,* although a little less robust.

Table 41 Ratio (M_3T/M_3 D) x 100 of fossil hominids and pongids, *Gorilla* and *Pan*

	n	$\bar{X}$	OR
Australopithecus africanus	3	89.8	87.5-92.9
R. punjabicus	3	83.0	79.2-85.7
D. (P.) africanus	4	66.1	53.5-76.5
D. (P.) nyanzae	3	61.6	57.1-68.0
D. (P.) major	2	68.2	62.5-73.9
D. (S.) silvalensis	3	74.8	69.5-82.5
D. fontani	3	65.7	61.0-70.6
D. laietanus	4	67.9	62.6-77.5
P. troglodytes (males)	10	65.7	58.0-74.5
P. troglodytes (females)	10	59.0	49.7-66.5
G. gorilla (males)	10	66.8	59.4-76.2
G. gorilla (females)	10	70.5	59.7-82.0
Pongo pygmaeus	6	67.4	56.0-75.0

Leakey's objections to the diagnosis continue (1967, p. 156),

> c) It goes on to say 'shorter face', but because no complete face of *Dryopithecus* (other than in the *Proconsul* group) has been found and certainly no complete face from gnathion to nasion in *Ramapithecus,* this seems to be a most unwise diagnostic character to attribute to the genus, in the present state of our knowledge.

It is obviously possible to misinterpret the diagnosis given by Simons and me (1965, p. 136). The shortness referred to in "shorter face" is anteroposterior and not superoinferior, as was inferred by Lewis when he named YPM 13799 "brevirostris."

Finally, (Leakey, 1967, p. 156),

> d) The character 'incisors and canines reduced in relation to cheek teeth when compared with *Dryopithecus*' may be valid for Asia but it is not true

> for specimens from East Africa which Simons and Pilbeam wish to include in *Ramapithecus.* While it may be true in respect of *Ramapithecus punjabicus (brevirostris)* (if indeed incisors of this genus and species are known in Asia, of which I am not aware) . . . it is certainly not true . . . in respect of comparisons of the incisors as between *Kenyapithecus* and the *Proconsul* group, which Simons and Pilbeam insist on including in the genus.

The canine of YPM 13799 must have been small both absolutely and relatively (as is the canine of "K. wickeri" which Leakey, 1962, p. 694 noted). In 1934 (p. 156), Lewis wrote of the incisors: "I^2–The root is present in the alveolus, but the crown has been lost. A small incisor close to the hominid type is indicated. I^1–Most of the alveolus has been preserved, and indicates that the size of the two incisors was approximately equal. The roots indicate that the incisors more nearly approached the vertical than is the case in the Simiidae known hitherto; the attendant slight prognathism is hominid."

To this account can be added the following brief comments. The lateral incisor root was no more than 16 mm long from cervix to tip. The root is broken above the cervix and is no more than 4 mm long mesiodistally and 5.5 mm broad labiolingually. The central incisor alveolus is preserved distally; the tooth root would have been no longer from cervix to tip than that of the lateral incisor. Such a root is both absolutely and relatively very small. The crown of the central incisor could hardly have been more than 9 mm long mesiodistally and 6.5 mm broad labiolingually.

These incisors are clearly small in absolute terms. The only pongid contemporary with YPM 13799 for which I have incisor measurements are for GSI D196, the palate originally described by Pilgrim as *Sivapithecus orientalis* (1927, p. 549), transferred by Lewis (1937a, p. 144) to *S. indicus,* and by Simons and me (1965, p. 125) to *D. (S.) indicus;* I now believe this to be a male *D. (S.) sivalensis.* The cheek teeth and lateral incisor root are preserved, as is the alveolus for the central incisor. An isolated upper central incisor of a large pongid is preserved in the Yale collections (YPM 16919). This specimen has only recently come to light, and has yet to be described. It fits the alveolus of GSI D196 and has been used as the incisor of D196 in the calculations. It may, in fact, represent the same individual as GSI D196.

In order to determine the relative size of the incisors, the crown area of the upper central incisors has been calculated (product of length and breadth) and expressed as a ratio of the sum of the crown areas of M^1 and M^2 (Table 42). The first two molars only were chosen since third molar crowns are not present in YPM 13799 and the palate of "K. wickeri". The central incisor

Table 42 Ratio (crown area of I^1/ crown area $M^1 + M^2$) x 100
in Dryopithecus and Ramapithecus

R. punjabicus	YPM 13799	*25.5
D. (S.) sivalensis	GSI D196/YPM 16919	*32.2
D. (P.) major	UMP 62-11	29.5
D. (P.) nyanzae	NMK 5, CMH3	21.2
D. (P.) africanus	NMK R1948,50	24.6

crown area has been estimated for YPM 13799 and this is clearly only a very rough approximation.

If pongids contemporary with *R. punjabicus* are considered, only one specimen is available, the composite of *D. (S.) sivalensis.* Here the incisor is relatively larger than in *R. punjabicus.* The palate of *D. (P.) major* is from older, early Miocene deposits and the ratio is slightly lower than in GSI D196, though still higher than *R. punjabicus.* The values for *D. (P.) nyanzae* and *D. (P.) africanus* are slightly below that for *R. punjabicus;* these individuals are geologically considerably older than the Indian form. If a trend towards incisor hypertrophy has occurred in the pongids then lower values for older species might be expected.

Since relatively small incisors are primitive for Pongidae, it is hardly surprising that early Miocene apes and late Miocene/early Pliocene hominids should both have relatively small anterior teeth. Seemingly, the Hominidae have retained the small incisors of their earlier Tertiary ancestors. (It should be remembered here that but a single specimen is recorded for each species noted above and the range of variation of incisor size within the species is unknown.)

In 1967 (p. 157) Leakey described an upper central incisor from the same level at Fort Ternan as the maxilla of "K. wickeri". Leakey believes that the incisor and maxilla belong to the same species. The dimensions of the incisor are: MDi L, 10.0 mm, and LaLi B, 6.5 mm, giving a crown area of 65 mm^2. The ratio of crown areas (if the incisor and maxillae are treated as coming from a single individual) is 26.3, 0.8 units above the estimate for YPM 13799 and below the values for the contemporary GSI D196 and the slightly earlier UMP 62–11. The ratio is greater than that for one *D. (P.) nyanzae* and 1.6 units above that of one *D. (P.) africanus.* Both these specimens are 5 million or more years older than East African *R. punjabicus.*

Figure 31 compares the maxillary dentitions of *D. (P.) africanus,* a pygmy chimpanzee *Pan troglodytes,* and the Fort Ternan *Ramapithecus.* All three have been brought to the same M^{1-2} length. The incisor from Fort Ternan is much smaller than that of *P. troglodytes* and is less hypsodont than geologically older *D. (P.) africanus.* So, considered in terms of crown height, the incisors of *Ramapithecus,* like the canines, are relatively smaller than those of Miocene to Recent apes. There is little difference between the East African and Indian specimens of *R. punjabicus* as far as incisor size is concerned, and there are no other significant differences, as has already been shown. The claim that they do not represent the same genus or species cannot be substantiated in this way.

The incisor of *Ramapithecus* from Fort Ternan is of interest, since it is the only complete one known. The specimen is described by Leakey (1967, p. 157):

> This tooth is remarkably like that of *Homo* and differs in a number of characters from the corresponding teeth of *Proconsul.* . . . Moreover, it has characters in common with the australopithecines, in particular in the cross-section of the root where it meets the crown. In the upper central incisors of *Proconsul,* the root at the junction with the crown is approximately trihedral, and has a greater diameter from the labial to the lingual aspect

> than from side to side. In the *Kenyapithecus wickeri* specimen, the cross-section is not trihedral but much more oval with the maximum diameter from side to side, while the labial-lingual diameter is reduced. The height of the crown of this tooth, which is practically unworn, is less than the width, and it is more compressed labio-lingually compared with the corresponding teeth of *Proconsul.* The region near the cutting edge is very thin providing a fine chisel edge very different from the upper incisors of *Proconsul,* where a marked medial thickening extends almost to the top of the crown.

The following dimensions are given (1967, p. 157), Crown width (MDi L), 10.0 mm, and Crown height (La H), 10.25 mm. Diameters of root at junction with crown, Bilateral (MDi), 7.5 mm, and Labio-lingual, 6.5 mm.

These dimensions do not agree with the statement that "the height of the crown . . . is less than the width." For comparison; dimensions for the central incisors of *D. (P.) nyanzae* and *africanus* are given in Appendix 2; their MDi lengths are lower, although the LaLi breadths are relatively closer to the Fort Ternan specimen.

In *D. (P.) major* (UMP 62–11) the crown dimensions of I^1 are, MDi L, 10.8 mm, and LaLi B, 9.1 mm. Unfortunately, the crown is so worn that features of the lingual surface cannot be seen. Like *R. punjabicus* from Fort Ternan, the MDi diameter of the root at the cervix (9.4 mm) exceeds the labiolingual diameter (8.7 mm). In this feature *D. (P.) major* differs from the two smaller species. At the cervix, the root of the incisor of *D. (S.) sivalensis* (YPM 16919) is 8.6 mm long mesiodistally and 8.1 mm broad labiolingually. Presumably the relative proportions at the cervix alter as the mesiodistal crown diameter increases.

The central incisor from Fort Ternan resembles those of hominids in its "shovel-shaped" morphology. However, not all hominids have central incisors in which the lingual surface lacks a median pillar. Robinson (1956, fig. 6a) has illustrated such a structure in *Australopithecus robustus.* In the only specimens of *A. africanus* (1956, fig. 7f) two small processes run centrally down the lingual surface from the gingival eminence. The central incisor of *D. (S.) sivalensis* from the Chinji (YPM 16919) was mildly shovel-shaped when unworn, although the lingual mesial and distal marginal ridges have almost disappeared through wear. There is a pronounced lingual bulging just below the cervix; there is no medial lingual thickening running down the crown. The central incisors of the subfossil orangutan, *Pongo pygmaeus palaeosumatrensis,* illustrated by Hooijer, show variations in crown lingual surface morphology. Some are moderately shovel-shaped with no central pillar (Hooijer, 1948, pl. 1, figs. 6 and 11) while others have these well developed (ibid., pl. 1, figs. 7, 8, 9, and 14). Finally, the composite *D. (P.) nyanzae* figured by MacInnes (1943, pl. 24) has incisors similar to those described by Leakey for *Ramapithecus.* Accordingly, the presence or absence of mesial, distal, or central ridges is variable in species of Hominoidea.

In his description of the East African *R. punjabicus,* Leakey wrote (1962, p. 695), "It must suffice to point out that, while it clearly represents a creature related, to some extent, to the Lower Miocene species, which Leakey and Le Gros Clark called *Sivapithecus africanus,* it is equally clearly not a true *Sivapithe-*

cus, as may be seen by the morphology of the upper canine and fourth upper pre-molar, and also by the presence of the canine fossa and the position of the root of the malar element of the malar maxillary process."

He concluded (p. 696), "when . . . [the Fort Ternan specimen] is allocated to a family, *Sivapithecus africanus* will have to join it there and be removed from the Pongidae." In the preceding paragraphs he had given no details of the similarities between "K. wickeri" and "S. africanus" which might necessitate the reclassification of the latter.

Before continuing with this account it is important to restate the fact that the material from Fort Ternan cannot be separated taxonomically from Indian *Ramapithecus* and that the discovery of the upper central incisor does not alter this conclusion. The generic nomen "Kenyapithecus" is therefore no longer available.

In his most recent papers, Leakey (1967 and 1968) has proposed that new material be added to the hypodigm of the species proposed by Clark and Leakey in 1950, *S. africanus.* Leakey regards this material as being distinct from *D. (S.) sivalensis.* The original holotype of "S. africanus" has already been mentioned and is BM(NH) M16649 from site R106, Rusinga (Fig. 28). The zygomatic process of this maxilla is situated above M^1 and is closer to the alveolar border than in *R. punjabicus.* This is probably a primitive character. It is most unlikely that the canine fossa was better developed than in other species of *Dryopithecus,* particularly in the presence of a presumed large canine jugum. The lowness of insertion of the zygomatic process seems to be a primitive character and is found in *D. (P.) major, D. (P.) africanus,* and, as far as can be seen in the holotype, *D. (P.) nyanzae.* In *D. (Proconsul)* the process is set either above the distal moiety of M^1 or the mesial part of M^2; the process is more distal in *D. (P.) major* UMP 62–11, possibly because this specimen has a sizeable anterior dentition and face, and also possibly because it is younger and therefore more evolved towards the condition seen in *G. gorilla.* A more forward position of the zygomatic process may be a primitive character for some Pongidae; without earlier material this cannot be determined. It is not confined to Hominidae, as Straus (1963, p. 149) has shown in his study of *Oreopithecus,* and the process is often situated above M^1 or M^{1-2} in *Pongo pygmaeus.* The condition seen in BM(NH) M16649 resembles that of *R. punjabicus,* although the morphologies of the lateral maxillary areas above the cheek teeth contrast strongly in the two groups. In BM(NH) M16649 there is none of the "tucking in" to be observed above the buccal roots of the premolars as in *R. punjabicus.* The way in which the zygomatic process merges with the alveolar area is also different.

The teeth of BM(NH) M16649 have been described in detail by Clark and Leakey (1951, p. 63), quoted above. All three preserved cheek teeth (P^3–M^1) have marked buccal and lingual slopes (see Table 39, p. 107). The cusps and crests are rather rounded; this roundness is increased by wear. It is not possible to tell whether or not this character is typical or otherwise for the population from which this individual is sampled.

The first premolar has two well-developed buccal roots (Fig. 31). The morphology of the buccal surface is very similar to that of *D. (P.) major,* UMP 62–11 (Fig. 18), particularly in the slope of the mesial buccal ridge and the superior extension of the enamel margin in the mesial half of the buccal surface. The mesial extension of the mesiobuccal corner of the crown has already been noted for UMP 62–11, GSI D299/300 (Gregory, Hellman, and Lewis, 1938, pl. 1, fig. 2a) and YPM 13837 (ibid., pl. 1, fig. 10a, pl. 7, fig. I). The condition is similar in BM(NH) M16649 and the mesial border is concave mesially. The occlusal slopes of the protocone and paracone are both steep and a central sulcus terminates the ridges running from these cusps towards the center of the occlusal surface. In these features it resembles *D. (P.) major* and *D. (S.) sivalensis* P^3's and contrasts strongly with *R. punjabicus.*

The morphology of P^4 is generally similar to P^3, although the mesiobuccal extension is not present. It contrasts with that of *R. punjabicus,* as Leakey (1962) noted, and compares with those described for *D. (S.) sivalensis*: GSI D299/300 (Gregory, Hellman, and Lewis, 1938, pl. 1, fig. 3a), GSI D1, and GSI 18065 (Prasad, 1964, pl. 20, fig. 3b). There is a slight distolingual cingulum.

The first molar is simple and low crowned. As in P^4, the buccal and lingual surface slope so that the cusp tips are relatively approximated (see Table 39, p. 107). It is morphologically similar to *D. (S.) sivalensis* first molars: GSI D299/300, BM(NH) M13365, and YPM 13834 (Fig. 30). A protoconule is present; the lingual cingulum is present only at the mesiolingual corner, as in YPM 13834. Figure 28 shows that the enamel is heaped-up on the lingual surfaces of all three preserved cheek teeth of BM(NH) M16649. This suggests either that other individuals within this species have cingula, or that individuals in preceding species had cingula, or both. The crown is somewhat lower than in Indian *D. (S.) sivalensis,* possibly a primitive feature.

Remane (1965, p. 281) has written of this specimen, "Die Zuordnung zu dem asiatischen Genus *Sivapithecus* ist provisorisch, die Reste könnten gut in die Gattung *Gorilla* oder vielleicht auch als Extremvariante zu *Proconsul major* gestellt werden. Aus diesem Rest dürfen daher vorläufig noch nicht paläontologisch-tiergeographische Schlüsse gezogen werden, etwa in dem Sinne: 'Die Gattung *Sivapithecus* erscheint zuerst im Miozän Afrikas.' "

Since a complete upper dentition of *D. (P.) major,* UMP 62–11, is now known, it can be seen that this specimen, BM(NH) M16649, does not represent any species in the subgenus *(Proconsul).* However, Remane's remark is reasonable in that it does make the point that BM(NH) M16649 has many pongid-like features.

One important pongid feature of BM(NH) M16649 which was first mentioned in 1965 by Simons and me (p. 113) is the presence above the roots of P^3 of the distoinferior part of a large canine alveolus curving back over the premolars (Fig. 28). The breadth of the mesial border of the first premolar also indicates that the canine would have been large.

In summary, this palate shows many pongid features and no unequivocal hominid characters. If this is a hominid ancestral to *R. punjabicus,* the number of similarities are very few; the anterior position of the zygomatic process is one, although this is not necessarily a hominid character. The number of resemblances to Late Miocene and Early Pliocene *D. (S.) sivalensis,* however, are more numerous.

Dimensions for BM(NH) M16649 have been given by MacInnes (1943, p. 168) and Clark and Leakey (1951, p. 67). Leakey gives two different sets of measurements (1967, tables 1 and 2). Measurements as defined in Chapter II are listed in Table 43.

A number of other maxillary specimens are referred by Leakey to the same species as BM(NH) M16649. These are left (NMK 300,111) and right (NMK 274,52) maxillae of one individual from Songhor, the left with P^4 and roots of C^1 and P^3, the right with P^3–M^1 and C^1 root. These specimens resemble BM(NH) M16649 in general features; NMK 300,111 has a canine fossa, although this is no better developed than in BM(NH) M16647 *(D. nyanzae),* GSI D196 *(D. sivalensis),* or in many *Pongo pygmaeus.* The palate of NMK 300,111 is shallow, like that of BM(NH) M16649. The canine root is preserved in both specimens; it is said to be set vertically in the maxilla of NMK 300,111, although no more so than in GSI D196, for example. The dimensions of the canine of NMK 274,52 would probably have been *11.9 mm (Max L) by *9.0 mm (Trans B) at the cervical border. The long axis was mesiodistal, as in pongids. For seven specimens of *D. (S.) sivalensis* from the Siwaliks the ranges for these dimensions are 10.5 to 16.6 mm and 8.7 to 12.5 mm.

Table 43 Measurements of East African Pongidae, non-Dryopithecus (Proconsul)

		BM(NH) M16649	NMK 300, 11	NMK 274, 52	NMK 333, 404	NMK 748, 7	NMK 1377	D. (S.) sivalensis
P^3	MDi L	7.8		6.2		6.9		7.8- 8.0 (2)[1]
	Max L	9.0		8.3		8.6	8.5[2]	8.9- 9.4 (2)
	BuLi B	12.5		10.7		11.5	10.0[2]	11.0-11.4 (2)
	Index Max L/B x 100	72.0		77.5		74.8	85.0	80.9-82.5 (2)
P^4	MDi L	8.1	7.8	7.0		7.6	6.0[2]	7.1- 7.8 (3)
	BuLi B	12.3	11.6	11.2		11.7	10.0[2]	11.3-12.0 (4)
	Index L/B x 100	65.8	67.2	62.5		64.9	60.0	60.6-66.5 (3)
M^1	MDi L	10.5		9.4				10.3-11.3 (7)
	BuLi B	11.8		10.9				11.4-12.6 (7)
	Index L/B x 100	89.0		86.2				78.6-93.4 (7)
M^2	MDi L	**11.0			10.0[2]			10.8-13.3 (9)
	BuLi B	**12.0			11.5[2]			12.6-15.4 (9)
	Index L/B x 100	**91.6			87.0			80.6-95.4 (9)

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[1] Number of specimens measured

[2] From Leakey (1967)

Two further maxillary fragments from Songhor have been assigned with the two described above. A right maxilla (NMK 748,7) contains P^3 and P^4, and a left fragment (NMK 1377) also contains these two teeth; a right M^2 (NMK 333,404) from Songhor has also been included. Of these, NMK 300,111 and 274,52 were originally classified as *D. (P.) nyanzae* (Clark and Leakey, 1951, p. 53), and NMK 333,404 as *D. (P.) africanus* (Clark and Leakey, 1951, p. 36). Such fragmentary specimens are very difficult to assign correctly.

One interesting contrast between *R. punjabicus* and *Dryopithecus* species is in the proportions of the premolar lengths. In the hominid species, the two premolars generally have closely similar lengths; in pongids P^3 is longer than

P^4 mainly because of the mesial extension of the buccal face of P^3. The ratios Max L P^3/MDi L P^4 × 100 are given in Table 44 below. The ratio in three specimens of *R. punjabicus* is lower than in earlier or contemporary pongids.

Leakey (1967, p. 160–161) has transferred an upper right central incisor (NMK 9, CMH9) from *D. (P.) nyanzae* (Clark and Leakey, 1951, p. 39–40) to his proposed new species. The specimen comes, according to Clark and Leakey (p. 39) from "Rusinga", no site being given. No locality data is available in the National Museum of Kenya Catalogue. Leakey (1967) states on p. 158 that the specimen comes from site R106 although in the description on p. 160–161 no exact locality is given. The tooth is large, dimensions 10 × 7.25 (p. 161) or 10.0 × 7.5 (Table 2, p. 162), and similar in morphology to the one which he referred to *R. punjabicus*. It should be emphasized again that the absence of a median lingual pillar does not prevent this incisor from being pongid, nor make it hominid; it is quite possible that incisors of female Siwalik *D. (S.) sivalensis* would have had similar dimensions and a similar morphology.

Table 44 Ratio (Max L P^3/ MDi L P^4) x 100 of fossil species, *Gorilla* and *Pan*

	n	$\bar{X}$	OR
D. (P.) africanus	2		110.9-129.2
D. (P.) nyanzae	3		110.2-120.7
D. (P.) major	1		134.1
D. (S.) sivalensis	1		118.6
BM(NH)M16649			111.1
NMK 274,52			118.5
NMK 748,7			113.1
NMK 1377			141.7
G. gorilla (males)	20	110.9	103.5-122.2
G. gorilla (females)	20	103.7	91.8-110.8
P. troglodytes (males)	14	114.5	102.6-130.0
P. troglodytes (females)	12	113.7	103.0-121.4
R. punjabicus	3		100.0-107.3[1]
A. robustus	4		90.0- 94.3
A. africanus	5		88.9-120.9

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[1] "K. wickeri" = **100.0

Leakey has also included in his proposed species three mandibular fragments, all of them containing part of the symphyseal area, and a more complete mandible, NMK Rs 1967, 394 (Leakey, 1968). These fragmentary specimens are so incomplete as to render their correct taxonomic assignment almost impossible. A piece of right ramus (NMK 71, CMH142) from site R106, Rusinga, which comes from the same site as BM(NH) M16649 (Leakey, 1967, p. 158, figs. 3a and 4a) is also listed by Leakey. This specimen was tentatively referred by Clark and Leakey (1951, p. 60) to *D. (P.) major*. The fragment is sectioned mesially just mesial to the right C_1 and distally midway through M_1. The roots of C_1 to P_4 are present and the mesial root of M_1. The specimen differs from *D. (P.) major* in a number of features. Leakey lists these (1967, p. 158). The first one is:

> a) At the level of P_4M_1 the depth of the corpus is only very slightly less than that seen in *Proconsul major,* but the thickness of the mandibular [*sic*], at this point, is totally different; the corresponding measurements at P_4M_1 are:

Proconsul major	Depth 41 mm	Thickness 22 mm
Kenyapithecus africanus	Depth 39.5 mm	Thickness 12 mm

My own measurements plus some from Leakey are in the following table.

Table 45 Mandibular measurements of East African early Miocene mandibles

		D. (P.) major			NMK
		NMK 190,1	BM(NH) M14086	NMK71 CMH142	Rs 1967,394 (from Leakey, 1968)
	D	41.0	36.5	38.0	34.0
P_4	T	21.0	17.0	15.5	13.5
	Index T/D x 100	51.2	46.5	40.8	39.7

A few sets of measurements are available for *D. (S.) sivalensis* from the Siwaliks and for *R. punjabicus* (Table 46).

Table 46 Mandibular measurements of R. punjabicus and D. sivalensis

		R. punjabicus		D. (S.) sivalensis	
		YPM 13814	YPM 13811	GSI D197	GSI D199
	D	*27.5	26.0	35.5	-
P_4	T	*12.5	11.5	14.5	13.0
	Index T/D x 100	*45.4	44.2	40.8	-

As far as other Early Miocene mandibles are concerned, NMK 71, CMH142 is relatively thin and gracile, as can be seen from the thickness-depth ratio. However, mandibles of *D. (S.) sivalensis* from the Silwaliks have in the region of P_4 thicknesses as low as 11.5 mm. The lowest recorded index is that of GSI D197 ("*S. himalayensis*" of Pilgrim, 1927). There is no evidence to indicate that this non-*D. (Proconsul)* feature is a hominid characteristic.

