BRITISH MUSEUM (NATURAL HISTORY)

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THE FORE-LIMB SKELETON AND ASSOCIATED REMAINS OF PROCONSUL AFRICANUS

J. R. NAPIER
and
P. R. DAVIS

LONDON
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by

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With 10 plates, 16 text-figures and 23 tables in the text

Preface by Sir Wilfrid Le Gros Clark, F.R.S.
(Professor of Anatomy, University of Oxford)

LONDON
PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

Issued May 1959

PRICE ONE POUND FIFTEEN SHILLINGS

BRITISH MUSEUM (NATURAL HISTORY)

FOSSIL MAMMALS OF AFRICA

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PREFACE

Most of the fossil relics of Miocene anthropoid apes discovered over the past twenty years in East Africa consist of jaws and teeth; thus, while of the greatest importance in demonstrating the remarkable diversity of types in existence at that early time, they have provided little information regarding the habits of life of these extinct creatures. Now, it is a distinctive feature of the Recent anthropoid apes that they manifest structural modifications of the limbs in adaptation to rather extreme habits of brachiation, that is, the mode of arboreal progression whereby the animal swings itself along from branch to branch in over-arm fashion. This is a functional specialisation in which the Recent apes are distinguished from other related groups of the higher Primates, and in the associated modifications of limb proportions and structure they also contrast strongly with all known types of the Hominidae. It has for long been a matter of importance, therefore, to determine whether the apes of Miocene times (some of which, it has been conjectured from their dental morphology, may have been closely related to the ancestral stock of the Hominidae) had already developed such divergent specialisations of the limbs. Fragmentary limb bones of *Limnopithecus macinnesi*, and others attributed to the large species *Proconsul nyanzae*, have already provided some evidence that this was not the case, for, although they show certain features indicating an approach to the limb structure of Recent apes, they evidently had not developed the adaptive features which are directly associated with the more extreme type of brachiation. Indeed, in a number of characters of the limb bones these particular species show a closer approximation to the quadrupedal monkeys.

The recent discovery of most of the arm and hand bones of *Proconsul africanus* is of quite unusual importance, since these comprise the first relatively complete specimens of the upper limb skeleton of a fossil anthropoid ape to be found. It was hoped, therefore, that a systematic comparative examination of these remains would provide much more certain evidence regarding the degree to which arboreal specialisation had proceeded in the Miocene apes. This hope has now been realised by the careful and prolonged studies of Dr. Napier and Dr. Davis, as recorded in the present monograph. The authors, it should be noted, employ the term "brachiation" with a somewhat broader connotation than is commonly done, for they define it as applying to all degrees of the use of the fore-limbs for grasping hand-holds above the head and swinging the body forward in arboreal progression, and they point out that such a mode of progression is of course widely practised by the arboreal quadrupedal monkeys as well as the anthropoid apes. But in the latter this brachiating habit has been developed to such an extreme as to replace quadrupedalism entirely, except in a very modified form. The combination in the upper limb skeleton of *Proconsul africanus* of characters typical of quadrupedal monkeys with those related to some degree of brachiation (a combination which might reasonably have been anticipated in primitive apes of the Early Miocene) appears to indicate that the specialised brachiating habits characteristic of the Recent Pongidae were not fully developed till much later.

Thus, the generalised nature of the upper limb of *Proconsul* (as determined by the authors of this monograph) has a special relevance for questions of the phylogeny of the several evolutionary radiations of the Hominoidea which, it has been inferred from general palaeontological evidence, were beginning to undergo diversification about this time. In particular, it is now clear that the question is no longer debatable whether a pongid stock should be excluded from hominid ancestry on the grounds that the Pongidae as a whole manifest a too divergent degree of specialisation in their limb morphology. For we now know for certain that in the earlier stages of the pongid sequence of evolution specialisations of such a type had not yet been established. But apart from general considerations, the comparative studies reported in this monograph have wide implications for all students of Primate phylogeny who recognise the importance of interpreting structural modifications of the limb skeleton in terms of functional specialisations.

W. E. Le Gros Clark

ACKNOWLEDGEMENTS

The authors are deeply indebted to Professor Sir Wilfrid Le Gros Clark for giving them the opportunity to study this unique material. His continual guidance and advice at all stages of this work have been a constant source of encouragement. They are further greatly indebted to him for his kindness in writing a preface to this monograph.

They would like to express their gratitude and to acknowledge the skill of Dr. L. S. B. Leakey and his staff at the Coryndon Museum, Nairobi, who carried out the critical task of development and preliminary identification of much of the fossil material contained in the blocks.