Leakey continues (p. 158):

> b) In the known mandibles of *Proconsul major* there is a clearly defined diastema between the lower 3rd premolar and the lower canine; in this specimen the anterior lingual root of the lower 3rd premolar is set far forward and extends well beyond the posterior rim of the alveolus of the canine, and there is no diastema. . . .
>
> c) In *Proconsul major* (as also in both the other species of the genus) the furthest posterior projection of the symphyseal region is set high in the mid-line and extends well back, so that its limit is almost in line with the lower 4th premolar. In this specimen the most backward part of the symphysis is not further back than the level of the front of the 3rd premolar, and may be even further forward.

d) In *Proconsul major* the inner wall of the corpus, in the region of the premolars, slopes slightly inwards, and the corpus itself is very thick. In this specimen the outer wall is at first straight, then turns slightly outwards.

e) The area of the root of the canine in *Proconsul major* is marked by a strong surface swelling of the anterior face of the mandible, giving a clear line of demarcation between the "chin" region and the lateral wall of the corpus. In this specimen, there is no such swelling and the root of the canine is much less massive.

f) The roots of the lower canines are more laterally compressed than in any *Proconsul,* and are orientated more antero-posteriorly and less transversely than in any species of *Proconsul* or Pongid.

g) The whole mandibular structure is gracile even though the corpus is very deep (39.5 mm).

h) The mental foramen lies relatively low on the corpus, and is situated beneath the 4th premolar, instead of below the 3rd premolar as in *Proconsul major.*

The following comments can be made. The specimen is not a *D. (Proconsul).* However, this does not automatically make it a hominid. For point b, a similar compression of the anterior part of the tooth row can be seen in some specimens of *D. (S.) sivalensis* (for example YPM 13811, see Lewis, 1934, pl. 11, fig. 1c), and also in some specimens of both sexes of *Pongo pygmaeus.* The symphyseal region, point c in Indian *D. (S.) sivalensis,* has a variable simian shelf. The most posterior part of the symphyseal midline may be as far forward as the distal border of P_3. The superior transverse torus is set farther forward than this. If it is assumed that ancestors of *D. (S.) sivalensis* and *D. fontani* (a closely related species from the later Miocene and early Pliocene of Europe), were generally without posteriorly projecting inferior transverse tori, some of them may have had a symphyseal morphology like that of NMK 71, CMH142. Point d also applies to certain *D. (S.) sivalensis* specimens from the Siwaliks, as does e. Point e applies to YPM 13811, as well as to AMNH 19411 (Gregory and Hellman, 1926, p. 22). Point f is certainly not a hominid feature. It applies to *D. fontaini.* Finally, the depth of the mental foramen below the alveolar border is very variable in pongid species and is of dubious taxonomic value. If this depth be expressed as a percentage of total rameal depth at the same point, the value of the ratio varies from 54.3 to 72.8 in a sample of 40 *G. gorilla* and from 59.2 to 73.9 in 26 *P. troglodytes.*

Although many of the features present in NMK 71, CMH142 also occur in specimens of *D. (S.) sivalensis* from the Silwaliks they do not occur in this combination in large males (NMK 71, CMH142 is male according to Leakey). However, this specimen is very similar to *D. fontani,* particularly the type specimen, Paris Museum No. AC 36 (see Fig. 30).

The roots of right C_1 to P_4 are retained in NMK 71, CMH142 and it is possible to obtain estimates, albeit poor ones, for some tooth dimensions. They are: for C_1, Max L = **14 mm, Trans B = **11 mm; for P_3, Max L = **12 mm, Trans B = **7 mm. The canine therefore was large, the first premolar roots were long, and, presumably, the crown was sectorial.

Leakey also describes another mandibular fragment, NMK 227,276, from the surface at Rusinga (1967, p. 158–159, figs. 3b, 4b, 5e). This specimen was described originally as *D. (P.) nyanzae* (Clark, 1952, p. 276) and may well be a member of that taxon. The specimen consists of the symphyseal region containing the roots of left P_3 to right P_3. Again, there is overlap between C_1 and P_3. The anterior surface of the symphysis is almost vertical in its superior half (Leakey, 1967, fig. 3b). In his figure 5e the section appears not to be oriented quite correctly, the infradentale being rotated posteriorly and gnathion anteriorly. There is no simian shelf; the symphysis is not as thick as in *D. (P.) major.* Symphyseal length is *37 mm and thickness *19.5 mm, giving a thickness-length ratio of *52.7; three *D. (P.) major* varied from 53.8 to 57.3.

According to Leakey (1967, p. 159), the symphyseal cross section "recalls that of the more primitive members of the genus *Homo* and of some australopithecines." Individuals of *Australopithecus* species, however, generally have projecting inferior tori (Scott, 1963). The similarity of NMK 227,276 to Pleistocene hominids may not imply a phylogenetic relationship, particularly since 17 million years separates this specimen and the Olduvai Gorge specimen illustrated by Leakey (Hominid 13, see 1967, fig. 5a). A number of symphyses of *D. (S.) sivalensis* from India are known, the one which preserves the midline most accurately is AMNH 19411 (Gregory and Hellman, 1926, p. 22, fig. 11). The main axis of the symphysis is probably somewhat less vertical than in NMK 227,276; there is no simian shelf, but instead "a nearly vertical area for the insertion of the digastric muscles" (Gregory and Hellman, 1926, p. 24). This specimen is from the Lower Chinji zone and is thus one of the oldest Siwalik pongids. Measurements of NMK 227,276 and AMNH 19411 are compared in Table 47.

Table 47 Symphyseal measurements of Dryopithecus

		NMK 227,276	AMNH 19411
Symphysis	D	*37	43.0
	T	*19.5	*17.8
Index T/D x 100		*52.7	*41.4
$\bar{I}$	B	*18.7	*18.5
C_1	B	*35.0	*35.5

The third mandibular fragment is NMK 417 from Songhor (Leakey, 1967, p. 160, figs. 4c and 5f). According to Leakey, it is very much smaller than NMK 71, CMH142 and NMK 227,276. Symphyseal dimensions are approximately 26 mm by 13 mm. This is almost certainly not conspecific with either NMK 71, CMH 142 or NMK 227,276. It probably represents *D. (P.) africanus.*

The more complete mandible described by Leakey (1968) again shows many differences from *D. (Proconsul)* species. However, these differences do not indicate hominid affinities. The symphyseal section resembles *D. (Sivapithecus)*; the inferior transverse torus projects posteriorly a little more than the superior torus [see Leakey, 1968, Fig. 1b(i)]. The canines are large and project above the occlusal plane of the cheek teeth. The P_3 is sectorial and unicuspid.

The long axes of the cheek tooth rows are concave buccally, rather than convex as in hominids. The contour of the dental arcade resembles that of primitive hominoids *(Aegyptopithecus, Aeolopithecus)* and is probably therefore a primitive trait. There are no features of the mandible which are specifically hominid, and none which would indicate any special affinity with *Ramapithecus.*

This mandible has been assigned by Leakey to "K. africanus," although the association of the mandible with the type maxilla, BM(NH) M16649, is by no means certain. No associated maxillary and mandibular specimens of "Kenyapithecus africanus" are known; consequently the mandibles have been referred to the same species as BM(NH) M16649 by "juggling." The mandible and lower dentition, as far as it is preserved, shows pongid features—large canines and elongate first premolars. The tooth row is compressed, although this feature can be observed in some *D. (S.) sivalensis* and in *D. (P.) major* (Fig. 18), as well as in dentitions of *R. punjabicus.* Symphyseal morphology is variable, as in *D. (Proconsul), D. (S.) sivalensis,* and *D. fontani,* and resembles the Eurasian species of *Dryopithecus.*

The maxillae also show pongid features, particularly in the size of the canine and the morphology of the first premolar; these characters are probably primitive. Features which could indicate hominid affinities are the canine fossa and the relatively anterior position of the zygomatic process. Canine fossae of this sort can, however, be observed in some *D. (Proconsul)* and *D. (S.) sivalensis,* and occasionally in living pongids, particularly the orangutan. As noted above, the relatively anterior position of the zygomatic process can also be observed in *Pongo pygmaeus* as well as in *D (S.) sivalensis* and is another reflection of facial shortness.

In his discussion, Leakey (1967, p. 161–162) states,

> It is, however, important to bear in mind that the differences between *Sivapithecus indicus* and *Sivapithecus sivalensis* appear to be marked, and that what is known as *Sivapithecus sivalensis* is possibly not a *Sivapithecus* at all. There seems to be no doubt that the species *Sivapithecus sivalensis* in India may stand much closer to the genus *Ramapithecus* than it does either to *Sivapithecus indicus* or to the true European *Dryopithecus* specimens, or even to . . . *Proconsul.* . . . This can be clearly established by examining the morphology of the molar and premolar teeth.

Leakey illustrates his article with a photograph of casts of the C^1–M^3 series of *D. (S.) sivalensis,* GSI D299/300 (1967, fig. 6c). The excellent illustrations given by Gregory, Hellman, and Lewis (1938), Gregory and Hellman (1926), Lewis (1934), and Prasad (1964) show that, as far as the upper dentitions are concerned, most *"S" sivalensis* and *"S. indicus"* are so similar as to constitute a single species. This species is no more variable than either subfossil or living *Pongo pygmaeus* (Pilbeam, in preparation). *D. (S.) sivalensis* is no more similar to *R. punjabicus* than is "K. africanus" from East Africa. They are superficially similar in that their cingula are either very reduced or totally absent.

Leakey (1967) concludes that the synonymy of *Kenyapithecus* with *Ramapithecus* and of *Sivapithcus africanus* with *D. (S.) sivalensis* must be rejected for the following reason (p. 162); "The diagnosis of *Ramapithecus* which has been given by Simons and Pilbeam states that, in the genus *Ramapithecus* the mandible is 'shallower' than in *Dryopithecus* and *Australopithecus.* This is certainly not true of *Kenyapithecus africanus,* where we have a mandibular fragment which is 39.5mm. deep at the level of the 4th premolar."

This statement involves some peculiar logic. The diagnosis of *R. punjabicus,* which is the diagnosis of a *species,* covered a Late Miocene and Early Pliocene group. Three mandibles are known which can be assigned to this species; these are all three shallow, both absolutely and relatively (see Table 41, p. 111). Although this species *may* contain individuals with deeper mandibles, this cannot be determined until more individuals are known. "Kenyapithecus africanus" is a *different* species and is from the Early Miocene. At least one of the three mandibles referred to this species (NMK 417) is as shallow as any of those referred to *R. punjabicus,* which invalidates the objection.

Since the synonymy of "K. wickeri" with *R. punjabicus* has already been demonstrated, the important point is to establish the relationship of "K. africanus" to *Ramapithecus*; is it ancestral or not? If it is ancestral, ought they to be placed in one genus?

The exact relationship between the Early Miocene and Pongidae discussed in this chapter and Late Miocene *D. (S.) sivalensis* and *D. fontani* cannot yet be accurately established. An African origin for Eurasian *Dryopithecus* is to be expected and some of these Early Miocene specimens make morphologically suitable ancestors. Until more complete material from the Early, Middle, and Late Miocene has been recovered, however, the solution to this problem, and the correct taxonomic allocation of the East African material, must remain open. Simons and I (1965) assigned some of the specimens to *D. (S.) sivalensis,* at that time believing the East African and Indian samples to be contemporaneous. This is now known to be unlikely, the Kenyan material probably being latest Early Miocene in age (see Table 1, p. 17). There are a number of morphological differences too, particularly in the mandibles. At the moment these pongids from East Africa are perhaps best described as *Dryopithecus* sp. indet. Phylogenetic relationship with *R. punjabicus* is improbable; a more probable association is with *D. (S.) sivalensis.*

CHAPTER IX. PONGID EVOLUTION: DISCUSSION AND CONCLUSIONS

AFRICAN DRYOPITHECINES

The *raison d'etre* of this study is the pongid material from Uganda, described in Chapters IV and V. It has been shown that this material is unlikely to be derived from more than a single species, *Dryopithecus (Proconsul) major.* The known fossil remains of this species show many features reminiscent of *Gorilla gorilla,* and thus the species is probably ancestral to the living ape. Comparison of the Ugandan material with that from Songhor and Koru in Kenya has demonstrated that this species is also represented at these sites. Its earliest known occurrence in East African sites is about 20 million years ago, and it probably persisted until at least 16 million years ago. This species, like *G. gorilla,* shows marked sexual size dimorphism; the males are characterized by large, projecting canines and relatively prognathous faces. The dentition exhibits a number of features anticipating those to be seen in gorillas, particularly in the morphology of canines and incisors. Some of the cheek teeth, however, show trends towards the lophodonty and hypsodonty characteristic of *G. gorilla.* The teeth also show many resemblances to other contemporary species of African *Dryopithecus. D. (P.) major* retains cingula on upper and lower molars. Of the three living pongid species, *G. gorilla* retains molar cingula most frequently (Korenhof, 1960; Frisch, 1965).

Dental and cranial changes in this lineage since the Miocene appear to have involved a general increase in size, a small differential hypertrophy of the anterior cheek teeth, increased lophodonty and hypsodonty of the cheek teeth, the loss of cingula, the development of long maxillary alveolar processes surrounding a deep palate, increased facial prognathism, the broadening of the anterior mandibular region, and the appearance of the simian shelf.

The postcranial material of *D. (P.) major* from East Africa shows that this species was approximately chimpanzee-sized, although somewhat more lightly built and active than the living species. The Miocene form was probably an arboreal quadrupedal form, perhaps with some knuckle-walking behavior. Morphologically the forelimbs, thorax, scapular, and vertebral column might have resembled those of quadrupeds like *Ateles* or *Lagothrix* rather than Old World forms like *Colobus* or *Hylobates.* As body size increased, more time would be spent on the ground and knuckle-walking behavior and adaptations would evolve fully.

The gorilla is a mainly herbivorous vegetarian living in thick, lush, rain forest at a variety of altitudes (see Schaller, 1963; Groves, 1967). In particular, the Eastern gorilla (*G. g. beringei* of most authors; *G. G. beringei* and *G. g. manyema* of Groves, 1967) inhabits upland country. *D. (P.) major* has been recovered from deposits at Napak, Moroto, Koru and Songhor. These sites preserve animals which presumably died on the forest-covered slopes of active volcanoes in habitats similar to those occupied by Eastern gorillas today. It is tempting to think that *D. (P.) major* lived in such an environment and that this species was already adapting to the more selectively vegetarian way of life of its Recent descendant. Traces only of *D. (P.) major* have been recovered from the Rusinga Island deposits. The sites on the island represent a variety of environments; savannah, swamp, lacustrine, and riverine.

The pongid material from Rusinga consists mainly of two further species of *D. (Proconsul), D. (P.) africanus* and *D. (P.) nyanzae. D. (P.) africanus* is much smaller than *D. (P.) major,* in size falling between *Symphalangus syndactylus* and *Pan troglodytes paniscus.* It is similar enough to *D. (P.) major* for them to be classified for the moment in the same subgenus. There are differences, however, in the relative proportions of the molars, in the morphology of the symphysis, and in the smoothness of the cranial vault. This last feature is correlated with the orthognathous face and the lightness of the masticatory apparatus in *D. (P.) africanus.* Although the cranial vault is not known in *D. (P.) major,* it is most unlikely that it was also rounded and delicately constructed. The forelimb of *D. (P.) africanus* is known from one tolerably complete specimen from Rusinga, and the species was probably mainly arboreal.

In a number of features—cranial, dental, and postcranial—*D. (P.) africanus* resembles *P. troglodytes* and is possibly ancestral to the living species. This relationship has already been tentatively suggested by a number of workers since Hopwood first described this species in 1933. It is found in Kenya at sites other than Rusinga, but it has not yet been recovered from Uganda. *D. (P.) africanus* is found with *D. (P.) major* at Songhor and Koru and, like living chimpanzees, probably lived in a variety of habitats ranging from savannah and open woodland to forested mountainside. In the Miocene, therefore, both proto-chimpanzees and proto-gorillas were probably small, lightly built, mainly arboreal creatures, the former probably lacking knuckle-walking adaptations. For the moment these two ancestral species are classified in one subgenus, although further material may indicate that they are better separated at the subgeneric level.

The third species, *D. (P.) nyanzae,* in size is midway between the other two species; the smallest individuals overlap *D. (P.) africanus* and the largest *D. (P.) major.* In overall morphology *D. (P.) nyanzae* is most similar to *D. (P.) major,* although it differs in having relatively smaller anterior teeth in general and first molars in particular (see Table 35). In these features *D. (P.) nyanzae* is more primitive than *D. (P.) major. D. (P.) nyanzae* seems to be contemporary with *D. (P.) major,* yet it is probable that this species, or a very similar species, was ancestral to *D. (P.) major. D. (P.) nyanzae* is found in abundance throughout the Rusinga beds, while so far it is virtually absent from the sites at Koru, Songhor, Moroto, and Napak which have yielded *D. (P.) major.* These differences may be due simply to random sampling fluctuations, or may be because there were genuine ecologic differences between the two species. The oldest of these East African sites may be sampled from a time when the evolution of *D. (P.) major* from a species very similar to *D. (P.) nyanzae* was barely completed.

In a number of publications, Leakey (see especially 1963) has proposed that the three species discussed above should be included in a family, Pronconsulidae, separate from the Pongidae. Pongidae would include the living great apes and other species of *Dryopithecus.* The classification of *D. (Proconsul)* has been discussed by Simons and me (1965, p. 105–111), and it has been shown there that the differences between *Dryopithecus* Lartet and *Proconsul* Hopwood cannot be regarded as significant at the generic level.

The characteristics of the various species of *D. (Proconsul)* which differ from those of the living pongids are to be regarded as primitive. Thus, the relatively orthognathous face, narrow symphyseal region, the absence of a simian shelf, the presence of well-developed molar cingula, the relatively small first molars, and the generalized cranial and postcranial morphology can be regarded as foreshadowing conditions seen in the living African great apes. As Remane comments (1965, p. 281), "*Proconsul* unterscheidet sich von den rezenten Pongidae weniger als die miozänen Vertreter vieler anderer Säugertierfamilien von ihren rezenten Arten."

Until recently, in the absence of known Miocene Hominidae, *D. (Proconsul)* has been regarded as some kind of "model" of the pre-Pleistocene hominids. Napier has stated (1963b, p. 185), "It is inevitable that *Proconsul* . . . should be considered in the search for the Tertiary ancestors of . . . Villafranchian hominids. Whatever the final status of *Proconsul* in the systematics of hominid evolution may turn out to be . . . it represents an important structural and functional stage in the phylogeny of hominid locomotion." Since it now seems that two of the *D. (Proconsul)* species are ancestral to the living African apes, or close to that ancestry, and since these Early and Middle Miocene species are almost certainly not ancestral to Late Miocene Hominidae, the viewpoint expressed by Napier should be re-examined. It is true that the forelimb and skull of *D. (P.) africanus* (nondentally, the best known of the species) are in many ways generalized and unspecialized compared with those of living apes. Whether or not Early and Middle Miocene hominids were generalized and unspecialized in the same ways is unknown, and an answer must depend on the recovery of Miocene hominid postcranial material.

One point that is clear; if the relationships suggested in this monograph are correct, then the lineages leading to *P. troglodytes* and *G. gorilla* were probably specifically distinct in the Early Miocene, twenty million years ago. Clark and Leakey (1951, p. 111–112) suggested that *D. (Proconsul)* species were ancestral to the African great apes. The similarities shown by these two living species have led some workers (i.e. Sarich and Wilson, 1967) to assume that their separation is relatively recent. In my view, at least some of these similarities ought now to be regarded as more probably parallelisms. The ancestral species, *D. (P.) africanus* and *D. (P.) major*, are sufficiently similar dentally and facially to be classified in the same subgenus; they are much more similar in these areas than are *P. troglodytes* and *G. gorilla*. This probably applies postcranially, too. It seems taxonomically most sensible to retain the two present-day species in separate genera for the moment, as Schultz (1966) has suggested.

The absence in *D. (Proconsul)* of the posteriorly projecting inferior transverse torus (basal plate or simian shelf) is an obvious point of difference between the Miocene species and their living descendants. As noted above, Leakey (1963, 1965) regards this feature as a major character separating *D. (Proconsul)* species from other pongids. However, if this character is viewed functionally and regarded as an adaptation to stresses in the anterior mandibular region associated with an increase in size of the dentition, particularly the incisors, its significance can be viewed in evolutionary perspective. A fossil species ought not to be removed from the ancestry of a living form simply because it differs in certain relatively minor points. If the differences have reasonable functional explanations, such a course becomes even more absurd. If evolution has occurred, descendants inevitably differ from ancestors.

EURASIAN DRYOPITHECINES

The African dryopithecines come from deposits between 20 and 18 million years old. Younger *Dryopithecus* have been found in European and Asian sites. Those from India have already been mentioned. The first European dryopithecine, *D. fontani,* appears in deposits of late Middle Miocene (Tortonian) age in France and Czechoslovakia; these sites are probably 15 or 16 million years old (see Table 1, p. 17). A number of specimens of *D. fontani* have been described from south-western France and a few teeth from the Vienna Basin in Czechoslovakia. These specimens were noted by Simons and me (1965, p. 83–85). Two specimens, the type mandible of *D. fontani* from St. Gaudens described in 1856 by Lartet, and a referred mandible from the same site described in 1890 by Gaudry, are in the Muséum National d'Histoire Naturelle, Paris. Through the courtesy of the director, M. J.-P. Lehman, I was able to examine these specimens. This work is not an appropriate place for a comprehensive discussion of the European dyropithecines. However, a number of relevant notes on these specimens will be included here.

The type specimen, Paris Museum no. AC 36, consists of right and left horizontal rami, the left with P_3–M_2 and M_3 alveolus, the right with broken C_1, P_3–M_2, and M_3 alveolus. A small fragment of symphysis containing the incisor alveoli is also preserved. This specimen is figured in Piveteau (1957, p. 198). At P_4, the horizontal ramus is deep (34.5 mm) and thin (12.5 mm); posteriorly it shallows and at M_3 is 28.0 mm deep. The tooth row is crowded anteriorly and the overlap between the mesial border of right P_3 and the distal border of C_1 is marked. The canine, first premolars, and second molars fall within the range of *D. (P.) nyanzae,* although P_4 and M_1 are somewhat larger. In view of the inferred trends within the several pongid lineages, this increase in relative size of P_4 and M_1 might be expected in a late Middle Miocene form. In fact, *D. fontani* M_1's are relatively no larger than those of *D. (P.) africanus* and *D. (P.) major* specimens (a point previously overlooked), although they are relatively larger than those of *D. (P.) nyanzae* (see Table 49).

The dentition of AC 36 is very similar to that of *D. (Proconsul);* the molars retain distinct buccal cingula. In both first and second molars the hypoconulid is shifted bucally.

The symphyseal fragment contains the incisor alveoli. The total incisor breadth was not great, 17 or 18 mm only. The incisors were not procumbent. The most superior 20 mm of the anterior part of the symphysis is preserved for some 7 mm on either side of the midline. This part of the anterior symphyseal contour was probably close to being vertical to the occlusal plane. The posterior border of the symphysis is poorly preserved, only the most superior 7 or 8 mm being present. Neither symphyseal thickness nor morphology can be gauged from this fragment.

The second specimen, Paris Museum no. 1872–2 or 1902–12b, has also been figured by Piveteau (1957, p. 198 and 199); an excellent photograph is included by Remane (1965, p. 282). The dentition, although not as crowded as in the type, is nevertheless morphologically and metrically very similar. This specimen has generally not been fully described (except by Remane, 1922), and a number of misconceptions about it are currently in the literature. For example, in 1953 (p. 179), Leakey wrote of *D. fontani,* "The simian shelf is well developed and the rows of cheek-teeth are parallel (for instance, in the specimen from the Middle Miocene of St. Gaudens in France)."

The symphysis of this specimen is fractured anteroposteriorly, and the right tooth row has been pushed lingually. This has affected in particular the more distal teeth. The left horizontal ramus has also been fractured between P_4 and M_1 and the distal part of the molar row rotated lingually. Although the tooth rows appear to be parallel, this is due to distortion. Originally, the internal contours of the tooth rows probably diverged slightly posteriorly; the outer contour would have been more markedly divergent. The tooth rows were probably no more parallel than in *D. (P.) major,* NMK 190,1 for example.

The symphysis is well preserved (see Fig. 3). The anterior margin slopes backward and downward as in *D. (P.) africanus.* The planum alveolare is long and gently sloping like that of *D. (P.) major.* The symphysis is 39.5 mm long and 21.5 mm thick in the midline and is therefore a little smaller than symphyses of supposed female *D. (P.) major,* although the proportions are similar (see dimensions in Chap. VI). What appears to be an inferior lingual torus is present on both horizontal rami below M_1 and M_2; the torus is present in a less developed form in the type and the thickness is probably emphasized in 1872–2 by lingual crushing of the basal parts of the rami. An inferior transverse torus is absent from the midline. This region has been examined microscopically and the absence is almost certainly not due to breakage or crushing. The most posterior part of the cross section is at the level of the superior transverse torus; the cross section of the symphysis is therefore very similar to that of *D. (P.) major.* These specimens show mandibular similarities with *D. (Proconsul),* and also to NMK 76, CMH142, assigned by Leakey (1967) to "Kenyapithecus africanus."

A third mandible of *D. fontani* from St. Gaudens, a left horizontal ramus with C_1 to M_3, was described in 1898 by Harlé. This specimen is illustrated by Piveteau (1957, p. 201). The resemblances between this specimen and some Asian *D. (S.) sivalensis* (e.g., AMNH 19412, see Gregory and Hellman, 1926, p. 23) are particularly marked. Cingula are more marked in the European specimens, however, and they are in this respect more primitive, resembling *D. (Proconsul)* species.

The upper dentition of Middle Miocene *D. fontani* is poorly known. What is preserved resembles that of *D. (S.) sivalensis* (see Gregory and Hellman, 1926, fig. 6B), although lingual cingula may be somewhat better developed.

Some *D. (S.) sivalensis* from the Siwaliks may be as old as Middle Miocene, although the majority of the known specimens are most probably younger than this. *D. (S.) sivalensis* molars tend either to lack cingula entirely or to have only small remnants preserved. The lingual borders of the upper molars bulge lingually, this bulging presumably representing the remains of the lingual cingulum. The buccal borders of the lower molars bulge in a similar way.

THE RELATIONSHIPS OF *DRYOPITHECUS* SPECIES

Although the three subgenera of *Dryopithecus* show varying degrees of expression of the cingulum, this feature is variable within genera and species of a number of mammals (e.g., *Hylobates,* see Frisch, 1965) and the differences do not seem to warrant generic distinction. In basic morphology, the teeth of the various *Dryopithecus* species are closely similar (see Fig. 30).

Table 48 includes ratios of lower molar lengths for various species of fossil hominoids. The first molar is relatively shortest in *D. (P.) nyanzae,* and this is presumably a primitive trait. The ratios in other species of *Dryopithecus,* although similar, are a little higher. If the ratios be compared to those in living pongids, it can be seen that in all lineages the first molars have increased relatively in size.

Table 48 Ratios of molar MDi L of Pongidae and Hominidae

	$(M_1/M_2) \times 100$			$(M_2/M_3) \times 100$		
	n	$\bar{X}$	OR	n	$\bar{X}$	OR
Propliopithecus haeckeli	1	103.1		1	88.9	
Aegyptopithecus zeuxis	2	84.0	82.3- 85.7	1	78.8	
D. (P.) africanus	4	85.2	80.0- 89.9	2	84.1	83.7- 84.5
D. (P.) nyanzae	4	78.2	75.4- 82.3	4	87.5	83.2- 92.8
D. (P.) major	4	86.0	81.7- 90.8	4	85.6	80.3- 93.3
D. sp. (Rs 1967,394)	1	78.2		1	93.8	
D. fontani	2	84.5	84.0- 85.0	2	93.0	92.3- 93.7
D. (S.) sivalensis	9	86.0	80.0- 93.7	7	92.7	83.8- 99.3
P. troglodytes	26	96.5	90.0-104.9	25	107.7	96.5-122.1
G. gorilla	40	89.3	85.3- 97.5	40	98.4	86.5-106.9
Pongo pygmaeus	20	93.3	85.5- 99.2	20	100.1	86.2-108.2
R. punjabicus	1	*90.1		3	96.7	94.4-100.0
Australopithecus africanus	3	88.5	86.4- 90.5	2	104.5	99.3-109.6
Australopithecus robustus	7	91.7	86.8- 97.3	4	95.4	92.5-101.2
Homo erectus	13	98.3	88.6-104.8	11	103.9	92.5-119.0

The ratio of second and third molar lengths is low in *D. (Proconsul)* species, the third molar being relatively elongated. Living pongids have approximately subequal second and third molar lengths, although in *P. troglodytes* M_3 is generally shorter than M_2. This is probably due to a reduction in size of M_3, perhaps quite recently. In *G. gorilla* and *Pongo pygmaeus* the ratio is approximately 100; trends in the lineages leading to these species seem therefore to have included an increase in size of M_2 relative to M_3 (see Appendix 3 for *D. (P.) major–G. gorilla* changes).

Dryopithecus species from the Middle and Late Miocene and Early Pliocene have somewhat longer M_2's relative to M_3 than in *D. (Proconsul)* species. The differences are probably due to the greater geological age of the African species; no doubt the later Miocene African contemporaries of Eurasian *Dryopithecus* would have produced similar ratios. It is of interest to note that the Early Miocene *Dryopithecus* species from Rusinga (Leakey, 1968) has a relatively small M_1, although the relative proportions of M_2 and M_3 are as in Eurasian *Dryopithecus.*

Table 49 includes ratios of M_3 talonid to trigonid breadths. This ratio gives some indication of the distal narrowing of M_3. Examination of the values obtained for living pongids and comparison with their putative ancestors suggests that a more triangular M_3 (hence giving a lower ratio) is primitive. The shape of M_3 is not constant in *D. (Proconsul), D. (P.) major* retaining the more primitive shape compared to the other two species. *G. gorilla* is also the most primitive of the living Pongidae in this character. *D. (S.) sivalensis, D. fontani* and *Pongo pygmaeus* are very similar to each other.

Table 49 Ratio of M_3 (Tal B/Tri B) x 100 in fossil and living pongids

	n	$\bar{X}$	OR
Propliopithecus haeckeli	1	93.1	
Aegyptopithecus zeuxis	1	87.4	
D. (P.) africanus	8	93.4	90.0- 96.4
D. (P.) nyanzae	5	92.4	89.6- 97.8
D. (P.) major	3	86.9	84.5- 89.5
D. fontani	1	94.2	
D. (S.) sivalensis	12	93.7	90.0-100.0
P. troglodytes	10	97.8	92.3-101.9
G. gorilla males	20	89.0	79.8- 99.3
Pongo pygmaeus	6	93.4	89.4- 96.8
R. punjabicus	3	94.2	92.6- 95.5

The functional significance of the changes reflected in these various ratios is not well understood. Presumably, an increase in surface area of the cheek teeth has been selected for in these primates in which crushing and grinding are important activities. As the more anterior smaller molars have increased relatively in size, the three molars have tended to subequality in length.

It is not only cheek teeth which have become enlarged, but incisors too. Table 41, p. 111, included values of the ratio comparing upper central incisor area to the combined areas of first and second molars. The value of this ratio for living pongid species was calculated using mean measurements from Ashton and Zuckerman (1950). These ratios show that the central incisors are relatively larger in living pongids than in *Dryopithecus* species. However, *D. (P.) major* (UMP 62–11) is very close to the mean values for *G. gorilla.* The lineages leading to chimpanzees and orangutans have shown a much greater increase in incisor size since the Miocene, and these living species have relatively much larger incisors than gorillas. One explanation of this might be that the Miocene ancestors of *G. gorilla* were becoming adapted to an herbivorous diet of shoots, stems, and leaves. Increasing adaptation since then has involved a general increase in tooth, jaw, skull, and body size, and some relative increase in size of the anterior cheek teeth. The incisors have increased little in relative size when compared with the rest of the dentition. Morphologic changes of cheek tooth crowns, however, have been important. In both chimpanzees and orangutans, however, the incisors are very large relative to the cheek teeth, see Table 50. Both species are frugivorous rather than herbivorous and large anterior teeth may have been selected for piercing the tough outer covers of fruits. Present-day chimpanzees often use their incisors for this purpose (Walker, personal communication). However, these phylogenetic and functional hypotheses can only be tested with the recovery of more, adequately dated, material, with proper stratigraphic and ecologic controls.

Although the Eurasian *Dryopithecus* species are at present classified in separate subgenera, *D. fontani* from Europe and *D. (S.) sivalensis* from the Siwaliks are closely related and should probably not be separated at the subgeneric level. Similar pairs of genera and species of other mammals are distributed in Europe and Asia during this period, and the two continents should be treated as a continuous land mass (or rather Europe should be regarded as a small westerly projection of Asia). Eurasian Middle Miocene *Dryopithecus* species almost certainly originated in Africa and presumably reached Eurasia no earlier than the Middle Miocene, some 16 or 17 million years ago. None of the known African species of *D. (Proconsul)* are obvious ancestors of the Eurasian species; however, there is a hint of such an ancestor in some of the East African sites, as I noted in the preceding chapter.

Table 50 Ratio (crown area of I^1/crown area M^1 and M^2) x 100 in living Pongidae

P. troglodytes (males)	43.1
P. troglodytes (females)	47.0
G. gorilla (males)	31.4
G. gorilla (females)	30.5
Pongo pygmaeus (males)	50.3
Pongo pygmaeus (females)	51.1

PONGID EVOLUTION

Sarich and Wilson (1967) have attempted to assess the relationships of living hominids and individual pongid species using immunological resemblances in serum albumins. They argue that albumins have evolved at a constant rate and that these proteins can be used as a "clock" which, once calibrated, will give the time of divergence of each living species. Sarich and Wilson conclude that, assuming a cercopithecoid/hominoid dichotomy in the Oligocene (the "clock" is calibrated with paleontological data), the hylobatids diverged from other hominoids ten million years ago, the proto-orangs eight million years ago, while the *Pan, Gorilla,* and *Homo* lineages have split only during the last five million years. More recently Sarich (1968) has revised this date to 3.5 million years.

Sarich and Wilson suggest that living apes and man are descended from a small Miocene dryopithecine which was already a "brachiator," like the gibbon —an arm-swinger with elongated upper limbs and other correlated scapular, thoracic, and lumbar features. They state (1967, p. 1202): "If the view that man and the African apes share a Pliocene ancestor and that all the living Hominoidea derive from a late Miocene form is correct, a number of the problems that have troubled students of this group are resolved. The many features of morphology, particularly in the thorax and upper limbs, which man and the living apes share in varying degrees, but which were not present in the Miocene apes, such as *Dryopithecus*, . . . and *Pliopithecus*, are then seen as due to recent common ancestry and not, as generally accepted, to parallel or convergent evolution." Several objections can be made to this viewpoint.

First, many of the biochemical assumptions may be rather too sweeping. For example, Barnicot, Jolly, and Wade (1967, p. 343–344) note: "An antiserum prepared against a given protein of one species can be used to test sera of other species and the reactions give information about antigenic similarities and differences. However, the relation between antigenic properties and protein structure is by no means fully understood so that the information provided by such immunological tests is much less explicit than chemical analysis." Until amino acid sequences of albumins are better understood, caution in interpreting immunological resemblances should be urged. Also the structure of other proteins should be considered in deriving phylogenies, for not all tell the same story. Barnicot, Jolly and Wade (1967, p. 352–353) have expressed this very well.

> The evidence provided by the structure of a single kind of protein, unique though it may be in the insight it allows into events at the gene level, does not necessarily give an unbiased view of the affinities of whole organisms. An obvious remedy for this is to look at more proteins, however laborious this may be. It is to be anticipated that in some lineages particular proteins will be found to have changed considerably whereas others have changed less. Indeed protein structures will probably prove to be a microcosm in which well-recognized evolutionary phenomena such as convergence and differential rates of change will often be exemplified.
>
> Students of molecular evolution naturally turn to paleontology for a time scale when they wish to calculate rates of change of proteins. To reverse this procedure and seek in proteins an evolutionary clock from which time can be read is likely to be fallacious and no more justifiable than in dealing with morphological characters. Although regularities in rates of structural change of proteins may emerge empirically there is no good reason to assume *a priori* that the underlying forces of mutation and selection pressure have remained constant.

Paleontological evidence should ideally be used as a framework in which the evolution of particular proteins, or morphological characters, can be studied.

Second, the evidence indicates that all Miocene hominoids so far recovered were basically quadrupedal. None of them can be described as "brachiators" in the sense that *Hylobates* is a brachiator.

Third, the paleontological evidence discussed in this paper indicates that, with some probability, proto-*Gorilla* and proto-*Pan* lineages can be traced back to the early Miocene, while early hominids are known from late Miocene deposits. If Sarich and Wilson are correct, these species became extinct, to be replaced later in time by another set of proto-*Gorilla,* proto-*Pan* and pre-*Homo* lineages. This would be a more unlikely set of parallelisms than those which Sarich and Wilson wish to explain away.

Fourth, the trend towards a forelimb-dominated type of locomotor-feeding behavior ("brachiation") in a small branch niche (Napier, 1967) is documented not only in Hominoidea, but in other primate taxa, too. For example, an extinct prosimian, *Palaeopropithecus* (Walker, 1967), and an extinct catarrhine, *Oreopithecus* (Straus, 1963), were both "brachiators." *Ateles* shows parallelistic changes also, particularly in thorax, scapula, and lower trunk. Evidently the trend towards this particular locomotor-feeding adaptation is widespread in primates and progresses to different levels in a number of living and extinct lineages. The various hominoid lineages could plausibly have evolved their "brachiating" adaptations in parallel from a quadrupedal ancestor already committed to the small branch niche.

Fifth, if we assume that the early Pliocene hominoid ancestor (after Sarich and Wilson, 1967) was a small "brachiator" and that the proto-orang of the middle Pliocene was a large "modified brachiator" or "fist-walker" (Tuttle, 1967) we are faced with the problem of transporting these highly arboreal animals, with few if any terrestrial adaptations, from Africa across the Arabian peninsula and continental India to their present forested habitat of Southeast Asia. It is highly unlikely that a forest, or even woodland, connection existed in East Africa and Arabia during the Pliocene (Howell, 1967). In the unlikely event that a common ancestor of the Hominoidea existed in the early Pliocene of Africa, the dispersal of highly arboreal forms like *Hylobates* and *Pongo* across arid terrain at this time seems improbable, to say the least.

In conclusion, the paleontological evidence suggests that the radiation of living hominoids had already occurred in the Miocene. Hominids are known from the late Miocene and one might infer that their ancestors are to be found in still earlier times, already differentiated from ancestral pongids. However, none of the early Miocene species discussed here show any dental or gnathic characters specially typical of hominids, and at present there is no evidence connecting any known early Miocene species with *Ramapithecus.* Nevertheless, hominid dental, gnathic, and (presumably) behavioral characters appear to be more ancient than often supposed, just as the differentiation of living pongid species occurs at an earlier time than has been generally thought.

As a final word I should like to point out that the fossil record of ancestral pongids is by no means as scanty as some recent workers have suggested (see Preface of Washburn and Jay, 1968). Nor can *Dryopithecus* species be written off as merely dental apes, with bodies like those of quadrupedal monkeys (Washburn, 1968). There are "quadrupeds" and then there are "quadrupeds." *Ateles* and *Cercocebus* may both be classified as arboreal quadrupeds, but they differ markedly both in behavior and in morphology. The Cercopithecoidea are a much more homogeneous group in locomotor terms than the Ceboidea, and to believe that, because *Dryopithecus* was a quadruped, it was therefore a cercopithecoid-like quadruped, is to make an unfortunate mistake. All evidence points to a much more flexible, ateline-like, type of quadrupedalism for *Dryopi-*

thecus. Thus hominoid characters of scapula, forelimb, thorax, and vertebral column might already have been to some extent present in "quadrupedal" *Dryopithecus* species. This seems also to have been the case for *Pliopithecus* (Walker, personal communication). This scheme would rule out a gibbon-type Miocene stage in hominoid evolution and would imply that *Pan* and *Gorilla* never went through a long-armed "brachiating" phase.

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Figures 14—31

FIGURE 14. Bivariate plot of P_4 Dryopithecus species, Pan troglodytes, and Gorilla gorilla with 95% equiprobability ellipses.

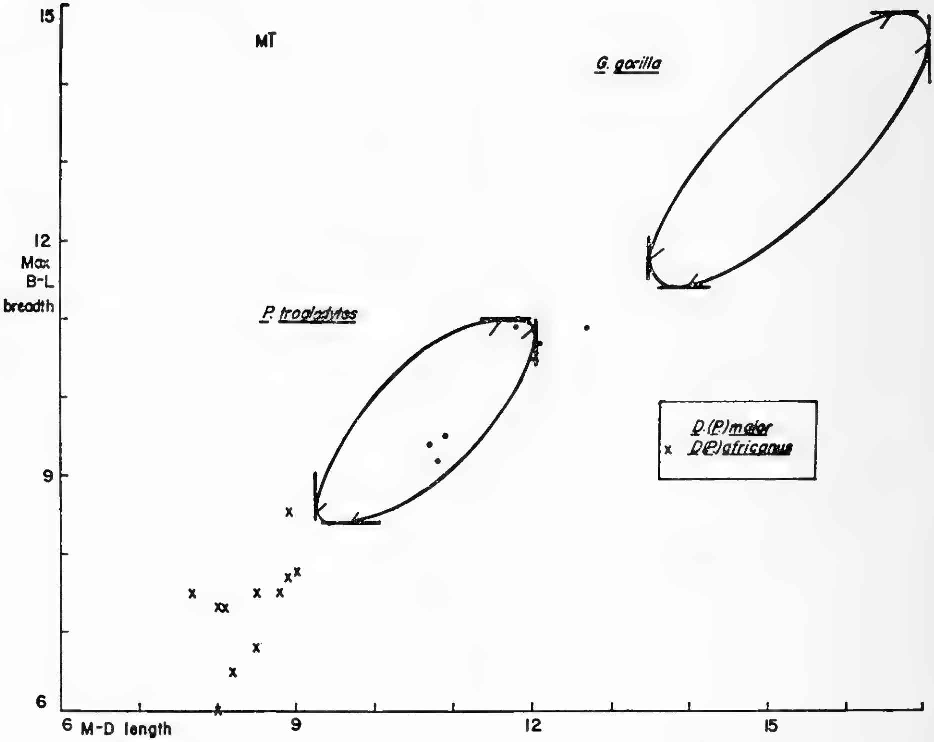


FIGURE 15. Bivariate plot of M_1 *Dryopithecus* species, *Pan troglodytes*, and *Gorilla gorilla* with 95% equiprobability ellipses.

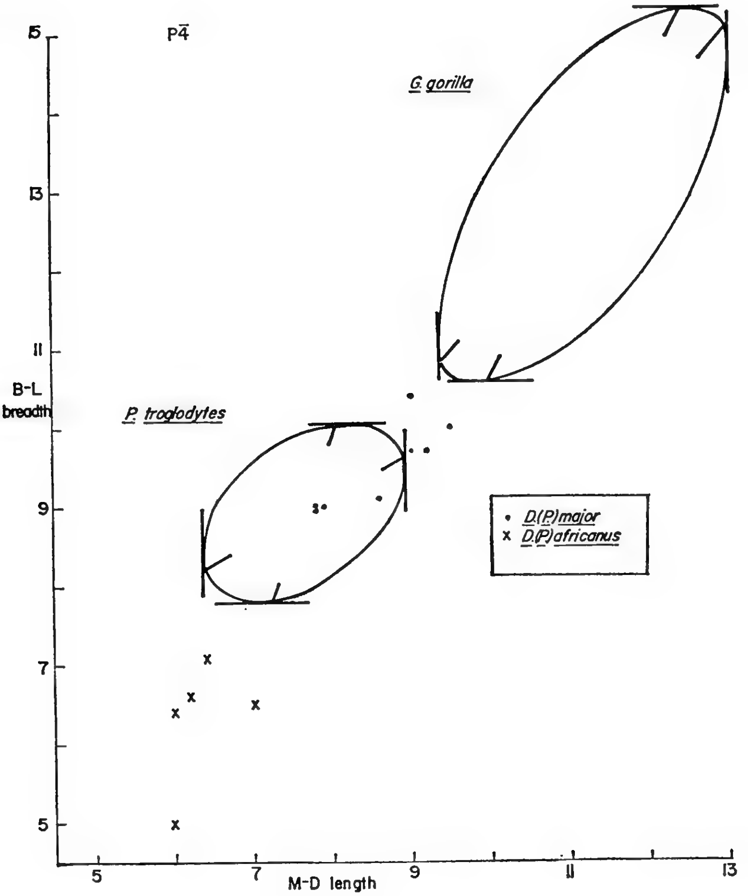


FIGURE 16. Bivariate plot of M_2 *Dryopithecus* species, *Pan troglodytes*, and *Gorilla gorilla* with 95% equiprobability ellipses.

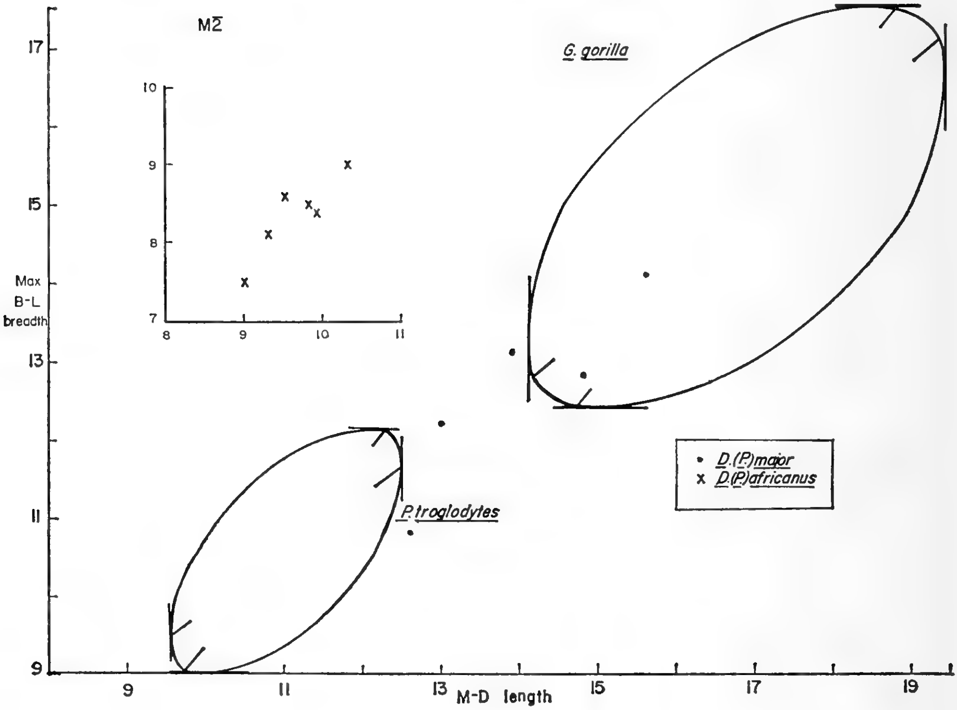
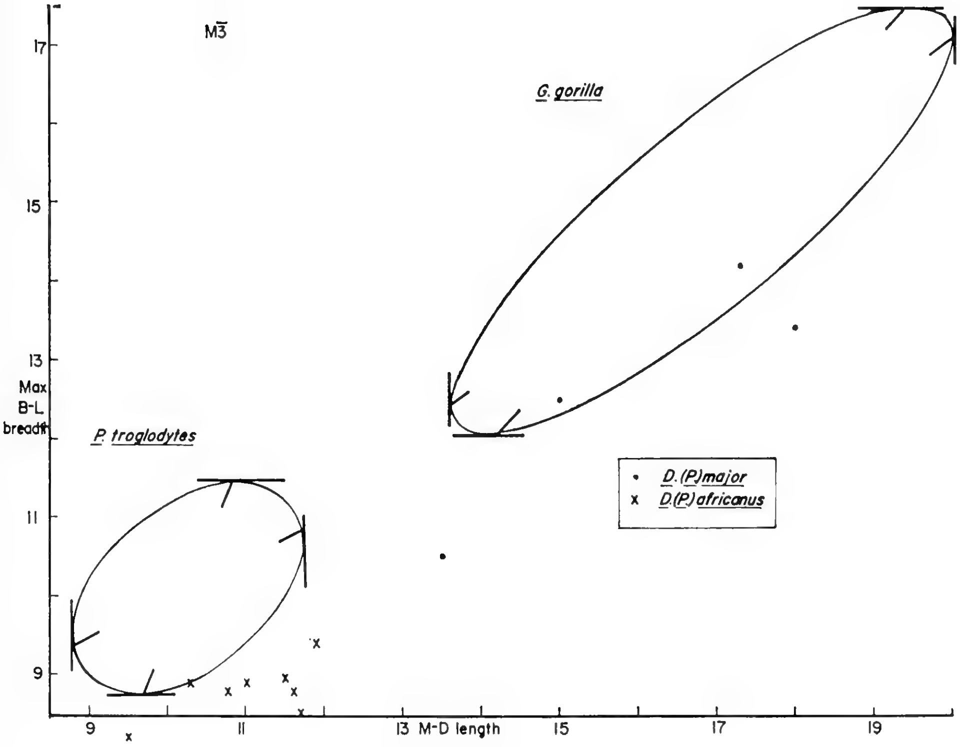


FIGURE 17. Bivariate plot of M_3 *Dryopithecus* species, *Pan troglodytes*, and *Gorilla gorilla* with 95% equiprobability ellipses.



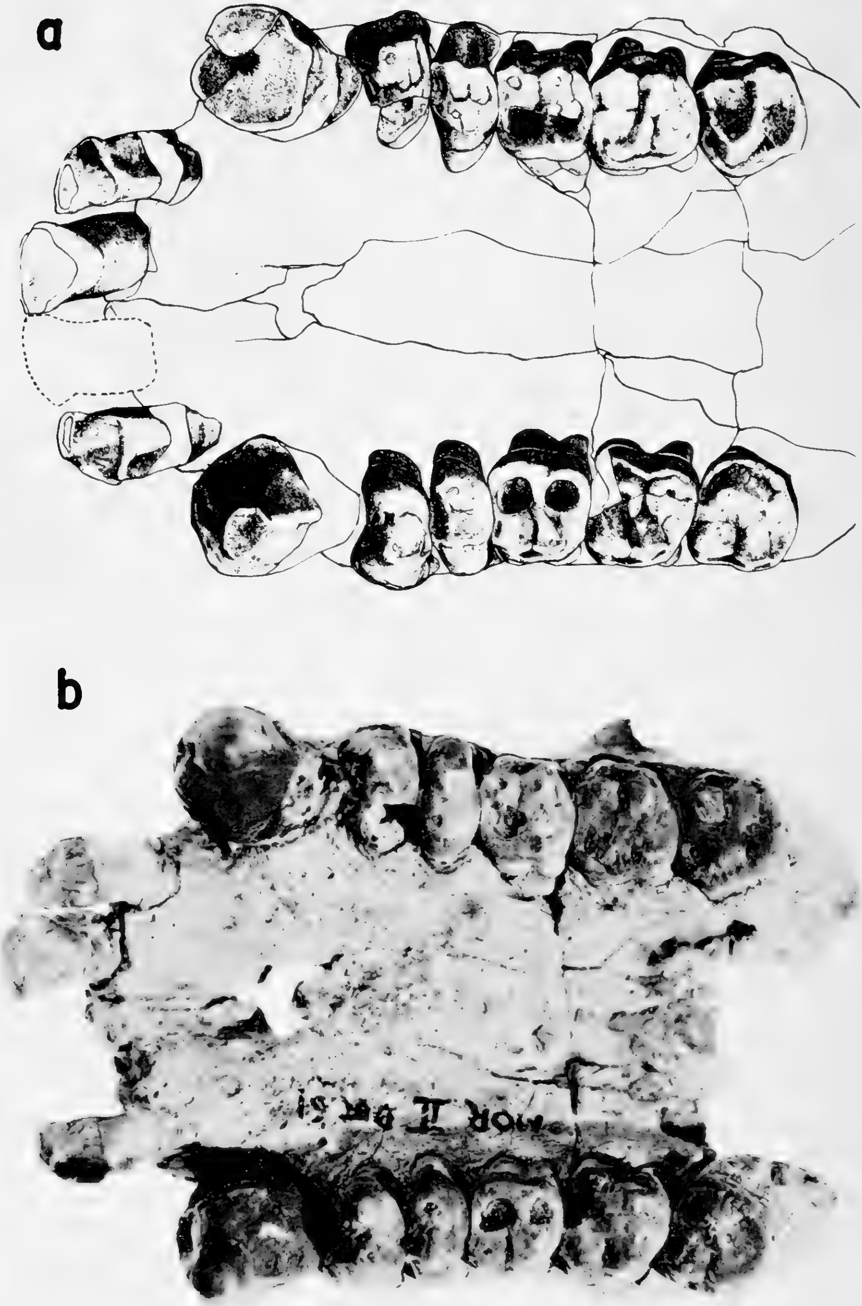


FIG. 18. a and b, occlusal views of UMP 62-11 from Moroto II. × 1.5.