Thanks are also due to Dr. Errol White, Keeper of the Department of Palaeontology, British Museum (Natural History), to Dr. K. P. Oakley for his great interest, to Dr. A. T. Hopwood for valuable advice, and to the many friends and colleagues who have interested themselves in this investigation and have provided comparative material for study. The authors are particularly indebted in this respect to Dr. F. C. Fraser and Miss J. E. King of the Osteology Department of the British Museum (Natural History), to Professor E. W. Walls of the Middlesex Hospital Medical School, to Professor J. D. Boyd of the Anatomy School, Cambridge, and to Miss Jessie Dobson, Curator of the Hunterian Collection at the Royal College of Surgeons, London. Professor J. D. Boyd was also kind enough to lend a notebook, the property of the late Professor A. Macalister, and now in the possession of the Anatomy School, Cambridge. Gratitude is expressed to Dr. W. Osman Hill, Prosector of the Zoological Society of London, who not only has provided material for study but has also generously supplied the authors with facts. Grateful thanks are due to Professor Ruth E. M. Bowden for her advice in many aspects of this investigation and for reading and criticising the manuscript.

The majority of the drawings were made by Mrs. A. Besterman, and the photographs were taken and prepared by Mrs. P. Thomas, with the exception of the photograph of the block of matrix containing the hand bones, for which grateful thanks are due to Dr. L. S. B. Leakey. Invaluable help is acknowledged from Mrs. E. Broome in the preparation of the manuscript and the tables.

The authors are also indebted to the Boise Fund of Oxford University for a grant towards the cost of the illustrations, and to the Medical Research Council for a grant to one of them (J.R.N.) for secretarial assistance in work on the evolution of prehensility of the hand in monkeys and apes.

J. R. Napier
P. R. Davis

I. INTRODUCTION

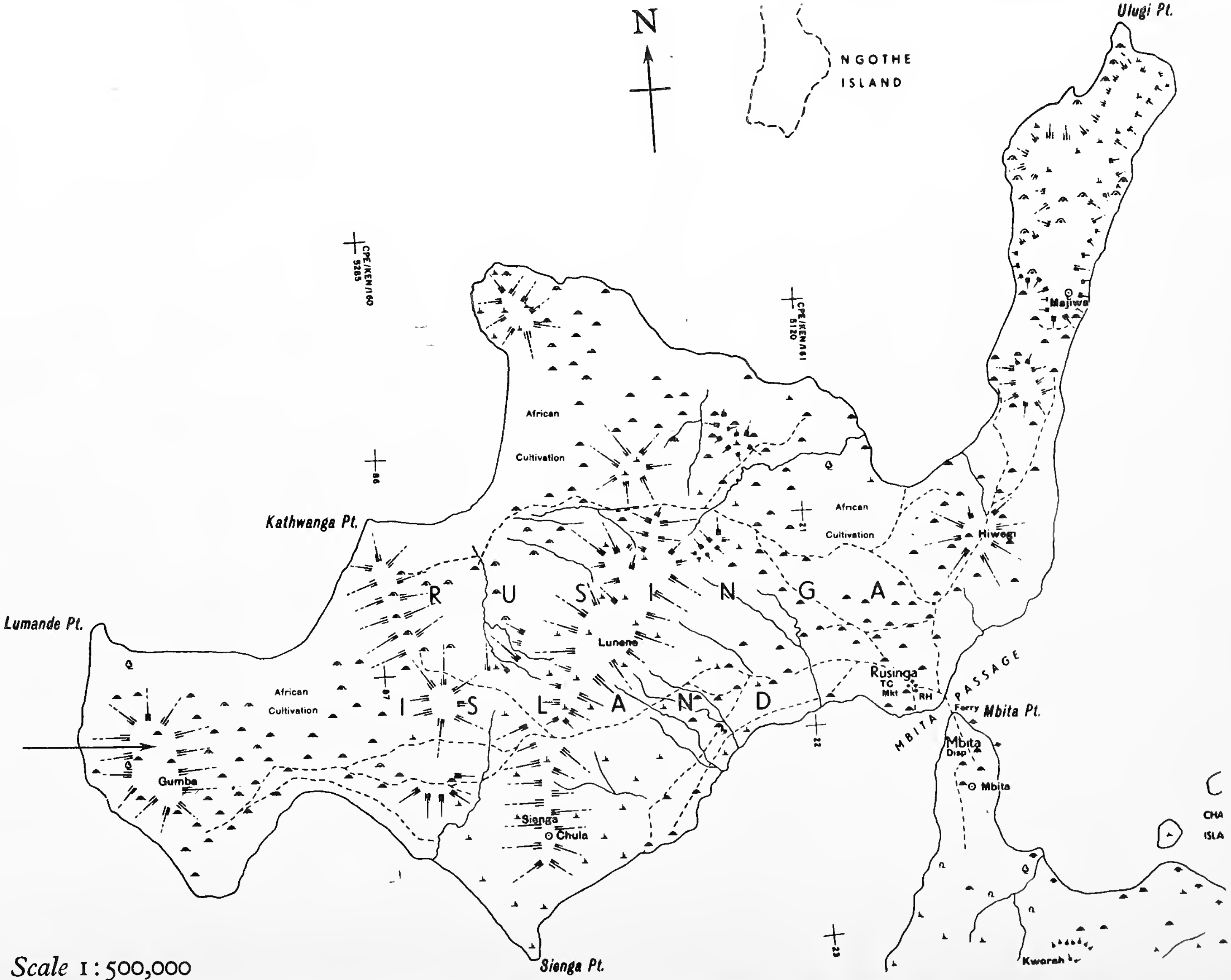
The fossil bones described in this paper were collected in 1951 from the Miocene sediments of Rusinga Island at the mouth of the Kavirondo Gulf of Lake Victoria. The bones are those of a single young adult of the genus *Proconsul* (Hopwood, 1933). The evidence provided by the upper and lower dentition, which were found closely associated with the limb fragments in the same block, indicates that the fossil bones are those of *P. africanus* Hopwood, the smallest of the three known species of the genus.