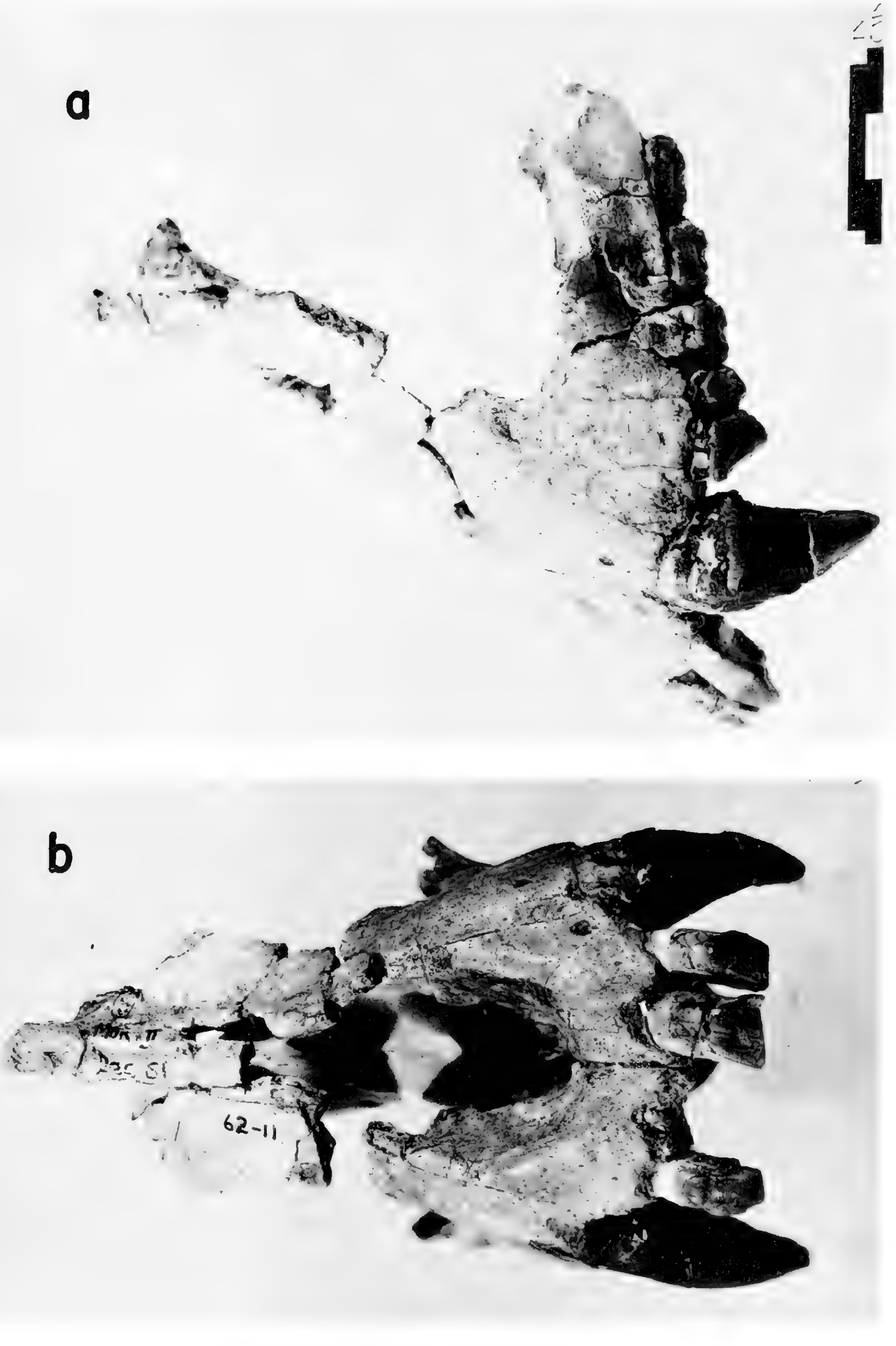


FIG. 19. a, lateral view of UMP 62-11 from Moroto II.
b, anterior view of UMP 62-11 from Moroto II.

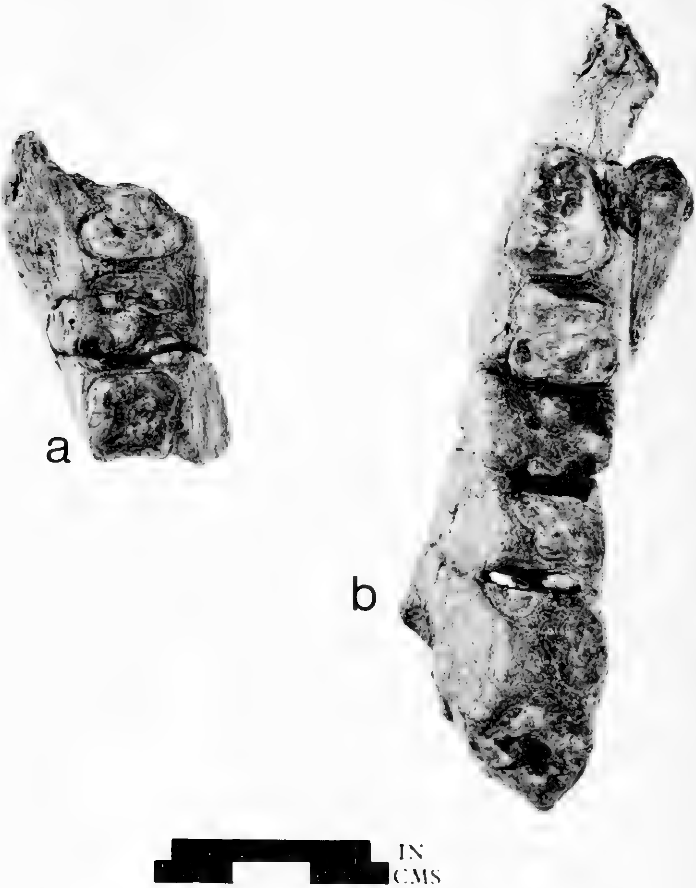


FIG. 20. a, occlusal view of UMP 62-10.
b, occlusal view of UMP 66-01.

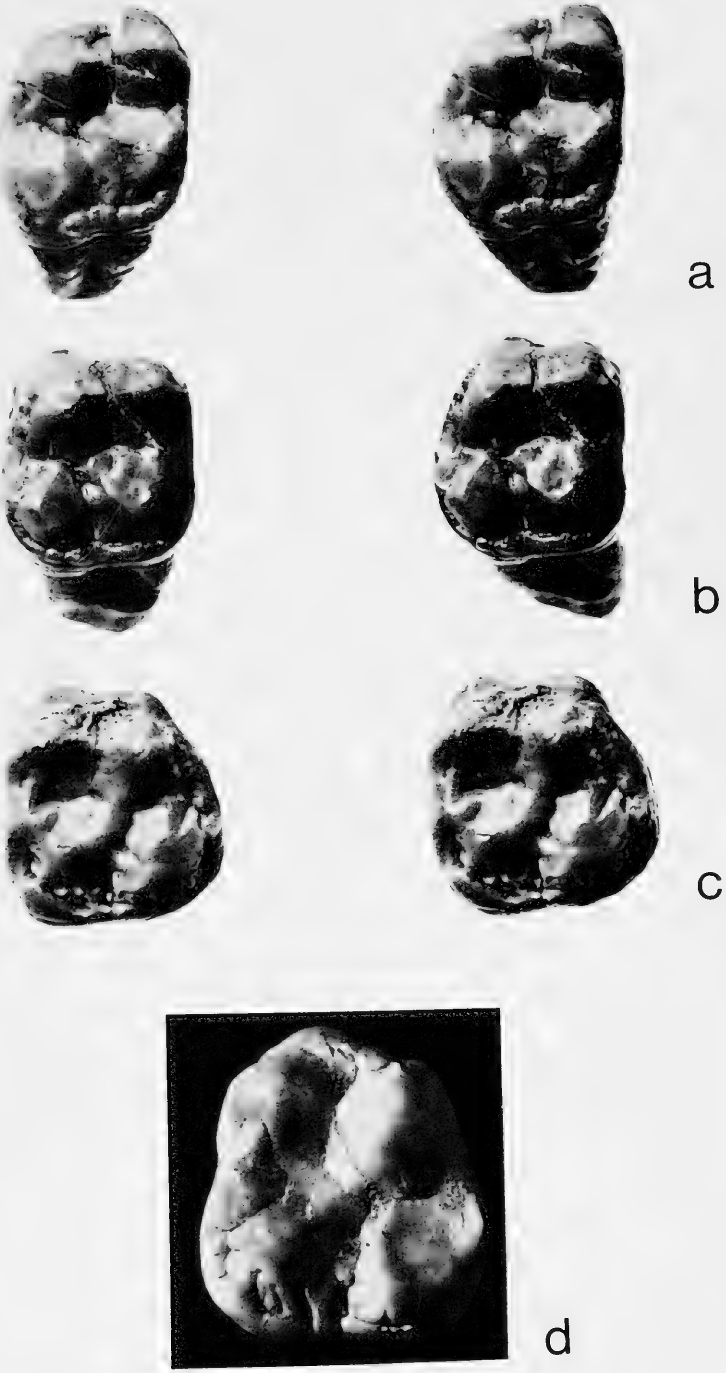


FIG. 21. Occlusal views of:
a, UMP 62-07 from Napak V, stereophotograph. × 2.2.
b, UMP 66-41 from Napak IV, sterephotograph. × 2.1.
c, UMP 62-08 from Napak V, stereophotograph. × 1.9.
d, NMK 405,381 from Songhor. × 2.6.

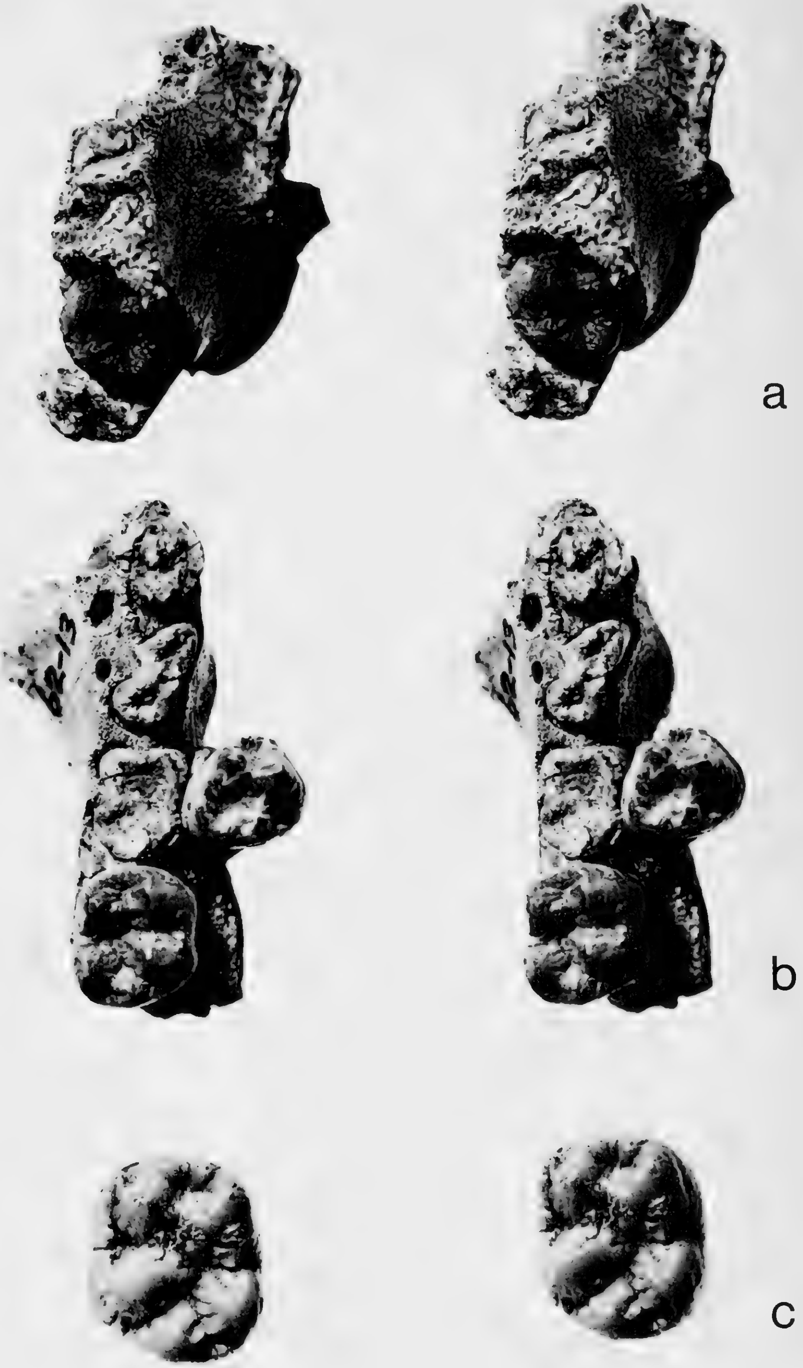


FIG. 22. Stereophotographs, occlusal views of:
a, UMP 62-06 from Napak V. × 1.6.
b, UMP 62-13 from Napak I. × 1.8.
c, UMP 62-14 from Napak I. × 2.3.

FIG. 22. Stereophotographs, occlusal views of:
d, UMP 62-15 from Napak I. × 2.4.
e, UMP 62-16 from Napak I. × 3.0.
f, UMP 66-02 from Napak V. × 3.0.

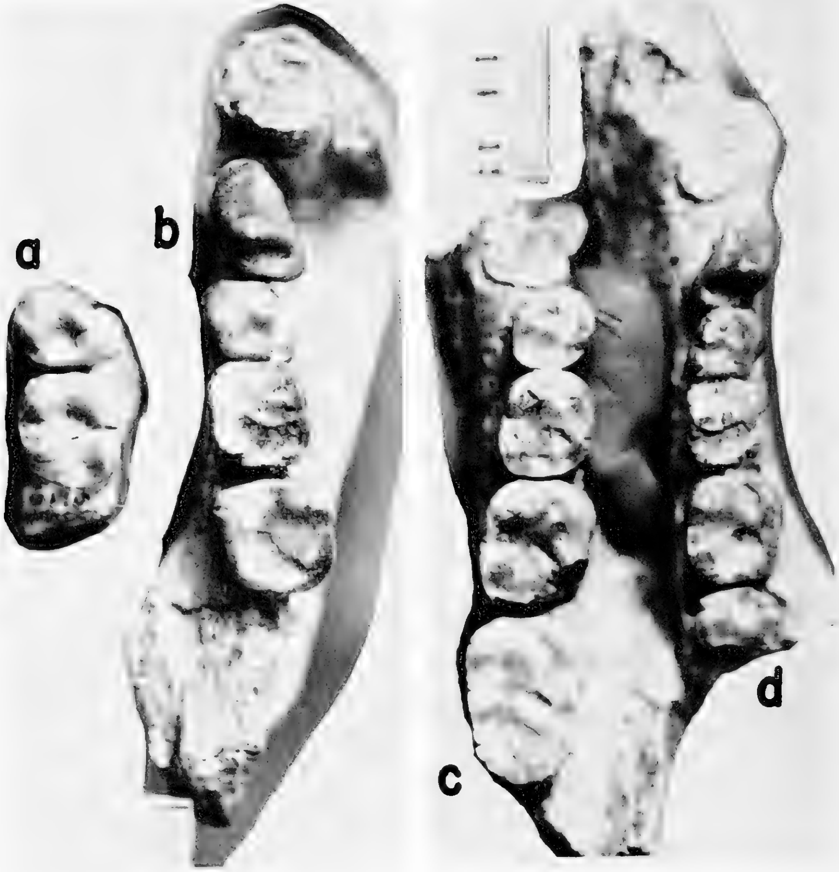


FIG. 23. Occlusal views of:
a, UMP 62-16. × 1.4.
b, BM(NH) M14086. × 1.4.
c, BM(NH) M14086. × 1.2.
d, BM(NH) M16648. × 1.2.

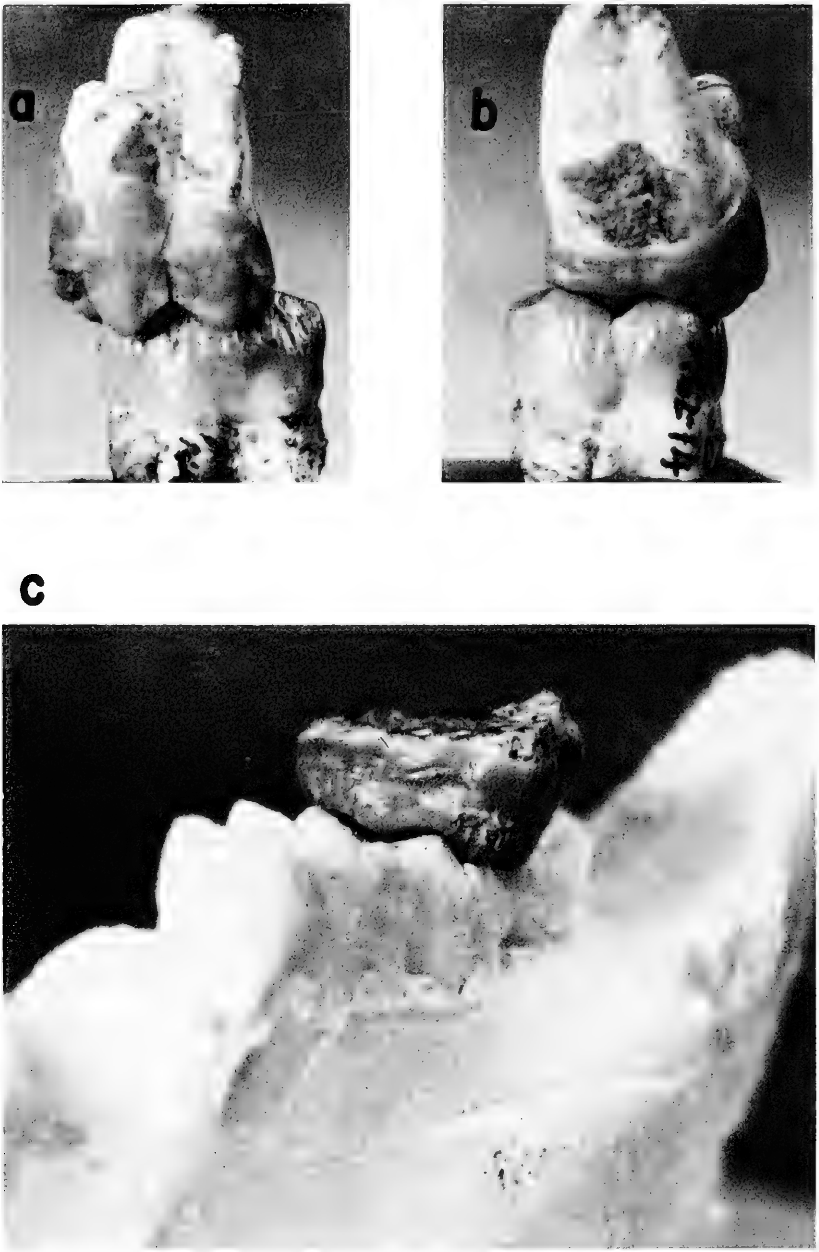


FIG. 24. a, buccal view of UMP 66-41(top) and UMP 62-14. × 2.4.
b, lingual view of UMP 66-41(top) and UMP 62-14. × 2.4.
c, lateral view of UMP 62-08(top) and NMK 190,1. × 2.2.

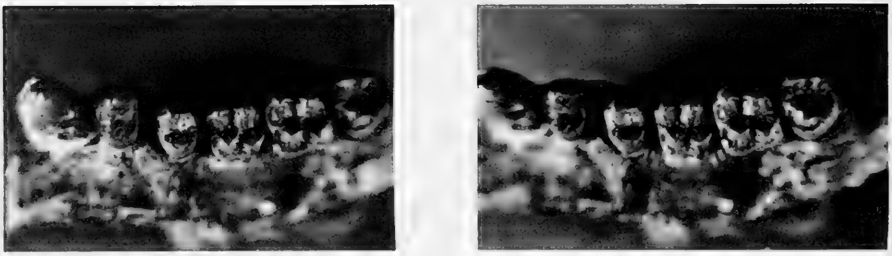


FIG. 25. Stereophotograph, occlusal view of BM(NH) M14084. × .85.

FIG. 26. Occlusal view of NMK 190,1 from Songhor. × 1.1.

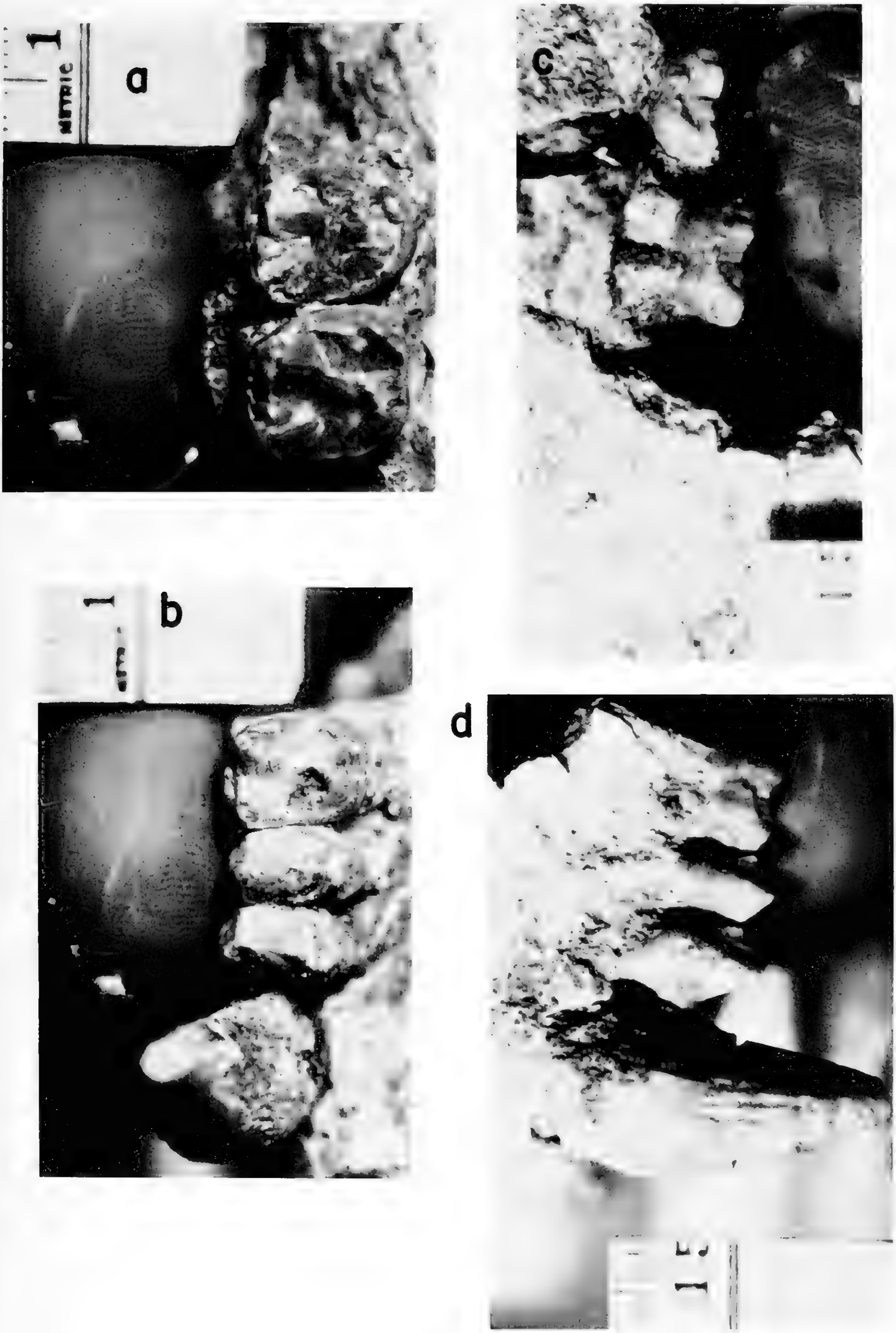


FIG. 27. BM(NH) M16647:

a, M^2, M^3. Occlusal view.
b, C^1, P^3, P^4, M^1. Occlusal view.
c, M^2, M^3. Buccal view.
d, C^1, P^3, P^4, M^1. Buccal view.

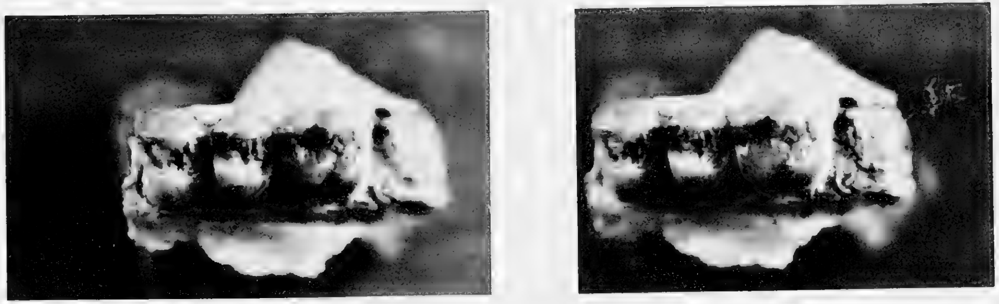


FIG. 28. Stereophotograph, occlusal view of BM(NH) M16649. × 1.6.

FIG. 29. Reconstruction of *Ramapithecus punjabicus*. Right maxilla, YPM 13799. Left maxilla, NMK Ft1272. Left M^3, GSI D186. × 1.6.

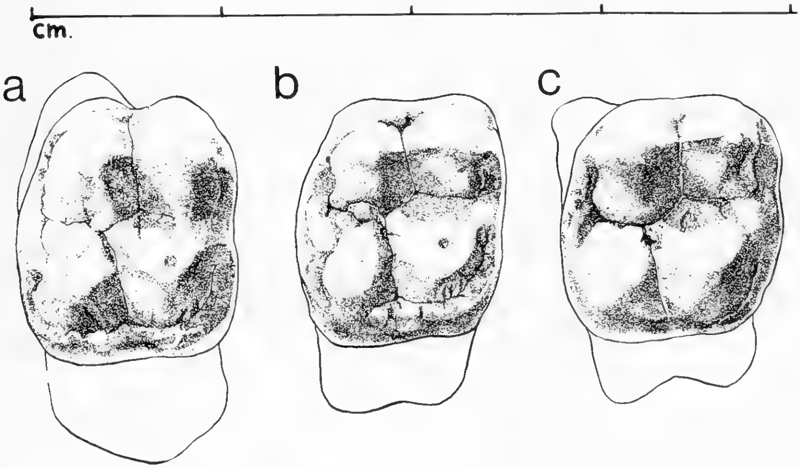


FIG. 30. Occlusal views of:
a, *D.* (*P.*) *major*, UMP 66-41.
b, *D.* (*P.*) *major*, UMP 62-07.
c, *D. indicus*, YPM 13834.

FIG. 31. a, *D.* (*P.*) *africanus.*
b, *Pan paniscus* (with incisor of *Ramapithecus*).
c, *Ramapithecus punjabicus.*
All brought to the same M^1, M^2 length.

APPENDICES

The following abbreviations have been used:

Spec no	Specimen number
Comp no	Computer card number

Material from the following institutions has been used in this study.

CODE	SOURCE
A	Anatomy Museum, Cambridge University
B	Zoology Department, British Museum (Natural History), London
C	Museum of Comparative Zoology, Cambridge University
D	Duckworth Laboratory of Physical Anthropology, Cambridge University
Z	Anthropologisches Institut der Universität, Zurich

APPENDIX 1a *Gorilla gorilla* male maxillae

Comp No		11001	11002	11003	11004	11005	11006	11007
Spec No		Z 6598	Z 4802	Z 6503	Z 4902	Z 6599	Z 6672	Z 6604
C^1	Max L	19.4	20.4	23.0	21.2	20.6	21.7	19.0
	Trans B	16.8	14.0	15.2	16.6	16.4	17.8	15.6
P^3	MDi L	10.5	10.6	11.6	12.0	10.8	11.4	10.5
	Max L	13.2	12.3	13.2	13.0	12.8	12.6	11.4
	BLi B	17.0	15.5	14.8	16.6	16.0	14.3	16.2
P^4	MDi L	10.8	10.8	11.6	11.2	10.7	11.4	11.0
	BLi B	15.8	14.7	15.4	16.8	15.0	14.6	16.0
M^1	MDi L	13.6	14.4	15.3	15.3	14.3	14.4	14.6
	BLi B	16.2	14.3	15.9	15.5	14.3	14.8	16.5
M^2	MDi L	16.3	15.4	17.9	16.8	14.7	16.2	15.8
	BLi B	16.8	16.4	16.9	17.8	15.5	17.0	17.0
M^3	MDi L	15.5	14.6	16.6	15.6	13.2	14.6	15.0
	BLi B	16.3	15.5	16.1	16.9	14.6	14.8	15.8
P^3—M^3	L	68.5	67.0	73.0	70.5	63.5	67.3	67.7
$\underline{I}$	B	39.5	40.4	*44.0	44.5	39.5	*43.0	42.3
C^1	B	78.3	69.4	*76.0	76.5	72.5	*74.0	79.4
P^4	B	70.8	67.8	75.5	73.5	68.3	64.5	78.6
M^3	B	75.8	70.8	76.5	70.2	68.7	68.5	71.3

Comp No		11008	11009	11010	11011	11012	11013	11014
Spec No		Z 6603	Z 6602	Z 6504	B 1939 913	B A25	B 919	B 25.1.4.2
C^1	Max L	23.2	22.3	20.8	19.9	19.2	21.3	23.2
	Trans B	16.6	17.3	16.0	14.8	13.3	16.2	16.7
P^3	MDi L	12.0	10.4	11.4	10.6	10.2	10.9	10.1
	Max L	12.5	12.0	11.7	12.3	11.0	12.2	11.6
	BLi B	15.2	15.4	14.0	15.0	14.3	17.0	16.8
P^4	MDi L	11.8	10.5	10.5	10.6	*10.3	*11.5	*10.8
	BLi B	15.1	15.0	15.2	14.4	14.3	16.0	*15.3
M^1	MDi L	15.8	14.4	14.3	*13.7	*14.4	15.1	*14.1
	BLi B	16.4	15.8	15.6	14.5	16.0	15.8	15.9
M^2	MDi L	17.0	15.3	15.3	*15.0	14.7	16.4	*15.4
	BLi B	16.7	16.6	16.8	16.1	16.3	16.4	16.8
M^3	MDi L	16.5	13.7	14.4	14.7	*14.3	*15.6	15.2
	BLi B	16.8	15.6	16.0	15.4	15.6	16.4	16.6
P^3—M^3	L	72.3	65.8	65.2	64.0	63.5	68.5	65.0
$\underline{I}$	B	-	44.5	44.8	38.5	36.3	40.5	40.7
C^1	B	*82.0	75.2	77.9	68.0	69.0	*68.3	78.0
P^4	B	71.5	*74.0	*73.0	68.8	69.0	66.6	73.2
M^3	B	77.8	71.3	67.7	70.0	68.1	68.3	71.7

APPENDIX 1a, continued

Comp No Spec No		11015 B 48. 436	11016 B 49. 603	11017 D Pr52. 0.3	11018 A G2	11019 A G28	11020 A D2
C^1	Max L	22.0	22.3	20.8	23.2	20.1	20.3
	Trans B	16.5	16.0	15.7	16.8	15.4	15.7
P^3	MDi L	10.0	11.4	9.7	12.2	10.4	11.2
	Max L	11.5	13.2	11.2	12.9	12.6	12.0
	BLi B	14.3	16.4	14.6	16.4	14.9	17.1
P^4	MDi L	11.1	*12.0	10.5	12.2	10.7	11.5
	BLi B	14.4	15.5	14.0	16.1	15.3	16.3
M^1	MDi L	14.8	16.2	14.0	16.7	14.8	16.1
	BLi B	14.1	16.0	14.7	17.4	15.6	17.1
M^2	MDi L	15.2	17.5	14.5	16.5	16.9	17.1
	BLi B	14.3	16.5	15.4	17.8	17.5	18.3
M^3	MDi L	14.5	17.0	15.0	14.7	*14.0	15.7
	BLi B	13.0	16.8	14.7	15.3	15.0	17.2
P^3—M^3	L	64.0	72.0	65.3	68.5	68.1	71.2
$\underline{I}$	B	39.2	42.6	42.6	43.3	*41.3	44.0
C^1	B	67.5	75.8	78.2	*79.0	80.1	*75.5
P^4	B	66.0	73.4	70.4	74.4	72.9	73.1
M^3	B	*70.5	76.6	65.8	71.4	75.3	71.5

		n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	95% CL
C^1	Max L	20	21.20 ± 0.31	1.37	6.55	19.0-23.2	18.32-24.08
	Trans B	20	15.97 ± 0.24	1.07	6.81	13.3-17.8	13.72-18.22
P^3	MDi L	20	10.90 ± 0.16	0.72	6.68	9.7-12.2	9.39-12.41
	Max L	20	12.28 ± 0.16	0.70	5.75	11.0-13.2	10.81-13.75
	BLi B	20	15.59 ± 0.23	1.04	6.79	14.0-17.1	13.41-17.77
P^4	MDi L	20	11.08 ± 0.12	0.55	5.02	10.3-12.2	9.92-12.24
	BLi B	20	15.26 ± 0.17	0.74	4.94	14.0-16.8	13.71-16.81
M^1	MDi L	20	14.82 ± 0.19	0.85	5.83	13.6-16.7	13.03-16.61
	BLi B	20	15.62 ± 0.21	0.92	5.98	14.1-17.4	13.69-17.55
M^2	MDi L	20	16.00 ± 0.22	1.00	6.34	14.5-17.9	13.90-18.10
	BLi B	20	16.65 ± 0.20	0.90	5.49	14.3-18.3	14.76-18.54
M^3	MDi L	20	15.02 ± 0.22	0.97	6.53	13.2-17.0	12.98-17.06
	BLi B	20	15.72 ± 0.22	1.00	6.46	13.0-17.2	13.62-17.82
P^3—M^3	L	20	67.60 ± 0.67	3.00	4.50	63.5-73.0	61.30-73.90
$\underline{I}$	B	19	41.66 ± 0.55	2.38	5.78	36.3-44.8	38.64-46.68
C^1	B	20	75.03 ± 1.00	4.46	6.02	67.5-82.0	65.65-84.41
P^4	B	20	71.27 ± 0.79	3.55	5.05	64.5-78.6	63.81-78.73
M^3	B	20	71.39 ± 0.75	3.36	4.77	65.8-77.8	64.34-78.44

APPENDIX 1b <u>Gorilla gorilla</u> female maxillae

Comp No		12001	12002	12003	12004	12005	12006	12007
Spec No		Z 1224	Z 6592	Z 5685	Z 6595	Z 6593	Z Fr. Cam.	Z 6600
C^1	Max L	14.6	14.3	14.6	15.9	14.4	14.6	12.5
	Trans B	10.7	12.7	12.5	11.5	11.7	12.2	10.3
P^3	MDi L	10.0	11.4	9.5	10.7	10.9	10.2	10.2
	Max L	11.4	11.8	9.9	11.6	11.2	11.0	10.3
	BLi B	15.3	16.3	14.3	16.4	16.2	15.6	13.5
P^4	MDi L	10.3	11.0	9.5	10.7	11.2	10.5	9.7
	BLi B	14.6	15.4	13.8	15.3	15.6	15.5	12.8
M^1	MDi L	14.3	14.5	12.7	15.4	15.3	13.5	13.4
	BLi B	14.8	15.5	14.8	15.8	15.5	15.7	13.4
M^2	MDi L	14.8	15.5	13.5	16.8	15.4	13.8	14.2
	BLi B	15.7	16.8	15.3	16.9	17.2	15.8	14.0
M^3	MDi L	14.7	13.8	12.0	15.9	15.3	13.0	12.6
	BLi B	15.2	16.8	14.6	15.4	16.2	15.8	13.0
P^3—M^3 L		62.3	65.6	57.7	67.8	67.7	52.3	59.8
$\overline{I}_1$	B	37.7	39.7	33.8	*37.0	40.2	37.7	36.3
C^1	B	59.0	74.0	65.3	58.8	52.7	57.2	45.2
P^4	B	63.8	71.2	66.7	*63.0	68.3	61.5	57.3
M^3	B	66.4	68.4	65.3	67.3	67.4	*66.7	56.6

Comp No		12008	12009	12010	12011	12012	12013	12014
Spec No		Z 6676	Z 6840	Z 6594	B 1939 935	B 1939 925	B 1939 933	B 1939 936
C^1	Max L	14.4	14.2	14.3	15.5	15.1	13.2	14.1
	Trans B	11.4	11.2	11.5	11.4	12.0	10.1	11.0
P^3	MDi L	10.2	10.4	9.7	10.5	10.3	9.8	9.2
	Max L	10.3	11.0	10.6	11.2	12.7	10.3	10.1
	BLi B	13.9	14.3	14.6	15.5	15.6	13.5	15.0
P^4	MDi L	10.4	10.3	10.3	*11.6	*11.9	9.7	11.0
	BLi B	13.9	14.2	14.2	15.6	-	13.2	15.6
M^1	MDi L	14.0	13.5	13.5	14.5	15.0	13.4	14.3
	BLi B	15.4	14.2	15.0	15.7	15.2	13.3	14.1
M^2	MDi L	14.1	15.4	13.4	15.6	16.2	14.7	15.0
	BLi B	15.7	16.4	14.7	16.6	15.5	14.6	16.0
M^3	MDi L	12.8	14.4	12.2	14.5	13.2	13.5	14.4
	BLi B	13.4	15.6	13.6	16.0	*14.0	13.6	15.9
P^3—M^3 L		61.3	64.4	50.5	*65.0	66.0	*62.0	62.7
$\overline{I}_1$	B	37.8	37.6	39.5	*38.0	42.6	34.0	36.7
C^1	B	52.2	57.2	61.4	60.0	63.6	53.5	60.3
P^4	B	52.5	61.7	61.2	62.8	*66.5	55.6	64.5
M^3	B	*66.0	63.4	58.3	*62.0	*65.0	58.2	67.1

APPENDIX 1b, continued

Comp No Spec No		12015 B 1939 927	12016 A G20	12017 A G21	12018 A G22	12019 A G23	12020 A G30
C^1	Max L	16.0	14.0	14.1	15.3	14.3	14.6
	Trans B	11.0	10.5	10.2	11.2	10.3	10.2
P^3	MDi L	10.6	9.4	9.5	10.9	10.7	9.8
	Max L	11.6	10.9	10.3	11.2	11.3	10.5
	BLi B	15.1	14.3	13.0	14.6	14.8	14.6
P^4	MDi L	10.9	10.3	10.4	11.7	10.2	9.8
	BLi B	14.9	13.8	12.6	14.6	14.6	14.2
M^1	MDi L	14.4	13.1	14.3	14.7	14.1	13.4
	BLi B	15.1	14.0	13.6	14.8	15.1	14.7
M^2	MDi L	15.2	13.7	15.2	15.0	15.0	13.8
	BLi B	16.0	14.2	14.6	16.0	15.5	15.1
M^3	MDi L	14.0	12.8	13.8	14.1	13.4	13.3
	BLi B	16.3	13.8	13.3	14.9	14.3	14.2
P^3—M^3	L	64.1	59.3	60.8	64.5	*60.0	58.0
I	B	39.0	37.4	35.5	41.7	37.3	34.1
C^1	B	55.0	*59.5	53.2	63.3	54.5	57.3
P^4	B	62.0	58.6	57.4	62.3	58.2	65.5
M^3	B	63.8	60.8	63.5	63.6	*62.0	66.8

		n	$\overline{X} \pm SE$	SD	V_{cor}	OR	95% CL
C^1	Max L	20	14.50 ±0.18	0.82	5.72	12.5–16.0	12.78–16.22
	Trans B	20	11.18 ±0.18	0.79	7.12	10.1–12.7	9.52–12.84
P^3	MDi L	20	10.20 ±0.13	0.58	5.79	9.2–11.4	8.98–11.44
	Max L	20	10.96 ±0.15	0.69	6.35	9.9–12.7	9.51–12.41
	BLi B	20	14.82 ±0.21	0.95	6.50	13.0–16.4	12.82–16.82
P^4	MDi L	20	10.57 ±0.15	0.68	6.50	9.5–11.9	9.14–12.00
	BLi B	19	14.44 ±0.22	0.94	6.62	12.6–15.6	12.46–16.42
M^1	MDi L	20	14.07 ±0.16	0.74	5.31	12.7–15.4	12.52–16.62
	BLi B	20	14.79 ±0.17	0.78	5.32	13.3–15.8	13.15–16.43
M^2	MDi L	20	14.82 ±0.20	0.92	6.27	13.4–16.8	12.84–16.75
	BLi B	20	15.63 ±0.20	0.90	5.86	14.0–17.2	13.74–17.52
M^3	MDi L	20	13.69 ±0.23	1.01	7.45	12.0–15.9	11.57–15.81
	BLi B	20	14.80 ±0.26	1.16	7.95	13.0–16.8	12.36–17.24
P^3—M^3	L	20	61.59 ±1.02	4.57	7.51	50.5–67.8	51.99–71.19
I	B	20	37.68 ±0.53	2.36	6.34	33.8–42.6	32.72–42.64
C^1	B	20	58.16 ±1.34	6.00	10.45	45.2–74.0	44.96–71.36
P^4	B	20	62.03 ±1.02	4.54	7.41	52.5–71.2	52.48–71.58
M^3	B	20	63.93 ±0.76	3.39	5.38	56.6–68.4	56.81–71.05

APPENDIX 1c *Gorilla gorilla* male mandibles

	Comp No Spec No	11001 Z 6598	11002 Z 4802	11003 Z 6503	11004 Z 4902	11005 Z 6599	11006 Z 6672	11007 Z 6604	11008 Z 6603	11009 Z 6602	11010 Z 6504	11011 B 1939 913	11012 B A25	11013 B 919	11014 B 25. L 4. 2
C_1	Max L	18.2	17.2	19.5	18.2	18.6	19.3	16.3	20.2	19.5	17.0	17.4	15.0	16.0	19.1
	Trans B	14.0	12.9	13.7	15.0	13.8	14.6	13.0	15.3	15.5	15.2	13.2	12.0	14.0	14.4
P_3	Max L	18.6	17.3	18.5	15.7	18.6	17.5	16.5	18.5	18.5	16.4	17.7	*15.1	18.0	17.7
	Trans B	12.2	10.9	11.5	13.2	12.6	10.7	13.5	13.8	12.8	12.3	12.0	10.4	10.3	11.9
P_4	MDi L	11.4	11.2	12.3	11.3	10.6	12.3	11.6	12.7	11.2	11.4	*11.5	*10.5	*11.5	*11.0
	BLi B	14.2	12.8	14.0	13.8	13.3	13.4	14.0	14.4	13.4	12.4	12.5	12.2	13.0	13.0
M_1	MDi L	15.4	15.3	16.4	15.8	14.8	15.5	15.3	16.8	15.4	15.2	*15.0	*15.0	16.2	15.0
	Max B	13.6	12.5	14.4	13.5	13.5	13.4	13.9	14.3	13.3	13.5	12.6	13.1	13.4	13.3
	Tri B	13.4	12.3	14.4	13.5	13.5	13.4	13.9	14.3	13.3	13.5	12.3	13.0	13.4	13.1
	Tal B	13.6	12.5	13.7	13.4	13.4	13.3	13.6	13.9	13.0	13.2	12.6	13.1	13.3	13.3
M_2	MDi L	17.3	16.4	18.6	17.4	15.3	17.4	17.8	19.2	16.1	17.0	*16.2	*16.1	*17.6	17.0
	Max B	15.5	15.2	16.2	16.0	14.6	16.1	16.1	16.8	15.2	15.2	15.2	14.5	15.4	15.7
	Tri B	14.5	14.6	16.2	16.0	14.6	16.1	16.1	16.8	15.2	15.2	14.6	14.5	15.4	15.7
	Tal B	15.5	15.2	15.6	15.8	14.1	15.5	15.3	16.2	14.2	14.6	16.2	13.7	14.4	15.4
M_3	MDi L	18.4	17.7	18.6	16.5	16.0	18.2	16.2	19.2	18.6	18.4	*17.1	17.2	18.0	19.0
	Max B	15.0	14.5	16.1	14.6	14.5	16.4	15.0	17.5	15.8	15.2	14.5	14.9	15.6	15.9
	Tri B	15.0	14.5	16.1	14.6	14.5	16.4	15.0	17.5	15.8	15.2	14.5	14.9	15.6	15.9
	Tal B	13.8	14.4	14.3	12.4	13.4	14.6	13.3	15.2	12.6	13.5	13.8	12.3	14.0	14.9
P_3-M_3	L	79.5	76.4	83.4	75.2	74.3	79.5	77.6	85.4	*77.0	73.5	75.0	71.4	78.3	76.3
$\bar{I}$	B	27.5	25.7	31.8	26.8	26.8	28.3	28.3	30.8	29.6	30.0	27.3	27.3	28.2	29.0
C_1	B	*54.0	51.3	61.2	55.8	55.3	58.4	55.3	64.6	*59.0	63.4	53.0	52.6	50.6	57.6
P_4	B	*59.0	57.3	64.6	62.8	*60.0	56.8	59.7	64.4	*64.8	*63.0	59.2	61.2	58.2	62.1
M_3	B	*68.0	*68.0	69.6	64.6	*66.0	*67.0	68.4	71.2	68.0	*65.0	64.3	65.4	65.2	66.4
P_4	D	*42.0	*35.0	*51.0	42.5	*46.0	43.8	*46.0	*49.0	42.3	44.6	46.0	39.8	43.4	49.3
	T	*20.0	21.5	*21.0	-	*21.0	20.0	-	-	23.3	-	-	-	-	-
M_3	D	*40.0	35.7	*48.0	*41.0	38.6	41.5	*40.0	45.8	40.5	43.8	45.2	39.8	43.4	45.2
	T	27.5	23.5	33.3	24.5	*25.0	25.6	30.5	32.8	26.3	27.3	28.0	24.6	25.8	28.4
Ment for D		*29.0	21.5	31.5	24.5	*30.0	28.5	27.5	32.2	27.3	28.5	25.0	22.0	26.3	30.2

APPENDIX 1c, continued

Comp No Spec No		11015 B 48. 436	11016 B 49. 603	11017 D Pr52. 0.3	11018 A G2	11019 A G28	11020 A D2	n	$\bar{X}$ ± SE	SD	V_{cor}	OR	95% CL
C_1	Max L	18.1	19.7	18.3	19.2	18.0	17.1	20	18.10 ± 0.31	1.37	7.66	15.0-20.2	15.22-20.98
	Trans B	13.9	13.7	13.3	15.1	14.1	14.4	20	14.06 ± 0.20	0.91	6.57	12.0-15.5	12.15-15.97
P_3	Max L	17.6	18.2	16.5	17.3	18.3	17.4	20	17.50 ± 0.22	1.00	5.97	15.1-18.6	15.40-19.60
	Trans B	11.4	12.6	11.6	13.2	12.1	11.4	20	12.05 ± 0.25	1.12	9.42	10.3-13.8	9.70-14.40
P_4	MDi L	*11.8	13.0	11.4	12.5	11.4	12.4	20	11.65 ± 0.15	0.68	5.90	10.5-13.0	10.22-13.18
	BLi B	13.5	13.7	13.4	14.3	12.7	13.3	20	13.37 ± 0.14	0.64	4.90	12.2-14.4	12.03-14.71
M_1	MDi L	15.9	16.2	15.2	16.2	16.0	16.8	20	15.67 ± 0.14	0.61	3.95	14.8-16.8	14.39-16.95
	Max B	13.2	13.2	13.6	13.9	13.9	14.0	20	13.51 ± 0.11	0.48	3.63	12.5-14.4	11.50-14.52
	Tri B	13.1	13.2	13.4	13.9	13.9	14.0	20	13.44 ± 0.12	0.55	4.14	12.3-14.4	12.28-14.60
	Tal B	13.2	13.0	13.6	13.8	13.7	13.8	20	13.35 ± 0.09	0.38	2.91	12.5-13.9	12.55-14.15
M_2	MDi L	*16.5	19.0	17.0	18.2	18.3	18.0	20	17.32 ± 0.23	1.04	6.10	15.3-19.2	15.14-19.50
	Max B	14.6	16.0	15.0	15.2	16.0	15.7	20	15.51 ± 0.14	0.61	3.98	14.5-16.8	14.19-16.83
	Tri B	14.6	16.0	15.0	15.2	16.0	15.7	20	**15.40 ± 0.16	0.70	4.60	14.5-16.8	13.98-16.95
	Tal B	14.2	15.3	14.5	14.6	15.3	14.5	20	15.01 ± 0.16	0.72	4.85	13.7-16.2	13.45-16.57
M_3	MDi L	16.4	18.5	16.5	18.2	17.8	17.5	20	17.60 ± 0.22	1.00	5.77	16.0-19.2	15.50-19.70
	Max B	14.1	16.2	14.7	15.3	15.4	15.3	20	15.33 ± 0.18	0.82	5.41	14.1-17.5	13.55-17.11
	Tri B	14.1	16.2	14.7	15.3	15.4	15.3	20	15.33 ± 0.18	0.82	5.41	14.1-17.5	13.55-17.11
	Tal B	13.3	14.1	13.6	13.5	12.5	12.6	20	13.61 ± 0.19	0.84	6.26	12.3-15.2	11.99-15.23
P_3 -M_3 L		74.1	79.6	73.3	79.6	79.0	80.0	20	77.42 ± 0.78	3.48	4.55	71.4-85.4	70.11-84.73
$\bar{I}$	B	25.0	30.0	28.2	29.7	28.0	30.2	20	28.43 ± 0.39	1.73	6.15	25.0-31.8	24.80-32.06
C_1	B	50.0	53.2	54.0	56.3	58.6	62.2	20	56.32 ± 0.95	4.24	7.62	50.0-64.6	47.41-65.23
P_4	B	57.4	63.6	61.0	64.3	59.5	62.6	20	61.08 ± 0.59	2.63	4.37	56.8-64.8	56.56-66.60
M_3	B	56.6	73.2	62.9	69.7	70.5	71.5	20	67.08 ± 0.82	3.68	5.59	56.6-73.2	59.35-75.81
P_4	D	39.0	42.0	43.5	43.1	45.0	37.8	20	43.56 ± 0.87	3.89	9.05	35.0-51.0	35.39-51.73
	T	-	-	-	-	-	-						
M_3	D	38.0	41.8	40.8	43.2	44.0	36.5	20	41.64 ± 0.71	3.19	7.77	35.7-48.0	34.94-48.34
	T	26.2	25.5	27.0	27.1	30.0	23.9	20	27.16 ± 0.62	2.75	10.26	23.5-33.3	21.38-32.94
Ment for D		23.6	27.4	28.5	28.9	29.4	24.5	20	27.17 ± 0.67	2.99	11.16	21.5-32.2	20.89-33.45