Although a large number of fossil bones of *Proconsul* have been discovered in the last ten years on Rusinga Island, Moboko Island and sites such as Songhor on the adjacent mainland of Kenya, limb bones have been poorly represented. The only previous discoveries relating to the upper limb include a portion of the shaft of the left humerus from Moboko (Le Gros Clark & Leakey, 1951) and two separate fragments of clavicles, one from Moboko, the other from Rusinga. The discovery of the fore-limb bones of *P. africanus* is therefore an event of considerable moment, for they constitute the oldest and most complete skeleton of the hominoid fore-limb so far known. It is clear that these bones belong to one of the most significant periods of Primate evolution; a period when the generalised catarrhine stock was emerging from a prolonged phase of arboreal quadrupedalism with its limited opportunities for adaptive radiation and was entering upon a phase that provided a diversity of environmental opportunity leading ultimately to the emergence of four distinct patterns of locomotion among the Anthropoidea: (1) arboreal quadrupedalism, (2) terrestrial quadrupedalism, (3) brachiation, (4) terrestrial bipedalism.

The fore-limb bones, which include part of the left humerus, the radius, a portion of the ulna and a number of bones of the hand, were associated with a well-preserved mandible with a complete dentition including the unerupted third molar on both sides, a portion of the right maxilla and premaxilla with the posterior premolar and first two molar teeth *in situ*, certain fragments of the occipital bone, a fully preserved right temporal bone and the following bones of the right foot: medial cuneiform, first metatarsal, the phalanges of the hallux and several other phalangeal and metatarsal fragments. An account is given of this associated material, but it is intended to make a more detailed analysis of the temporal bone and of the skull as a whole at a later date.

Geological and Palaeo-geographical Considerations

The fossil bones were recovered by Dr. T. Whitworth during the course of a geological survey a few hundred yards north-west of the summit of Kiakanga Hill on the Gumba Peninsula in south-west Rusinga (Fig. 1). The site consisted of a small circular pipe-like body of fine, green tuff which was very compact and lacked clear bedding. The pipe appeared to cut vertically through a group of bedded sediments termed the Flaggy Series (Whitworth, 1953), and probably represented an



Scale 1 : 500,000

FIG. 1. Map of Rusinga Island showing site of discovery (arrowed) of the Gumba skull and limb bones.

in-filled pot-hole of Miocene age. A profusion of mammalian fossils found in this restricted pocket suggests that, for a certain time, the pot-hole may have acted as a trap for unwary animals that came there to drink.

The Flaggy Series of Gumba are probably equivalent to the Kathwanga and Kuru Series of Northern Rusinga (Whitworth, 1953) which are regarded by Shackleton (1951) as the youngest group of bedded Miocene sediments on the island. It is thus probable that the material filling in the pot-hole may be of a slightly later date than any member of the main sedimentary sequence on Rusinga, and its mammalian fossils a little younger than the other Miocene fossils collected there. It is not yet possible to give an absolute stratigraphic date for the fossil. Whitworth (personal communication), however, does not consider that the difference in age can be very great, since the mammals preserved in the pipe seem to be indistinguishable, on superficial examination, from the species which characterise the bedded Miocene rocks of the island.