APPENDIX 1d <u>Gorilla gorilla</u> female mandibles

Comp No		12001	12002	12003	12004	12005	12006	12007	12008	12009	12010
Spec No		Z 1224	Z 6592	Z 5685	Z 6595	Z 6593	Z Fr. Cam.	Z 6600	Z 6676	Z 6840	Z 6594
C_1	Max L	*13.5	13.8	13.4	14.6	14.4	13.2	12.0	13.0	13.2	12.7
	Trans B	9.6	10.7	11.4	11.0	10.3	10.7	10.3	11.5	10.6	10.7
P_3	Max L	15.2	16.4	14.3	15.7	16.0	14.6	15.4	14.0	15.2	14.6
	Trans B	11.0	10.8	9.8	11.4	10.4	11.2	8.2	11.0	11.5	11.4
P_4	MDi L	10.2	11.6	9.8	11.0	10.2	10.6	11.3	10.6	11.3	10.6
	BLi B	10.5	13.6	11.7	13.7	14.4	13.0	11.2	12.4	14.2	12.8
M_1	MDi L	14.6	14.6	14.5	16.5	15.3	14.6	13.6	15.2	15.2	15.2
	Max B	12.5	13.5	12.6	14.0	13.7	13.2	11.8	13.4	13.4	13.4
	Tri B	12.3	13.5	12.6	14.0	13.6	12.2	11.6	13.2	13.0	13.4
	Tal B	12.5	13.3	12.4	13.7	13.7	13.2	11.8	13.4	13.4	12.9
M_2	MDi L	16.2	17.0	15.3	17.7	16.4	16.5	14.7	16.0	17.8	15.6
	Max B	14.2	16.5	13.5	16.0	15.2	15.2	12.8	14.3	16.0	14.0
	Tri B	14.2	16.5	13.3	16.0	15.2	14.7	12.7	14.3	16.0	14.0
	Tal B	13.7	15.0	13.5	15.2	15.0	15.2	12.8	14.3	16.0	13.6
M_3	MDi L	15.7	16.4	15.2	17.2	16.8	17.2	14.2	15.4	18.2	14.6
	Max B	14.2	15.5	13.4	15.6	15.7	15.8	12.4	14.2	16.2	13.7
	Tri B	14.2	15.5	13.4	15.6	15.7	15.8	12.4	14.2	16.2	13.7
	Tal B	13.3	13.3	12.0	13.6	15.0	13.3	11.6	13.3	15.5	11.7
P_3 -M_3	L	*72.0	*75.0	70.7	*77.0	74.8	*71.0	66.6	*70.0	75.4	69.3
$\overline{I}$	B	24.9	*29.0	26.3	25.4	29.8	*26.0	24.7	27.6	24.9	28.3
C_1	B	43.3	*54.0	47.4	45.3	*46.0	42.8	40.8	*48.0	43.2	43.7
P_4	B	43.7	*62.0	*53.0	43.5	*58.0	*42.0	47.8	55.2	52.2	51.3
M_3	B	61.4	64.5	57.3	44.3	66.4	*64.0	53.2	62.4	61.6	64.2
P_4	D	37.2	*42.0	39.3	38.5	37.6	36.3	33.6	38.3	40.4	35.8
M_3	D	35.5	39.2	36.4	36.4	36.4	37.8	*35.0	34.7	39.2	34.4
	T	25.4	23.4	28.5	25.7	23.8	27.0	23.5	25.8	26.7	24.7
Ment for D		20.8	30.6	25.4	24.6	27.5	23.4	19.5	26.6	28.8	24.2

APPENDIX 1d, continued

Comp No Spec No		12011 B 1939 935	12012 B 1939 925	12013 B 1939 933	12014 B 1939 936	12015 B 1939 927	12016 A G20	12017 A G21	12018 A G22	12019 A G23	12020 A G30
C_1	Max L	13.6	12.6	11.3	-	13.2	-	11.8	12.4	12.1	12.4
	Trans B	10.3	10.5	9.1	-	10.4	-	9.2	9.8	9.9	9.9
P_3	Max L	15.2	15.9	13.7	15.0	16.0	14.4	13.7	13.8	14.1	14.2
	Trans B	10.5	11.4	8.9	10.0	11.1	9.8	9.1	9.7	10.1	9.9
P_4	MDi L	11.0	12.1	10.6	11.3	10.8	10.3	10.8	10.4	10.7	*10.3
	BLi B	12.4	13.4	11.0	12.7	13.2	11.3	12.0	11.9	12.6	12.3
M_1	MDi L	15.0	15.6	14.3	15.2	15.5	14.6	15.0	14.1	14.7	14.3
	Max B	12.1	13.7	11.6	12.5	13.5	11.8	12.2	11.9	12.4	12.7
	Tri B	12.1	13.3	11.6	12.5	13.5	11.8	11.8	11.3	12.1	12.7
	Tal B	12.1	13.7	11.4	12.5	13.2	11.7	12.2	11.9	12.4	12.1
M_2	MDi L	*15.7	17.1	16.2	16.0	*16.8	15.5	16.3	15.8	15.7	15.1
	Max B	14.7	15.1	13.2	14.4	15.7	13.5	13.0	12.8	13.9	14.2
	Tri B	14.7	15.1	13.2	14.4	15.7	13.5	13.0	12.6	13.9	14.2
	Tal B	13.8	14.9	13.0	14.1	14.6	12.1	12.9	12.8	13.0	13.4
M_3	MDi L	15.2	*17.1	15.4	15.7	18.0	14.7	15.8	15.2	15.6	16.4
	Max B	13.9	14.0	13.3	14.1	14.6	12.8	13.2	13.1	13.7	14.4
	Tri B	13.9	14.0	13.3	14.1	14.6	12.8	13.2	13.1	13.7	14.4
	Tal B	12.1	13.4	12.0	12.6	12.3	10.8	11.2	11.6	11.3	13.5
P_3 -M_3	L	70.2	74.9	66.9	70.5	75.5	68.6	69.2	68.8	68.6	65.7
$\overline{I}$	B	25.8	28.8	25.2	25.6	27.0	27.5	23.2	*24.0	28.8	25.0
C_1	B	44.3	50.1	42.1	-	43.8	*43.8	41.4	*42.0	44.3	*44.0
P_4	B	54.2	58.1	49.1	54.3	55.7	51.8	50.3	51.6	*51.0	51.0
M_3	B	61.1	62.8	62.8	64.8	64.7	60.5	62.6	58.6	*64.0	60.4
P_4	D	36.9	39.9	31.0	33.5	36.1	34.8	34.6	34.3	33.0	36.4
M_3	D	36.8	37.0	-	36.2	36.3	32.1	31.7	33.0	29.1	32.6
	T	22.0	25.0	21.7	23.4	24.2	25.1	26.0	23.2	22.7	26.7
Ment for D		22.0	26.4	21.0	21.0	22.0	20.8	21.2	22.1	20.7	25.4

APPENDIX 1d, continued

		n	$\bar{X} \pm SE$	SD	V_{cor}	OR	95% CL
C_1	Max L	18	13.00 ± 0.21	0.88	6.88	11.3-14.6	11.13-14.87
	Trans B	18	10.33 ± 0.16	0.66	6.50	9.1-11.5	8.93-11.73
P_3	Max L	20	14.87 ± 0.19	0.85	7.24	13.7-16.4	13.08-16.66
	Trans B	20	10.36 ± 0.21	0.94	9.19	8.2-11.5	8.39-12.33
P_4	MDi L	20	10.76 ± 0.12	0.54	5.05	9.8-12.1	9.63-11.89
	BLi B	20	12.52 ± 0.24	1.06	8.61	10.5-14.4	10.30-14.74
M_1	MDi L	20	14.88 ± 0.14	0.63	4.29	13.6-16.5	13.56-16.20
	Max B	20	12.80 ± 0.17	0.75	6.00	11.6-14.0	11.22-14.38
	Tri B	20	12.61 ± 0.18	0.79	6.38	11.3-14.0	10.95-14.27
	Tal B	20	12.68 ± 0.16	0.73	5.86	11.4-13.7	11.15-14.21
M_2	MDi L	20	16.22 ± 0.18	0.81	5.09	14.7-17.8	14.52-17.92
	Max B	20	14.41 ± 0.25	1.18	7.85	12.8-16.5	11.93-16.89
	Tri B	20	14.36 ± 0.25	1.14	8.01	12.6-16.5	11.96-16.76
	Tal B	20	13.95 ± 0.23	1.04	7.58	12.1-16.0	11.77-16.13
M_3	MDi L	20	16.00 ± 0.25	1.12	7.08	14.2-18.2	13.65-18.35
	Max B	20	14.19 ± 0.24	1.08	7.71	12.4-16.2	11.92-16.46
	Tri B	20	14.19 ± 0.24	1.08	7.71	12.4-16.2	11.92-16.46
	Tal B	20	12.67 ± 0.28	1.24	9.91	10.8-15.5	10.07-15.27
P_3 —M_3	L	20	71.04 ± 0.75	3.33	4.75	65.7-77.0	64.04-78.04
$\overline{I}$	B	20	26.39 ± 0.41	1.86	7.12	23.2-29.8	22.49-30.29
C_1	B	20	44.74 ± 0.74	3.24	7.35	40.8-54.0	37.94-51.54
P_4	B	19	52.23 ± 1.09	4.76	9.23	42.0-62.0	42.23-62.23
M_3	B	19	61.96 ± 0.71	3.10	5.06	53.2-66.4	54.45-68.47
P_4	D	20	36.50 ± 0.62	2.77	7.69	31.0-42.0	30.68-42.32
M_3	D	19	35.25 ± 0.60	2.61	7.50	29.1-39.2	29.77-41.73
	T	20	24.73 ± 0.40	1.79	7.32	21.7-28.5	20.97-28.49
Ment for D		20	23.70 ± 0.69	3.11	13.27	19.5-30.6	17.17-30.23

APPENDIX 1e *Pan troglodytes* male maxillae

Comp No Spec No		21001 Z	21002 Z	21003 Z	21004 Z	21005 Z	21006 Z	21007 Z
C^1	Max L	12.9	14.9	15.3	14.0	12.5	13.6	15.6
	Trans B	10.6	9.6	13.0	10.4	10.0	10.5	13.2
P^3	MDi L	6.8	7.6	7.4	7.2	7.6	7.2	7.4
	Max L	7.0	8.3	7.4	8.0	8.6	8.0	7.8
	BLi B	11.0	10.4	11.3	-	10.3	10.2	10.7
P^4	MDi L	6.6	6.8	7.2	6.6	7.3	7.5	7.6
	BLi B	9.8	9.6	10.7	-	10.4	9.8	10.5
M^1	MDi L	9.5	9.2	10.4	9.8	10.2	9.6	10.6
	BLi B	10.6	10.4	11.2	-	10.8	10.7	11.7
M^2	MDi L	9.6	9.6	10.0	9.3	10.4	9.8	10.5
	BLi B	11.2	11.0	11.7	-	11.5	11.5	12.3
M^3	MDi L	-	9.0	8.2	-	-	* 9.8	9.4
	BLi B	-	11.0	10.5	-	-	12.0	11.3
P^3—M^3 L		41.6	42.4	43.3	42.4	47.3	43.3	46.2
$\underline{I}$	B	37.6	*37.0	36.4	35.6	39.9	34.4	40.2
C^1	B	57.0	56.5	56.6	58.8	56.3	59.0	61.6
P^4	B	55.7	58.4	55.8	56.6	53.8	55.0	62.3
M^3	B	57.2	60.4	53.2	53.5	49.5	53.8	57.8

Comp No Spec No		21008 Z	21009 Z	21010 Z	21011 B 87 12.2	21012 D Pr53. 0.2	21013 A P15	21014 C E 7117A
C^1	Max L	15.4	15.4	13.4	*12.0	12.3	14.3	14.0
	Trans B	12.2	11.9	11.4	* 8.7	9.6	10.8	10.7
P^3	MDi L	7.5	7.4	6.5	* 8.0	8.0	6.4	6.7
	Max L	8.5	7.4	7.5	* 8.7	9.1	8.1	8.4
	BLi B	10.8	10.7	10.2	*10.0	11.1	* 9.4	10.0
P^4	MDi L	7.2	7.2	6.7	* 7.0	7.0	6.8	7.0
	BLi B	10.2	10.5	10.2	*10.0	10.5	10.3	* 9.8
M^1	MDi L	10.4	9.5	10.2	*10.6	* 9.5	10.2	9.0
	BLi B	11.7	11.2	11.3	*11.6	-	11.7	10.9
M^2	MDi L	11.0	10.0	11.3	10.4	11.1	9.3	10.0
	BLi B	11.7	11.6	12.4	11.6	12.8	11.6	11.2
M^3	MDi L	9.3	9.5	9.3	8.6	10.3	8.7	9.3
	BLi B	12.2	10.7	12.0	* 8.8	11.7	10.3	10.8
P^3—M^3 L		44.3	42.3	43.7	44.1	46.0	41.6	42.3
$\underline{I}$	B	38.6	38.2	36.5	38.6	38.7	38.5	34.9
C^1	B	57.9	60.2	57.8	55.7	59.2	62.3	57.8
P^4	B	60.5	56.5	58.3	59.4	*60.5	57.6	56.6
M^3	B	56.2	55.5	57.2	56.8	58.2	56.1	54.2

APPENDIX 1e, continued

		n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	95% CL
C^1	Max L	14	13.96 ± 0.33	1.23	8.95	12.0-15.6	11.33-16.59
	Trans B	14	10.90 ± 0.35	1.31	12.21	8.7-13.2	8.10-13.70
P^3	MDiL	14	7.26 ± 0.13	0.50	7.05	6.4- 8.0	6.19- 8.33
	Max L	14	8.06 ± 0.16	0.59	7.46	7.0- 9.1	6.80- 9.32
	BLi B	13	10.47 ± 0.15	0.53	5.14	9.4-11.3	9.32-11.62
P^4	MDi L	14	7.04 ± 0.08	0.32	4.56	6.6- 7.6	6.35- 7.73
	BLi B	13	10.18 ± 0.10	0.35	3.47	9.6-10.7	8.42-10.94
M^1	MDi L	14	9.91 ± 0.14	0.53	5.43	9.0-10.6	8.78-11.04
	BLi B	12	11.15 ± 0.13	0.47	4.27	10.4-11.7	10.12-12.18
M^2	MDi L	14	10.16 ± 0.17	0.65	6.47	9.3-11.3	8.77-11.55
	BLi B	13	11.70 ± 0.14	0.51	4.47	11.0-12.8	10.60-12.80
M^3	MDi L	11	9.22 ± 0.18	0.58	6.45	8.2-10.3	7.94-10.50
	BLi B	11	10.98 ± 0.30	1.00	9.30	8.8-12.2	9.78-12.18
P^3—M^3 L		14	43.63 ± 0.48	1.78	4.16	41.6-47.3	39.82-47.44
I	B	14	37.46 ± 0.46	1.72	4.66	34.4-40.2	33.78-41.14
C^1	B	14	58.34 ± 0.53	1.99	3.47	55.7-62.3	54.08-62.50
P^4	B	14	57.64 ± 0.64	2.39	4.23	53.8-62.3	52.53-62.75
M^3	B	14	55.69 ± 0.72	2.69	4.92	49.5-60.4	49.93-61.47

APPENDIX 1f <u>Pan troglodytes</u> female maxillae

Comp No Spec No		22001 Z	22002 Z	22003 Z	22004 Z	22005 Z	22006 Z
C^1	Max L	10.9	11.7	11.2	11.7	11.0	12.2
	Trans B	8.7	9.2	8.6	8.2	9.0	8.8
P^3	MDi L	6.9	6.4	6.7	7.2	7.0	7.3
	Max L	8.0	7.5	8.0	8.3	8.0	8.3
	BLi B	9.8	10.0	10.6	10.3	11.0	10.8
P^4	MDi L	6.8	7.3	6.8	7.0	6.6	7.3
	BLi B	9.8	10.2	10.5	10.3	10.2	10.8
M^1	MDi L	9.4	9.5	9.6	10.5	9.5	10.6
	BLi B	9.9	11.7	11.7	11.0	10.6	11.7
M^2	MDi L	9.7	9.6	9.8	10.2	9.3	10.7
	BLi B	10.2	12.4	12.0	11.2	11.4	12.2
M^3	MDi L	9.5	–	8.4	9.2	8.4	9.2
	BLi B	10.6	–	11.2	10.3	10.9	11.3
P^3–M^3 L		43.5	43.3	42.3	44.8	40.8	*46.0
$\bar{I}$	B	34.4	35.6	36.4	34.7	35.6	*38.0
C^1	B	57.3	*55.0	56.3	53.2	*58.0	56.8
P^4	B	52.6	59.3	58.7	58.4	*59.0	*59.0
M^3	B	56.7	*55.5	60.8	*58.0	56.5	*60.0

Comp No Spec No		22007 Z	22008 Z	22009 Z	22010 Z	22011 B 1939 3366	22012 A P9
C^1	Max L	10.8	11.4	10.5	12.0	11.2	10.7
	Trans B	8.9	–	9.3	9.2	9.0	8.6
P^3	MDi L	7.0	7.5	6.3	7.3	7.3	7.3
	Max L	8.0	8.0	6.8	7.8	8.5	8.0
	BLi B	10.3	–	10.4	11.8	11.0	9.9
P^4	MDi L	6.7	7.2	6.6	7.4	7.0	7.1
	BLi B	9.5	–	10.2	10.4	10.1	9.6
M^1	MDi L	10.4	10.6	9.4	9.4	9.8	9.3
	BLi B	11.7	–	10.8	11.2	11.3	11.7
M^2	MDi L	9.6	10.8	9.8	10.4	10.7	9.0
	BLi B	11.7	–	10.7	11.4	11.6	11.0
M^3	MDi L	–	9.0	8.7	8.9	10.3	8.5
	BLi B	–	–	10.0	10.7	12.0	10.8
P^3–M^3 L		*42.0	45.9	43.0	43.8	45.0	42.6
$\bar{I}$	B	36.3	36.8	36.5	39.6	36.0	34.3
C^1	B	56.5	51.2	54.8	55.4	50.8	50.0
P^4	B	60.6	57.6	57.2	58.0	53.2	56.7
M^3	B	*59.0	55.5	57.2	58.0	50.7	54.0

APPENDIX 1f, continued

		n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	95% CL
C^1	Max L	12	11.28 ± 0.15	0.53	4.84	10.5-12.2	10.11-12.45
	Trans B	11	8.86 ± 0.10	0.33	3.77	8.2- 9.3	8.12- 9.60
P^3	MDi L	12	7.02 ± 0.11	0.38	5.54	6.3- 7.5	6.18- 7.86
	Max L	12	7.93 ± 0.13	0.44	5.62	6.8- 8.5	6.96- 8.90
	BLi B	11	10.54 ± 0.18	0.59	5.71	9.8-11.8	9.22-11.86
P^4	MDi L	12	6.98 ± 0.08	0.28	4.13	6.6- 7.4	6.36- 7.60
	BLi B	11	10.15 ± 0.12	0.27	3.89	9.5-10.8	9.55-10.75
M^1	MDi L	12	9.83 ± 0.15	0.53	5.48	9.3-10.6	8.66-11.00
	BLi B	11	11.21 ± 0.18	0.59	5.41	9.9-11.7	9.89-12.53
M^2	MDi L	12	9.97 ± 0.17	0.59	6.01	9.0-10.8	8.67-11.27
	BLi B	11	11.44 ± 0.20	0.65	5.83	10.2-12.4	9.99-12.89
M^3	MDi L	10	9.01 ± 0.19	0.59	6.67	8.4-10.3	7.68-10.34
	BLi B	9	10.87 ± 0.20	0.59	5.56	10.0-12.0	9.51-12.23
P^3 -M^3	L	12	43.58 ± 0.46	1.60	3.74	40.8-46.0	40.06-47.10
$\overline{I}$	B	12	36.18 ± 0.44	1.51	4.27	34.3-39.6	32.86-39.50
C^1	B	12	54.61 ± 0.78	2.70	5.05	50.0-58.0	48.67-60.55
P^4	B	12	57.53 ± 0.69	2.39	4.25	52.6-60.6	52.27-62.79
M^3	B	12	56.83 ± 0.79	2.74	4.92	50.7-60.8	50.80-62.86

APPENDIX 1g *Pan troglodytes* male mandibles

Comp No		21001	21002	21003	21004	21005	21006	21007	21008	21009	21010	21011	21012	21013	21014	n	$\bar{X}$ ± SE	SD	V_{cor}	OR	95% CL
Spec No		Z	Z	Z	Z	Z	Z	Z	Z	Z	Z	B 87 12.2	D Pr53, 0.1	A P15	C E 7117A						
C_1	Max L	11.6	12.8	15.3	12.8	12.2	12.4	13.3	13.8	14.8	14.6	11.2	14.0	-	12.0	13	13.12±0.35	1.27	9.83	11.2-15.3	10.38-15.86
	Trans B	9.6	9.3	12.2	10.6	10.6	10.6	10.4	10.7	11.4	11.2	9.0	11.2	*11.5	10.4	14	10.62±0.24	0.88	8.43	9.0-12.2	8.64-12.60
P_3	Max L	10.8	11.7	11.2	10.7	10.2	11.8	10.8	11.6	11.4	11.0	11.0	12.1	10.3	10.3	14	11.06±0.16	0.60	5.49	10.2-12.1	9.78-12.34
	Trans B	7.8	7.5	8.2	7.2	9.8	7.5	8.0	8.0	8.4	8.2	8.1	8.9	8.2	7.1	14	8.06±0.19	0.69	8.77	7.1- 9.8	6.58- 9.54
P_4	MDi L	6.8	7.2	8.0	7.0	7.3	8.0	7.7	8.5	7.5	7.8	9.0	8.8	7.4	8.0	14	7.79±0.17	0.65	8.55	6.8- 9.0	6.40- 9.18
	BLi B	8.7	8.3	9.3	8.9	9.8	9.0	8.8	9.2	9.2	8.8	9.2	9.8	8.5	*8.4	14	8.99±0.12	0.46	5.22	8.3- 9.8	8.00- 9.98
M_1	MDi L	10.3	10.2	10.8	10.3	11.3	10.7	10.2	10.6	11.3	10.4	11.4	12.2	*10.4	10.1	14	10.73±0.16	0.61	5.78	10.1-12.2	9.42-12.04
	Max B	9.6	8.8	9.8	9.6	10.2	9.6	9.4	9.7	10.2	9.8	10.7	11.0	9.9	9.0	14	9.81±0.16	0.59	6.11	8.8-11.0	8.55-10.07
	Tri B	9.6	8.5	9.2	9.5	9.9	8.8	9.0	9.3	9.6	9.4	10.0	10.9	9.9	8.9	14	9.46±0.16	0.61	9.70	8.5-10.9	8.15-10.77
	Tal B	9.4	8.8	9.8	9.6	10.2	9.6	9.4	9.7	10.2	9.8	10.7	11.0	9.6	9.0	14	9.77±0.16	0.60	9.90	8.8-11.0	8.48-11.06
M_2	MDi L	10.7	10.2	11.3	10.6	12.0	11.0	11.2	10.8	11.8	10.7	11.6	12.6	10.7	10.4	14	11.11±0.18	0.68	6.21	10.2-12.6	9.55-12.67
	Max B	10.8	9.6	10.5	10.6	11.5	10.6	10.5	11.1	11.1	10.3	11.0	12.3	10.5	9.8	14	10.73±0.18	0.68	6.41	9.6-12.3	9.27-12.39
	Tri B	10.8	9.3	10.3	10.6	11.3	9.9	10.5	10.3	10.4	10.2	11.0	12.3	10.5	9.3	14	10.48±0.20	0.77	7.45	9.3-12.3	8.83-12.13
	Tal B	10.4	9.6	10.5	10.3	11.5	10.6	10.3	11.1	11.1	10.3	10.0	11.0	9.6	9.8	14	10.44±0.16	0.58	5.68	9.6-11.5	9.20-11.68
M_3	MDi L	9.8	10.0	-	9.2	11.6	11.0	10.5	11.2	11.3	10.5	*9.7	10.8	9.3	10.3	13	10.40±0.21	0.77	7.54	9.2-11.6	8.74-12.06
	Max B	10.4	9.6	-	9.4	11.0	10.6	11.4	10.4	10.2	9.6	9.8	11.3	9.8	9.5	13	10.23±0.19	0.69	6.86	9.4-11.4	8.74-11.72
	Tri B	10.4	9.6	-	9.4	10.8	10.6	11.4	10.3	10.2	9.6	9.8	11.3	9.8	9.5	13	10.21±0.19	0.67	6.69	9.4-11.4	8.76-11.66
	Tal B	9.6	9.4	-	9.2	11.0	10.5	10.7	10.4	10.2	9.5	9.3	9.9	9.0	9.2	13	9.84±0.18	0.66	6.79	9.0-11.0	8.41-11.27
P_3—M_3	L	47.8	48.2	*53.0	47.8	51.2	53.3	48.2	51.6	54.3	50.0	50.0	54.4	47.1	46.9	14	50.27±0.72	2.70	5.47	46.9-54.4	44.49-56.05
$\bar{I}$	B	27.9	*28.0	28.3	27.9	28.5	*29.0	28.7	31.7	30.3	29.4	29.5	31.0	29.1	27.2	14	29.04±0.34	1.27	4.44	27.2-31.7	26.32-31.76
C_1	B	47.3	46.8	46.4	45.3	45.2	45.3	48.6	48.8	48.9	46.7	47.6	51.0	*52.0	46.1	14	47.57±0.56	2.09	4.47	45.2-52.0	43.10-52.04
P_4	B	49.2	52.2	49.2	50.2	51.6	50.3	51.6	54.4	55.8	47.3	53.6	54.8	*51.0	48.2	14	51.39±0.68	2.56	5.07	47.3-55.8	45.91-56.87
M_3	B	55.4	57.6	*51.0	52.4	56.4	51.0	51.0	56.5	56.5	53.3	56.8	57.9	54.3	54.4	14	54.61±0.67	2.50	4.66	51.0-57.9	49.26-59.96
P_4	D	27.4	27.6	28.5	28.3	27.5	28.7	36.2	*35.0	29.4	32.5	32.0	31.2	29.8	25.5	14	29.97±0.82	3.06	10.38	25.5-36.2	23.42-36.52
M_3	D	27.5	27.5	27.0	29.4	29.3	26.7	34.5	30.4	28.5	32.6	30.7	29.5	28.3	24.4	14	29.02±0.68	2.55	8.93	24.4-34.5	23.56-34.48
	T	18.5	20.5	17.6	19.5	17.3	17.7	20.0	19.2	20.0	20.6	17.6	16.9	19.1	17.2	14	18.69±0.35	1.31	7.11	16.9-20.6	15.89-21.49
Ment for	D	19.5	18.5	19.8	17.8	17.3	17.8	25.2	22.5	18.2	22.5	24.6	21.2	19.6	15.1	14	19.96±0.77	2.89	14.73	15.1-25.2	13.78-26.14

APPENDIX 1h Pan troglodytes female mandibles

Comp No Spec No		22001 Z	22002 Z	22003 Z	22004 Z	22005 Z	22006 Z	22007 Z	22008 Z	22009 Z	22010 Z	22011 B 1939 3366	22012 A P9	n	$\bar{X}$ ± SE	SD	V_{cor}	OR	95% CL
C_1	Max L	10.9	11.8	10.3	10.3	11.6	-	11.2	11.8	10.8	11.0	11.0	*11.0	11	11.06 ± 0.16	0.52	4.77	10.3-11.8	9.90-12.22
	Trans B	8.5	9.2	8.8	8.7	8.8	-	8.8	9.4	9.0	9.3	8.8	* 8.0	11	8.85 ± 0.12	0.39	4.52	8.0- 9.4	7.98- 9.72
P_3	Max L	11.4	11.8	10.7	11.4	11.0	11.5	10.7	11.7	10.8	11.2	10.6	11.0	12	11.15 ± 0.12	0.41	3.76	10.6-11.8	10.25-12.05
	Trans B	7.2	7.6	7.0	7.0	7.0	7.3	7.3	8.3	7.6	8.2	7.6	7.4	12	7.46 ± 0.13	0.43	5.94	7.0- 8.3	6.51- 8.41
P_4	MDi L	7.2	7.8	7.4	7.6	7.0	7.9	7.4	7.5	7.8	7.7	7.3	7.4	12	7.50 ± 0.08	0.27	3.67	7.0- 7.9	6.91- 8.09
	BLi B	8.0	8.8	8.4	8.8	9.0	9.8	8.8	9.4	8.5	8.9	9.0	8.5	12	8.83 ± 0.14	0.47	5.43	8.0- 9.8	7.80- 9.86
M_1	MDi L	9.8	9.9	10.0	10.8	10.6	10.8	10.7	11.4	10.0	10.4	10.6	11.3	12	10.53 ± 0.15	0.53	5.10	9.8-11.4	9.36-11.70
	Max B	9.1	9.7	9.3	9.7	8.8	9.7	10.2	10.5	9.6	9.6	9.3	9.9	12	9.62 ± 0.13	0.46	4.91	8.8-10.5	8.61-10.63
	Tri B	8.3	9.6	9.2	9.6	8.6	9.6	9.9	10.5	9.6	9.2	9.3	9.4	12	9.40 ± 0.16	0.57	6.18	8.3-10.5	8.15-10.65
	Tal B	9.1	9.7	9.3	9.7	8.8	9.7	10.2	10.5	9.3	9.6	9.2	9.9	12	9.58 ± 0.14	0.48	5.10	8.8-10.5	8.52-10.64
M_2	MDi L	10.3	11.0	10.5	10.8	10.7	11.7	10.2	11.6	10.5	11.3	11.0	11.2	12	10.90 ± 0.15	0.49	4.57	10.2-11.7	9.82-11.98
	Max B	9.5	10.7	10.2	9.9	9.8	10.8	10.7	11.6	10.6	10.6	10.2	10.1	12	10.39 ± 0.16	0.56	5.50	9.5-11.6	9.16-11.62
	Tri B	9.3	10.7	10.2	9.9	9.6	10.4	10.6	11.6	10.6	10.2	10.2	9.6	12	10.24 ± 0.18	0.62	6.14	9.3-11.6	8.88-11.60
	Tal B	9.5	10.3	9.8	9.6	9.8	10.8	10.7	11.6	10.4	10.6	10.0	10.1	12	10.27 ± 0.17	0.60	5.96	9.5-11.6	8.95-11.59
M_3	MDi L	10.3	9.7	10.2	9.8	10.0	10.6	10.0	9.5	10.2	9.8	10.6	10.4	12	10.09 ± 0.10	0.35	3.57	9.5-10.6	9.32-10.86
	Max B	9.7	9.6	9.8	10.2	9.6	10.3	10.2	10.7	10.2	9.9	9.7	9.7	12	9.97 ± 0.10	0.35	3.56	9.6-10.7	9.20-10.74
	Tri B	9.6	9.6	9.8	10.2	9.6	10.3	10.2	10.7	10.2	9.8	9.7	9.7	12	9.95 ± 0.10	0.36	3.67	9.6-10.7	9.16-10.74
	Tal B	9.7	9.3	9.5	9.1	9.3	10.2	10.0	10.2	9.6	9.9	9.7	9.6	12	9.68 ± 0.10	0.35	3.71	9.1-10.2	8.91-10.45
P_3–M_3	L	48.8	49.5	48.8	50.0	49.8	52.0	49.4	52.0	48.7	50.3	47.9	49.7	12	49.74 ± 0.36	1.24	2.55	47.9-52.0	47.01-52.47
$\bar{I}$	B	26.4	29.3	28.9	27.5	29.3	28.6	29.6	29.7	30.0	30.3	26.5	31.0	12	28.93 ± 0.42	1.45	5.11	26.4-31.0	25.74-32.12
C_1	B	48.0	43.7	44.6	41.8	48.0	48.0	47.1	43.8	45.8	46.2	41.2	*42.5	12	45.06 ± 0.72	2.48	5.62	41.2-48.0	39.61-50.51
P_4	B	45.9	52.0	52.5	51.3	54.3	52.0	54.0	51.6	50.6	52.8	46.1	47.6	12	50.89 ± 0.82	2.85	5.72	45.9-54.3	44.62-57.16
M_3	B	53.3	56.5	56.8	55.6	54.4	56.5	59.5	54.0	55.2	56.2	50.3	53.0	12	55.11 ± 0.67	2.34	4.33	50.3-59.5	49.96-60.26
P_4	D	32.0	33.0	32.6	28.6	29.3	33.0	27.8	29.2	31.6	30.3	27.3	25.2	12	29.99 ± 0.73	2.52	8.57	25.2-33.0	24.44-35.54
M_3	D	31.3	29.8	31.8	28.6	29.0	31.7	28.4	27.3	29.8	29.4	24.7	27.3	12	29.09 ± 0.59	2.06	7.22	24.7-31.8	24.56-33.62
	T	17.6	14.8	16.5	15.3	17.5	21.0	17.3	18.2	18.0	19.0	17.3	16.2	12	17.39 ± 0.48	1.65	9.70	14.0-21.0	13.76-21.02
Ment for	D	22.5	24.4	23.5	19.4	20.4	22.8	20.0	19.5	20.9	20.4	16.2	16.9	12	20.58 ± 0.72	2.48	12.29	16.2-24.4	15.13-26.03

APPENDIX 11 <u>Gorilla gorilla</u> male crania

	D Pr52. 0.3	A DC 2	A G 29	A G 37	A G 27	A G 26	A G 13	A G2	A G 28	C E71 26B	n	$\bar{X} \pm$ SE	SD	V$_{cor}$	OR	95%CL
Nasal height	96.1	91.2	97.4	96.8	94.4	97.2	106.3	90.1	99.4	89.5	10	95.8±1.6	5.0	5.4	89.5-106.3	84.5-106.1
Nasal breadth	38.3	40.0	34.8	39.9	37.4	38.1	40.7	33.4	40.2	36.3	10	37.9±0.9	2.9	7.9	33.4- 40.7	31.3- 44.5
Breadth across lacrimal crests	24.1	16.9	34.2	21.3	25.8	31.1	34.9	29.0	30.3	*21.0	10	26.9±1.9	6.0	22.9	16.9- 34.9	13.3- 40.5
Thickness lateral orbital margin	13.0	16.6	15.2	15.4	17.3	14.5	15.9	15.5	17.3	17.2	10	15.8±0.4	1.4	8.8	13.0- 17.3	12.4- 19.2
Orbital height zygomaticofrontal to inferior border	28.6	31.3	34.5	*32.0	27.4	27.5	27.2	23.2	27.4	30.2	10	28.9±1.0	3.2	11.2	23.2- 34.5	28.9- 36.1
Nasospinale-alveolare	29.5	37.0	*31.0	*29.0	31.1	42.1	37.1	38.0	34.6	31.6	10	34.1±1.4	4.3	13.0	29.5- 42.1	24.3- 43.9
Breadth across infraorbital foramina	60.8	61.7	69.2	59.8	*68.0	64.4	*53.3	60.2	26.0	59.2	10	61.9±1.5	4.8	8.0	53.3- 69.2	51.0- 72.8
Left infraorbital for. to left antr. lacrimal crest	38.7	43.7	34.5	42.4	*41.0	35.3	42.6	40.6	38.7	*39.0	10	39.7±0.9	3.0	7.8	34.5- 43.7	32.8- 46.6
Alveolar length	*107.0	103.3	101.3	*109.0	98.7	105.8	*106.0	104.5	108.9	*98.5	10	104.3±1.2	3.7	3.7	98.5-109.0	95.9-112.7
Alveolar breadth at M^2	69.1	75.3	72.5	72.5	72.9	73.2	72.9	74.4	76.2	68.2	10	72.7±0.8	2.5	3.5	68.2- 76.2	67.1- 78.3
Alveolar breadth at C^1	78.5	75.2	69.2	77.2	84.5	72.3	76.4	76.5	77.3	64.4	10	75.2±1.7	5.5	7.5	64.4- 84.5	62.8- 87.6
Palatal depth at C^1 /P^3	10.8	8.0	7.5	9.9	9.2	6.3	8.2	11.0	16.2	*9.5	10	9.7±0.8	2.4	25.7	6.3- 16.2	4.2- 15.2
Palatal depth at M^2	17.0	11.0	12.4	17.8	23.0	17.1	16.8	18.5	24.3	*11.0	10	16.9±1.4	4.5	27.6	11.0- 24.3	6.6- 27.2

APPENDIX 1j _Gorilla gorilla_ female crania

	D Pr 52. 0.4	A G 20	A G 21	A G 22	A G 19	A G 23	A G 30	A G 31	A G 38	A G 15	n	X ± SE	SD	V_{cor}	OR	95% CL
Nasal height	77.7	76.5	78.1	68.6	*77.0	83.0	80.1	72.0	78.3	85.2	10	77.7±1.5	4.6	6.1	68.6-85.2	67.2-88.2
Nasal breadth	32.1	29.3	32.6	34.8	34.2	28.0	39.7	32.1	30.6	32.6	10	32.6±0.9	2.8	8.8	28.0-39.7	26.3-38.9
Breadth across antr. lacrimal crests	21.2	*22.0	19.5	20.6	20.4	15.3	19.2	18.7	16.4	23.4	10	19.7±0.8	2.5	12.7	15.3-23.4	12.2-25.2
Thickness lateral orbital margin	6.7	10.6	11.7	12.1	9.6	12.6	8.8	10.8	12.6	14.8	10	11.0±0.7	2.3	21.2	6.7-14.8	5.8-16.2
Orbital height zygomaticofrontal to inf. border	*29.0	27.6	29.5	*30.0	28.5	30.4	31.4	31.2	27.1	29.6	10	29.4±0.6	1.4	4.9	27.1-31.4	26.2-32.6
Nasospinale-alveolare	21.3	26.1	26.2	25.3	30.4	27.1	37.5	29.0	31.3	26.4	10	28.1±2.0	4.4	15.9	21.3-37.5	18.3-37.9
Breadth across infra-orbital foramina	56.1	*50.0	59.6	54.9	51.2	49.0	50.6	53.2	*52.2	55.0	10	53.2±1.5	3.3	6.3	49.0-59.6	45.9-60.5
Left infraorbital foramen to left antr. lacrimal crest	31.0	*31.0	41.4	29.1	33.2	33.1	36.1	34.3	33.2	37.2	10	34.0±1.6	3.6	10.7	29.1-41.4	26.0-42.0
Alveolar length	86.0	82.1	85.3	86.4	*81.0	80.6	89.5	87.5	83.4	88.0	10	85.0±1.4	3.1	3.7	80.6-89.5	78.1-91.9
Alveolar breadth at M^2	69.1	62.6	65.6	66.7	64.2	65.6	66.6	66.0	62.1	68.8	10	65.7±1.0	2.3	3.6	62.1-69.1	60.5-70.9
Alveolar breadth at C^1	61.4	58.1	52.2	61.0	58.9	54.4	56.5	64.1	55.2	59.7	10	58.2±1.9	4.2	7.5	52.2-64.1	48.6-67.8
Palatal depth at C^1/P^3	14.4	8.9	*9.5	*10.0	*9.0	8.2	13.0	8.6	12.8	8.5	10	10.3±1.0	2.2	22.0	8.2-14.4	5.3-15.3
Palatal depth at M^2	20.6	13.9	*11.0	*15.0	14.6	12.8	22.4	17.5	16.2	14.7	10	15.9±1.6	3.5	22.2	11.0-22.4	8.1-23.7

APPENDIX 1k *Pan troglodytes* crania

	A P5	D Pr 53. 0.1	D Pr 53. 0.9	A P 11	C E 7117A	A P 10	A P 17	A P 20	A P 18	A P9	n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	95% CL
Nasal height	58.1	55.1	59.4	59.8	*55.0	53.7	54.2	54.0	42.1	48.9	10	54.0 ± 1.7	5.3	10.0	42.1-59.8	42.0-56.0
Nasal breadth	28.6	27.8	25.5	25.0	25.4	25.1	24.7	22.5	26.0	21.0	10	25.2 ± 0.7	2.2	9.0	21.0-28.6	20.1-30.3
Breadth across antr. lacrimal crests	20.0	26.3	23.4	21.5	21.0	20.1	21.1	18.0	20.8	13.7	10	20.6 ± 1.0	3.3	16.5	13.7-26.3	13.1-28.1
Thickness lateral orbital margin	9.9	7.6	10.8	9.9	9.9	8.7	7.9	8.3	8.9	8.8	10	9.1 ± 0.3	1.0	11.5	7.6-10.8	6.8-11.4
Orbital height zygomaticofrontal to inf. border	23.8	*21.0	*23.0	*25.8	22.6	20.4	20.1	19.0	22.6	17.7	10	21.6 ± 0.8	2.4	11.5	17.7-25.8	16.1-27.1
Nasospinale-alveolare	31.8	28.2	39.2	33.3	29.9	26.7	25.8	25.0	28.2	25.3	10	29.3 ± 1.4	4.4	15.5	25.0-39.2	19.3-39.3
Breadth across infraorbital foramina	50.2	42.9	57.0	48.3	52.3	48.4	51.0	52.3	48.6	50.7	10	50.2 ± 1.1	3.6	7.4	42.9-57.0	41.9-58.3
Left infraorbital foramen to left antr. lacrimal crest	31.9	21.8	31.5	27.8	26.9	24.7	27.8	25.1	24.8	27.5	10	27.0 ± 1.0	3.1	11.8	21.8-31.9	20.0-34.0
Alveolar length	67.8	67.4	75.9	69.8	66.5	*66.0	*68.0	67.1	*65.0	*63.0	10	67.7 ± 1.0	3.2	4.9	63.0-75.9	60.4-75.0
Alveolar breadth at M^2	58.6	63.2	62.4	56.6	54.8	58.3	56.1	55.6	55.6	58.6	10	58.0 ± 0.9	2.9	5.1	54.8-63.2	51.5-64.5
Alveolar breadth at C^1	60.4	56.3	*62.4	59.2	57.3	53.8	52.8	55.9	*54.0	50.3	10	56.2 ± 1.2	3.7	6.7	50.3-62.4	47.8-64.6
Palatal depth at C^1/P^3	7.2	*8.0	*6.0	*8.0	*6.0	5.5	5.2	*2.0	*9.0	5.5	10	6.2 ± 0.6	2.0	32.6	2.0- 9.0	1.7-10.7
Palatal depth at M^2	12.1	14.8	13.4	11.9	*12.0	*13.0	11.2	*10.0	*13.0	12.8	10	12.4 ± 0.4	1.3	11.8	10.0-14.8	9.5-15.3

APPENDIX 2a *Dryopithecus (Proconsul) africanus* maxillae

Site		Kathwanga									
Spec No NMK:		220, 138	547, 670	569, 1403	570, 1404	593, 1988	686, 313	34,CMH 101	688, 315	41,CMH 112	51, 1499
I^C	MDi L	-	7.5	-	7.5	-	-	-	6.9	8.7	-
	LaLi B	-	5.7	-	5.7	-	-	-	5.5	6.8	-
C^1	Max L	-	-	-	-	8.0	8.0	*9.0	-	-	-
	Trans B	-	-	-	-	7.0	6.3	*7.3	-	-	-
P^3	MDi L	-	-	-	-	-	-	*4.6	-	-	-
	Max L	-	-	-	-	-	-	*5.0	-	-	-
	BLi B	-	-	-	-	-	-	*8.6	-	-	-
P^4	MDi L	-	-	-	-	-	-	*4.4	-	-	5.2
	BLi B	-	-	-	-	-	-	*8.0	-	-	9.1
M^1	MDi L	-	-	7.8	-	-	-	*7.4	-	-	8.0
	BLi B	-	-	9.3	-	-	-	*8.5	-	-	9.8
M^2	MDi L	8.8	-	-	-	-	-	-	-	-	8.6
	BLi B	10.5	-	-	-	-	-	-	-	-	10.4
M^3	MDi L	-	-	-	-	-	-	-	-	-	-
	BLi B	-	-	-	-	-	-	-	-	-	-

Site		Kiahera	Hiwegi				R100-112			
Spec No NMK:		218, 103	131, 342	507, 94	557, 1040	715, 156	1948, 50	216, 48	531, 286	550, 777
I^C	MDi L	8.1	7.7	-	-	-	7.0	7.6	-	-
	LaLi B	6.1	6.0	-	-	-	6.3	5.5	-	-
C^1	Max L	-	9.5	8.8	9.8	-	10.4	-	-	-
	Trans B	-	7.6	6.3	8.3	-	8.2	-	-	-
P^3	MDi L	-	-	-	-	-	5.4	-	-	-
	Max L	-	-	-	-	-	6.1	-	-	-
	BLi B	-	-	-	-	-	10.8	-	-	-
P^4	MDi L	-	-	-	-	-	5.5	-	-	-
	BLi B	-	-	-	-	-	10.1	-	-	-
M^1	MDi L	-	-	-	-	-	8.2	-	7.4	7.5
	BLi B	-	-	-	-	-	9.6	-	8.7	8.9
M^2	MDi L	-	-	-	-	-	9.2	-	7.6	-
	BLi B	-	-	-	-	-	11.0	-	9.5	-
M^3	MDi L	-	-	-	-	8.3	8.1	-	-	-
	BLi B	-	-	-	-	11.5	11.0	-	-	-

Site		Koru			Songhor						
Spec No BM(NH):		M14 081	M14 084	M14 085	NMK: 95, CMH24	191, 2	409, 385	8'62	145 '62	201, 45	301, 112
I^C	MDi L	-	-	-	-	-	-	-	-	-	-
	LaLi B	-	-	-	-	-	-	-	-	-	-
C^1	Max L	-	11.6	-	-	-	-	-	-	9.4	-
	Trans B	-	9.1	-	-	-	-	-	-	7.5	-
P^3	MDi L	-	6.0	-	-	-	-	-	-	-	-
	Max L	-	7.5	-	-	-	-	-	-	-	-
	BLi B	-	9.7	-	-	-	-	-	-	-	-
P^4	MDi L	-	5.8	-	-	-	5.4	-	5.6	-	-
	BLi B	-	9.3	-	-	-	7.8	-	9.7	-	-
M^1	MDi L	7.0	8.0	7.9	-	9.0	-	7.0	-	-	-
	BLi B	8.8	10.0	9.2	-	9.9	-	8.0	-	-	-
M^2	MDi L	7.8	9.2	-	9.4	-	-	-	-	-	-
	BLi B	9.7	11.5	-	10.4	-	-	-	-	-	-
M^3	MDi L	-	8.2	-	-	-	-	-	-	-	8.8
	BLi B	-	10.6	-	-	-	-	-	-	-	11.4

APPENDIX 2b *Dryopithecus africanus* mandibles

Site		Kathwanga						
Spec No NMK:		134, 465	183, 1097	268, 893	690, 317	185, 1228	58, CMH129	51 1499
C_1	Max L	7.5	-	-	-	-	-	8.7
	Trans B	5.3	-	-	-	-	-	6.8
P_3	Max L	-	-	-	-	-	-	8.5
	Trans B	-	-	-	-	-	-	5.8
P_4	MDi L	-	-	7.0	-	-	-	6.0
	BLi B	-	-	6.5	-	-	-	6.4
M_1	MDi L	-	-	-	9.0	9.1	7.7	8.9
	Max B	-	-	-	7.8	7.9	7.5	7.7
	Tri B	-	-	-	7.8	7.8	-	7.4
	Tal B	-	-	-	7.4	7.9	-	7.7
M_2	MDi L	-	-	-	-	-	9.5	9.9
	Max B	-	-	-	-	-	*8.6	8.4
	Tri B	-	-	-	-	-	*8.6	8.3
	Tal B	-	-	-	-	-	7.9	8.4
M_3	MDi L	-	10.8	-	-	-	-	-
	Max B	-	8.8	-	-	-	-	-
	Tri B	-	8.8	-	-	-	-	-
	Tal B	-	8.3	-	-	-	-	-
$P_3 — M_3$ L		-	-	-	-	-	-	-
$\overline{I}$ B		-	-	-	-	-	-	-
C_1 B		-	-	-	-	-	-	-
P_4 B		-	-	-	-	-	-	-
M_3 B		-	-	-	-	-	-	-
P_4	D	-	-	-	-	-	-	-
	T	-	-	-	-	-	-	-
M_3	D	-	-	-	-	-	19.6	-
	T	-	-	-	-	-	*15.0	-

Site		Kiahera	Hiwegi						
Spec No NMK:		262, 635	8, CMH8	35,CMH 102	131, 342	542, 583	545, 628	573, 1558	578, 1778
C_1	Max L	-	-	-	8.3	-	-	-	-
	Trans B	-	-	-	6.5	-	-	-	-
P_3	Max L	-	-	-	-	-	-	8.0	-
	Trans B	-	-	-	-	-	-	4.8	-
P_4	MDi L	-	-	6.2	-	-	-	5.3	-
	BLi B	-	-	6.6	-	-	-	-	-
M_1	MDi L	-	-	8.1	-	-	-	*8.0	-
	Max B	-	-	7.3	-	-	-	7.3	-
	Tri B	-	-	7.1	-	-	-	7.3	-
	Tal B	-	-	7.3	-	-	-	7.3	-
M_2	MDi L	-	-	9.8	-	-	-	*10.0	-
	Max B	-	-	8.5	-	-	-	-	-
	Tri B	-	-	8.4	-	-	-	-	-
	Tal B	-	-	8.5	-	-	-	-	-
M_3	MDi L	-	-	11.7	-	10.3	11.6	-	9.5
	Max B	-	-	8.5	-	8.9	8.8	-	8.2
	Tri B	-	-	8.5	-	8.9	8.8	-	8.2
	Tal B	-	-	7.9	-	8.4	8.3	-	7.9
$P_3 — M_3$ L		-	-	43.0	-	-	-	-	-
$\overline{I}$ B		-	-	-	-	-	-	-	-
C_1 B		-	-	-	-	-	-	-	-
P_4 B		-	-	-	-	-	-	-	-
M_3 B		-	-	-	-	-	-	-	-
P_4	D	*22.0	23.3	-	-	-	-	19.5	-
	T	*10.0	10.5	-	-	-	-	11.0	-
M_3	D	-	21.7	-	-	-	-	-	-
	T	-	11.6	-	-	-	-	-	-

APPENDIX 2b, continued

Site		R100-112						Koru	
Spec No NMK:		140, 599	147, 645	1948, 50	514, 282	637, 260	640, 417	BM(NH) M14087	NMK 618,2
C_1	Max L	8.5	8.2	9.5	-	8.7	-	-	10.4
	Trans B	6.0	6.2	6.4	-	7.0	-	-	8.2
P_3	Max L	*9.0	-	9.3	9.6	-	-	-	-
	Trans B	5.0	-	6.0	7.0	-	-	-	-
P_4	MDi L	-	-	6.4	-	-	-	-	-
	BLi B	-	-	7.1	-	-	-	-	-
M_1	MDi L	-	-	8.5	-	-	-	-	-
	Max B	-	-	7.5	-	-	-	-	-
	Tri B	-	-	7.5	-	-	-	-	-
	Tal B	-	-	7.5	-	-	-	-	-
M_2	MDi L	-	-	10.3	-	-	-	-	-
	Max B	-	-	9.0	-	-	-	-	-
	Tri B	-	-	9.0	-	-	-	-	-
	Tal B	-	-	8.6	-	-	-	-	-
M_3	MDi L	-	-	11.5	-	-	-	11.9	-
	Max B	-	-	9.0	-	-	-	9.4	-
	Tri B	-	-	9.0	-	-	-	9.4	-
	Tal B	-	-	8.4	-	-	-	8.6	-
P_3—M_3 L		-	-	43.5	-	-	-	-	-
$\bar{I}$	B	-	-	-	-	-	15.6	-	-
C_1	B	-	-	-	-	-	-	-	-
P_4	B	-	-	-	-	-	-	-	-
M_3	B	-	-	-	-	-	-	-	-
P_4	D	25.5	-	20.0	-	-	-	-	-
	T	11.6	-	10.0	-	-	-	-	-
M_3	D	-	-	-	-	-	-	-	-
	T	-	-	-	-	-	-	-	-

Site		Songhor												
Spec No NMK:		90, D4	91, 9	94, 21	113, F3104	196, 16	334, 405	380, 1	381, 2	406, 382	139, '62	143, '62	144, '62	384, 5
C_1	Max L	8.5	-	-	-	8.3	-	-	-	-	10.3	-	-	*11.0
	Trans B	6.8	-	-	-	7.2	-	-	-	-	7.5	-	-	*7.5
P_3	Max L	-	-	-	-	-	-	-	-	-	-	-	-	-
	Trans B	-	-	-	-	-	-	-	-	-	-	-	-	-
P_4	MDi L	-	-	6.0	-	-	-	-	-	-	-	-	-	-
	BLi B	-	-	5.0	-	-	-	-	-	-	-	-	-	-
M_1	MDi L	-	-	8.0	-	-	-	8.2	-	8.8	-	8.5	8.8	-
	Max B	-	-	6.0	-	-	-	6.5	-	7.5	-	6.8	7.5	-
	Tri B	-	-	-	-	-	-	6.5	-	7.5	-	-	7.5	-
	Tal B	-	-	-	-	-	-	6.4	-	7.3	-	-	7.1	-
M_2	MDi L	-	-	9.0	*8.0	-	-	9.3	-	-	-	-	-	-
	Max B	-	-	7.5	-	-	-	8.1	-	-	-	-	-	-
	Tri B	-	-	-	-	-	-	8.1	-	-	-	-	-	-
	Tal B	-	-	-	-	-	-	7.5	-	-	-	-	-	-
M_3	MDi L	-	-	-	*10.0	-	9.5	11.0	10.2	-	-	-	-	-
	Max B	-	-	-	-	-	7.0	8.9	7.0	-	-	-	-	-
	Tri B	-	-	-	-	-	-	8.9	-	-	-	-	-	-
	Tal B	-	-	-	-	-	-	8.1	-	-	-	-	-	-
P_3—M_3 L		-	-	-	-	-	-	-	-	-	-	-	-	-
$\bar{I}$	B	-	*15.0	-	-	-	-	-	-	-	-	-	-	-
C_1	B	-	*24.0	-	-	-	-	-	-	-	-	-	-	-
P_4	B	-	-	-	-	-	-	-	-	-	-	-	-	-
M_3	B	-	-	-	-	-	-	-	-	-	-	-	-	-
P_4	D	-	*22.5	-	-	-	-	*27.0	-	-	-	-	-	-
	T	-	10.4	-	-	-	-	*12.0	-	-	-	-	-	-
M_3	D	-	-	-	*17.5	-	-	*22.0	*15.0	-	-	-	-	-
	T	-	-	-	12.0	-	-	*14.5	-	-	-	-	-	-

APPENDIX 2c *Dryopithecus* (*Proconsul*) *nyanzae* maxillae

Site		Kathwanga				Kiahera	Hiwegi					R100-112
Spec No NMK:		594,1969	25,CMH32	50,CMH121	722,550	166,993	155,712	BM(NH) M16647	5,CMH3	566,1342	694,2542	44,CMH115
I^C	MDi L	9.6	-	-	-	-	-	-	8.4	*9.6	9.4	8.8
	LaLi B	6.8	-	-	-	-	-	-	6.8	6.7	7.4	7.4
C^1	Max L	-	-	-	-	-	-	15.8	14.0	-	-	-
	Trans B	-	-	-	-	-	-	12.0	10.9	-	-	-
P^3	MDi L	-	-	-	-	-	5.7	7.0	7.0	-	-	-
	Max L	-	-	-	-	-	7.0	8.2	7.5	-	-	-
	BLi B	-	-	-	-	-	10.5	11.8	10.8	-	-	-
P^4	MDi L	-	-	-	-	-	5.8	6.8	6.8	-	-	-
	BLi B	-	-	-	-	-	11.0	12.0	11.0	-	-	-
M^1	MDi L	-	-	9.8	-	9.0	8.4	9.6	8.9	-	-	-
	BLi B	-	-	11.3	-	9.8	10.8	12.0	11.3	-	-	-
M^2	MDi L	-	10.9	-	11.7	10.3	10.0	12.4	12.3	-	-	-
	BLi B	-	12.4	-	14.0	11.3	11.6	13.7	13.8	-	-	-
M^3	MDi L	-	-	-	-	-	10.0	11.3	11.5	-	-	-
	BLi B	-	-	-	-	-	12.8	14.1	13.6	-	-	-

APPENDIX 2d *Dryopithecus* *(Proconsul)* *nyanzae* mandibles

Site		Kathwanga									Kiahera			Hiwegi					R100-112				
Spec No NMK:		125, 143	186, 1229	7, CMH7	23, CMH30	24, CMH31	39, CMH110	374, 692	562, 1145	620, 1	181, 1043	538, 486	539, 487	1, CMH1	4, CMH4	6, CMH5	65, CMH136	560, 1056	38, CMH109	64, CMH135	141, 600	144, 603	151 683
C_1	Max L	-	-	-	-	-	-	12.0	12.8	-	-	-	-	10.8	12.8	-	-	-	*9.6	-	-	-	-
	Trans B	-	-	-	-	-	-	10.5	10.5	-	-	-	-	8.7	10.0	-	-	-	*6.0	-	-	-	-
P_3	Max L	-	-	-	-	-	-	-	12.0	10.2	-	-	12.9	8.9	10.0	10.8	-	-	9.8	-	-	10.6	-
	Trans B	-	-	-	-	-	-	-	7.4	6.3	-	-	7.7	6.5	7.0	-	-	-	-	-	-	6.5	
P_4	MDi L	-	-	7.6	-	-	-	-	7.4	-	-	-	-	7.4	8.0	6.8	-	-	-	-	6.5	-	-
	BLi B	-	-	7.9	-	-	-	-	7.8	-	-	-	-	7.8	8.4	7.3	-	-	-	-	7.4	-	-
M_1	MDi L	-	9.7	9.6	-	-	-	-	8.9	9.8	9.3	-	-	8.4	10.0	8.9	-	9.8	-	-	9.6	-	9.5
	Max B	-	8.6	8.6	-	-	-	-	8.6	-	7.8	-	-	7.8	8.7	7.9	-	7.9	-	-	8.7	-	8.3
	Tri B	-	8.4	-	-	-	-	-	7.8	-	7.7	-	-	7.5	8.4	7.8	-	7.9	-	-	8.3	-	8.0
	Tal B	-	8.6	-	-	-	-	-	8.6	-	7.8	-	-	7.8	8.7	7.9	-	7.6	-	-	8.7	-	8.3
M_2	MDi L	-	-	-	10.7	12.7	11.8	-	11.8	12.0	-	-	-	10.2	13.0	11.4	-	-	-	12.6	-	-	-
	Max B	-	-	-	10.0	10.7	9.7	-	10.4	-	-	-	-	9.0	11.5	9.7	-	-	-	11.4	-	-	-
	Tri B	-	-	-	9.8	10.7	9.7	-	10.0	-	-	-	-	8.6	11.3	9.4	-	-	-	10.9	-	-	-
	Tal B	-	-	-	10.0	10.4	9.2	-	10.4	-	-	-	-	9.0	11.5	9.7	-	-	-	11.4	-	-	-
M_3	MDi L	14.3	-	-	-	-	-	-	13.7	14.4	-	14.3	-	11.6	14.0	13.7	13.7	-	-	-	-	-	-
	Max B	11.6	-	-	-	-	-	-	11.2	-	-	11.0	-	9.4	12.4	9.4	11.8	-	-	-	-	-	-
	Tri B	11.6	-	-	-	-	-	-	11.2	-	-	11.0	-	9.4	12.4	9.4	11.8	-	-	-	-	-	-
	Tal B	10.4	-	-	-	-	-	-	-	-	-	*10.0	-	9.2	11.4	-	10.8	-	-	-	-	-	-
P_3—M_3	L	-	-	-	-	-	-	-	55.2	-	-	-	-	44.5	54.8	-	-	-	-	-	-	-	-
$\overline{I}$	B	-	-	-	-	-	-	-	*22.0	-	-	-	-	*19.9	-	-	-	-	-	-	-	-	-
C_1	B	-	-	-	-	-	-	-	*40.0	-	-	-	-	*35.5	-	-	-	-	-	-	-	-	-
P_4	B	-	-	-	-	-	-	-	-	-	-	-	-	*40.0	-	-	-	-	-	-	-	-	-
M_3	B	-	-	-	-	-	-	-	-	-	-	-	-	*50.0	-	-	-	-	-	-	-	-	-
P_4	D	-	-	-	-	-	-	-	*30.0	-	-	-	-	33.2	-	27.5	-	-	-	-	-	-	-
	T	-	-	-	-	-	-	-	12.0	-	-	-	-	15.7	-	15.5	-	-	-	-	-	-	-
M_3	D	-	-	-	-	-	-	-	*28.0	-	-	-	-	33.5	-	23.4	-	-	-	-	-	-	-
	T	-	-	-	-	-	-	-	16.0	-	-	-	-	*20.0	-	15.9	-	-	-	-	-	-	-

APPENDIX 2e *Dryopithecus* (*Proconsul*) *major* maxillae

Site		Moroto			Napak								Songhor		
Spec No UMP:		62-11 L	62-11 R	62-12	66-03	62-03	62-04	62-05	62-07	66-41	62-08	62-09	NMK: 102, CMH35	405, 381	101, CMH34
I^C	MDi L	10.8	-	-	-	-	-	-	-	-	-	-	-	-	-
	LaLi B	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-
C^1	Max L	*18.6	-	17.6	-	*18.7	19.6	18.8	-	-	-	-	-	-	-
	Trans B	*15.7	-	16.1	-	*15.7	16.0	16.1	-	-	-	-	-	-	-
P^3	MDi L	8.0	8.2	-	-	-	-	-	-	-	-	-	-	-	-
	Max L	10.6	10.7	-	-	-	-	-	-	-	-	-	-	-	-
	BLi B	-	14.6	-	-	-	-	-	-	-	-	-	-	-	-
P^4	MDi L	7.9	8.0	-	-	-	-	-	-	-	-	-	-	-	-
	BLi B	14.8	14.7	-	-	-	-	-	-	-	-	-	-	-	-
M^1	MDi L	*11.7	*11.6	-	-	-	-	-	*11.4	12.0	-	-	-	-	-
	BLi B	12.7	12.6	-	-	-	-	-	*13.9	14.0	-	-	-	-	-
M^2	MDi L	*13.1	*13.1	-	-	-	-	-	-	-	15.1	15.2	12.7	14.4	12.0
	BLi B	14.0	14.1	-	-	-	-	-	-	-	17.3	-	15.3	16.3	13.6
M^3	MDi L	12.8	12.7	-	-	-	-	-	-	-	-	-	-	-	-
	BLi B	14.4	14.3	-	-	-	-	-	-	-	-	-	-	-	-
I^L	MDi L	8.6	8.7	-	* 8.2	-	-	-	-	-	-	-	-	-	-
	LaLi B	10.2	10.1	-	*10.1	-	-	-	-	-	-	-	-	-	-

APPENDIX 2f *Dryopithecus* *(Proconsul)* *major* mandibles

Site		Moroto	Napak						Koru	Songhor						
Spec No UMP:		62-10 66-01	62-06	62-13	62-14	62-15	62-16	66-02	BM(NH) M14086	BM(NH) M16648	190,1	277,55	272,56	382,3	383,4	604,69
C_1	Max L	**16.0	-	-	-	-	-	-	*13.5	-	15.1	-	-	-	-	-
	Trans B	**12.0	-	-	-	-	-	-	* 9.5	-	12.5	-	-	-	-	-
P_3	Max L	**16.0	-	-	-	-	-	-	12.7	**14.0	**13.0	-	-	*16.0	16.0	14.4
	Trans B	** 9.5	-	-	-	-	-	-	7.2	** 9.0	** 8.2	-	-	* 9.0	9.0	9.8
P_4	MDi L	** 9.5	*10.3	8.6	-	-	7.9	7.8	7.8	9.2	9.0	-	9.0	-	-	-
	BLi B	**10.0	-	9.1	-	-	9.0	9.0	9.0	9.7	9.7	-	10.6	-	-	-
M_1	MDi L	**11.8	-	10.8	12.0	12.7	10.7	-	*10.9	12.1	11.8	-	-	-	-	-
	Max B	*11.0	-	9.2	10.5	10.9	*9.4	-	9.5	10.7	10.9	-	-	-	-	-
	Tri B	*10.8	-	9.0	10.2	10.6	*9.4	-	9.3	10.2	10.9	-	-	-	-	-
	Tal B	*11.0	-	9.2	10.5	10.9	9.4	-	9.5	10.7	10.8	-	-	-	-	-
M_2	MDi L	*13.0	-	-	-	-	-	-	*12.6	14.8	13.9	15.6	-	-	-	-
	Max B	*12.2	-	-	-	-	-	-	10.8	*12.8	13.1	14.1	-	-	-	-
	Tri B	*12.2	-	-	-	-	-	-	10.8	12.8	13.1	14.1	-	-	-	-
	Tal B	*11.9	-	-	-	-	-	-	10.2	*12.8	12.5	13.5	-	-	-	-
M_3	MDi L	15.0	-	-	-	-	-	-	*13.5	18.0	17.3	-	-	-	-	-
	Max B	12.5	-	-	-	-	-	-	*10.5	13.4	14.2	-	-	-	-	-
	Tri B	12.5	-	-	-	-	-	-	*10.5	13.4	14.2	-	-	-	-	-
	Tal B	*10.4	-	-	-	-	-	-	-	12.0	12.0	-	-	-	-	-
P_3 -M_3	L	**64.0	-	-	-	-	-	-	*54.0	**65.6	**63.0	-	-	-	-	-
I	B	**23.0	-	-	-	-	-	-	*20.0	-	21.2	-	-	-	-	-
C_1	B	**49.5	-	-	-	-	-	-	*42.0	-	*46.0	-	-	-	-	-
P_4	B	**54.5	-	-	-	-	-	-	*48.0	-	*51.0	-	-	-	-	-
M_3	B	**60.5	-	-	-	-	-	-	-	-	*58.5	-	-	-	-	-
P_4	D	-	-	-	-	-	-	-	36.5	-	41.0	-	-	-	-	-
	T	-	-	-	-	-	-	-	17.0	-	21.0	-	-	-	-	-
M_3	D	-	-	-	-	-	-	-	*32.0	-	34.5	-	-	-	-	-
	T	24.5	-	-	-	-	-	-	*20.0	24.0	25.5	-	-	-	-	-

APPENDIX 3. Statistics of Dryopithecus (Proconsul), Gorilla gorilla and Pan troglodytes

		D. (P.) africanus					D. (P.) nyanzae					D. (P.) major				
		n	$\bar{X}$ SE	SD	V_{cor}	OR	n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	n	$\bar{X} \pm$ SE	SD	V_{cor}	OR
C^1	Max L	9	9.4±0.38	1.14	12.2	8.0-11.6	2	14.9	-	-	14.0-15.8	4	19.5	-	-	17.6-19.3
	Trans B	9	7.5±0.32	0.96	13.2	6.3- 9.1	2	11.5	-	-	10.9-12.0	4	15.9	-	-	15.7-16.1
P^3	Max L	3	6.2	-	-	5.0- 7.5	3	7.9	-	-	7.0- 8.2	1	10.7	-	-	-
	BLi B	3	9.7	-	-	8.6-10.8	3	11.0	-	-	10.5-11.8	1	14.6	-	-	-
P^4	MDi L	6	5.3	-	-	4.4- 5.8	3	6.5	-	-	5.8- 6.8	1	8.0	-	-	-
	BLi B	6	9.0	-	-	7.8-10.1	3	11.3	-	-	11.0-12.0	1	14.8	-	-	-
M^1	MDi L	12	7.9±0.19	0.66	8.5	7.0- 9.0	4	9.2	-	-	8.4- 9.8	3	11.7	-	-	11.4-12.0
	BLi B	12	9.2±0.18	0.64	7.1	8.0-10.0	4	11.4	-	-	10.8-12.0	3	13.5	-	-	12.6-14.0
M^2	MDi L	8	8.9±0.31	0.88	10.2	7.6-10.3	5	11.5	-	-	10.0-12.4	6	13.8	-	-	12.0-15.2
	BLi B	8	10.5±0.25	0.71	7.0	9.5-11.5	5	13.5	-	-	11.6-14.0	5	15.3	-	-	13.6-17.3
M^3	MDi L	4	8.4	-	-	8.1- 8.8	3	10.9	-	-	10.0-11.5	1	12.8	-	-	-
	BLi B	4	11.1	-	-	10.6-11.5	3	13.5	-	-	12.8-14.1	1	14.4	-	-	-
C_1	Max L	13	9.0±0.29	1.03	11.7	7.5-11.0	4	12.1	-	-	10.8-12.8	3	14.9	-	-	13.5-16.0
	Trans B	13	6.7±0.24	0.86	13.1	5.3- 8.2	4	9.9	-	-	8.7-10.5	3	11.3	-	-	9.5-12.5
P_3	Max L	5	8.9	-	-	8.0- 9.6	7	10.8	-	-	8.9-12.9	6	14.4	-	-	12.7-16.0
	Trans B	5	5.7	-	-	4.8- 7.0	6	6.9	-	-	6.3- 7.7	6	8.8	-	-	7.2- 9.8
P_4	MDi L	6	6.2	-	-	5.3- 7.0	6	7.3	-	-	6.5- 8.0	9	8.8±0.27	0.80	9.3	7.3-10.3
	BLi B	5	6.3	-	-	5.0- 7.1	6	7.8	-	-	7.3- 8.4	8	9.5±0.22	0.61	6.6	9.0-10.6
M_1	MDi L	11	8.6±0.14	0.48	5.7	7.7- 9.0	12	9.5±0.14	0.49	5.3	8.4-10.0	8	11.6±0.25	0.72	6.4	10.7-12.7
	Max B	11	7.2±0.17	0.56	8.0	6.0- 7.8	11	8.3±0.12	0.40	4.9	7.8- 9.7	8	10.3±0.27	0.76	7.6	9.2-11.0
M_2	MDi L	8	9.5±0.26	0.73	7.9	8.0-10.3	9	11.8±0.31	0.93	8.1	10.1-13.0	5	14.0	-	-	12.6-15.6
	Max B	6	8.4	-	-	7.5- 9.0	8	10.3±0.31	0.87	8.7	9.0-11.5	5	12.6	-	-	10.8-14.1
M_3	MDi L	11	10.7±0.27	0.88	8.4	9.5-11.9	8	13.8±0.33	0.93	7.0	11.6-14.5	4	16.0	-	-	13.5-18.0
	Max B	10	8.5±0.26	0.83	10.0	7.0- 9.4	7	11.0	-	-	9.4-12.4	4	12.7	-	-	-

APPENDIX 3, continued

		G. gorilla					P. troglodytes				
		n	$\bar{X} \pm$ SE	SD	V_{cor}	OR	n	$\bar{X} \pm$ SE	SD	V_{cor}	OR
C^1	Max L	40	17.85 ± 0.56	3.57	20.1	12.5-23.2	26	12.72 ± 0.33	1.66	13.2	10.5-15.6
	Trans B	40	13.58 ± 0.41	2.60	19.3	10.1-17.8	25	10.00 ± 0.29	1.43	14.4	8.2-13.2
P^3	Max L	40	11.62 ± 0.15	0.95	8.3	9.9-13.2	26	8.00 ± 0.10	0.52	6.6	6.8- 9.1
	BLi B	40	15.21 ± 0.17	1.06	7.0	13.0-17.1	24	10.50 ± 0.11	0.55	5.2	9.4-11.8
P^4	MDi L	40	10.82 ± 0.10	0.66	6.1	9.5-12.2	26	7.01 ± 0.06	0.30	4.3	6.6- 7.6
	BLi B	39	14.86 ± 0.15	0.93	6.3	12.6-16.8	24	10.16 ± 0.07	0.36	3.6	9.5-10.8
M^1	MDi L	40	14.44 ± 0.14	0.87	6.1	12.7-16.7	26	9.87 ± 0.10	0.52	5.3	9.0-10.6
	BLi B	40	15.20 ± 0.15	0.94	6.2	13.3-17.4	23	11.18 ± 0.11	0.52	4.7	9.9-11.7
M^2	MDi L	40	15.41 ± 0.18	1.12	7.3	13.4-17.9	26	10.07 ± 0.12	0.62	6.2	9.0-11.3
	BLi B	40	16.14 ± 0.16	1.03	6.4	14.0-18.3	24	11.58 ± 0.12	0.58	5.1	10.2-12.8
M^3	MDi L	40	14.35 ± 0.19	1.19	8.3	12.0-17.0	21	9.12 ± 0.13	0.58	6.4	8.2-10.3
	BLi B	40	15.26 ± 0.18	1.17	7.7	13.0-17.2	20	10.93 ± 0.18	0.82	7.6	8.8-12.2
C_1	Max L	38	15.66 ± 0.46	2.84	18.3	11.3-20.2	24	12.18 ± 0.29	1.43	11.9	10.3-15.3
	Trans B	38	12.89 ± 0.33	2.05	16.8	9.1-15.5	25	9.84 ± 0.23	1.14	11.7	8.0-12.2
P_3	Max L	40	16.19 ± 0.25	1.61	10.0	13.7-18.6	26	11.10 ± 0.10	0.51	4.6	10.2-12.1
	Trans B	40	11.21 ± 0.21	1.34	12.0	8.2-13.8	26	7.78 ± 0.13	0.65	8.5	7.0- 9.8
P_4	MDi L	40	11.21 ± 0.12	0.75	6.8	9.8-13.0	26	7.65 ± 0.10	0.52	6.9	6.8- 9.0
	BLi B	40	12.94 ± 0.15	0.97	7.5	10.5-14.4	26	8.92 ± 0.09	0.46	5.3	8.0- 9.8
M_1	MDi L	40	15.28 ± 0.12	0.73	4.8	13.6-16.8	26	10.63 ± 0.11	0.57	5.4	9.8-12.2
	Max B	40	13.15 ± 0.11	0.72	5.5	11.6-14.4	26	9.72 ± 0.10	0.53	5.5	8.8-11.0
M_2	MDi L	40	16.77 ± 0.17	1.08	6.5	14.7-19.2	26	11.02 ± 0.12	0.60	5.5	10.2-12.6
	Max B	40	14.96 ± 0.17	1.05	7.1	12.8-16.8	26	10.57 ± 0.12	0.64	6.1	9.5-12.3
M_3	MDi L	40	16.80 ± 0.21	2.90	7.9	14.2-19.2	25	10.25 ± 0.12	0.61	6.1	9.2-11.6
	Max B	40	14.76 ± 0.18	1.11	7.5	12.4-17.5	25	10.10 ± 0.11	0.56	5.6	9.4-11.4

Date Due

~~DEC 31 1983~~

~~reserve - fall 1985~~

~~reserve spring 86~~
~~Bio 99ht~~