As Le Gros Clark & Leakey (1951) have pointed out, the precise age of these beds is still somewhat equivocal. An early Miocene date has been generally accepted for the East African fossils (Andrews, 1911; Hopwood, 1933; Arambourg, 1933; Le Gros Clark & Leakey, 1951; MacInnes, 1956, 1957). Some doubt, however, has been cast on this dating by the presence in the deposits of mammalian genera usually associated with later Miocene horizons in other parts of the world; further work, now proceeding, may serve to elucidate this problem.

The palaeo-geography of the Kavirondo Gulf region in early Miocene times is clearly a matter of considerable importance in a study of the locomotor adaptations of *Proconsul.* The work of Dr. Kathleen Chesters (1957) on the palaeobotany of this region has somewhat altered the generally accepted picture of Miocene East Africa, that is, a region of open savannah and of scattered forests in the neighbourhood of water-courses. Her work has shown that, in this area, tropical rain forests abounded and contained great trees and an abundance of climbing plants, similar in these respects to the rain forests of equatorial Africa. The forests appeared to have extended to the edge of the numerous water-courses and lakes which formed the lacustrine and volcanic Kavirondo basin. There is reason to believe that between the forests there were open spaces or glades. The absence of swamps and the presence of open spaces of savannah-like terrain are points of some importance in the ecology of *Proconsul.*

Method of Study

After reconstruction, the fossil limb material has been compared with the limbs of certain modern Primates selected by reason of their particular locomotor habits. Certain safeguards relating to the age and source of the comparative material have had to be observed. It has not been possible to determine the sex of the fossil and therefore comparative material from both sexes has been employed.

The epiphyses of the long bones of the Gumba specimen are still open, with the exception of that for the medial epicondyle. The metacarpal and phalangeal epiphyses and those for the distal end of the radius and ulna were found lying separately in the matrix, and allocation of these to their appropriate shafts added to the difficulties of reconstruction. The extent of the epiphyseal ossification corresponded closely with the dental age, which was assessed on the basis of the unerupted third molars in both upper and lower jaws. The specimen therefore appears to be equivalent to the Juvenile 2 category of Schultz's classification (1941). The close correspondence between the epiphyseal and dental age, together with the circumstances of recovery, make it reasonably certain that the jaw and limb bones belonged to the same individual.

Schultz's classification is based on dental age alone, but his studies of the sequence of closure of the epiphyses in the orang and the chimpanzee (1940, 1941) make it possible to correlate the dental and epiphyseal ages in these forms. It was clearly important that only specimens whose epiphyseal ages were comparable with that of the fossil specimen should be used for this particular study. In fact, however, it proved impossible to obtain sufficient comparative material of an exactly similar age.

The material used is listed in Table I and, with one or two exceptions, the specimens are classified as either "Juvenile 2" or "Young adult". The designation of "Young adult" does not figure in Schultz's age grouping. For the purpose of our study, this category is defined as including those animals in which the permanent dentition is fully erupted, but in which certain epiphyses are still open, notably those of the proximal end of the humerus and the distal end of the radius and ulna. Such a grouping appears to be sufficiently valid for our purpose. It can be seen in Table I that in several specimens the skull was not available; in these individuals, the age group designation is based on the epiphyseal age alone, using Schultz's criteria (1941). A considerable amount of adult material has also been used in this investigation where a large sample was necessary for certain statistical methods. However, adult material has been used discretely and employed only where it was reasonably certain that there was unlikely to be any significant difference between it and Juvenile 2 material.

For comparative specimens wild-shot material was used as far as possible, but as it proved difficult to obtain sufficient specimens of the desired epiphyseal age from this source alone, captive material had to be employed in some cases. The status of each specimen is indicated in the table.

The comparative material has been selected on the basis of adaptive locomotor type rather than that of taxonomic affinity, for it has seemed to us that the purpose of this present study should be to elucidate the locomotor habits of *P. africanus* as far as is possible with the material at our disposal. Prior to the discovery of the present material the only available limb-bones attributable to *Proconsul* were a fragment of the humeral shaft (probably *P. nyanzae*), the upper extremity of the femur, the talus and the calcaneum. From these fragments Le Gros Clark & Leakey (1951) were unable to draw any definite conclusions regarding the locomotor habits of *Proconsul*. In general, however, they believed the animal to be "an active running and leaping creature, and in no way specialised for a purely arboreal habitat". In their study of the contemporary East African Lower Miocene form *Limnopithecus macinnesi*, Le Gros Clark & Thomas (1951) showed that certain features of the forelimb skeleton resemble that of the modern gibbon. They concluded, however, that *Limnopithecus* was not a brachiating animal "like the modern gibbon", but was nevertheless actively arboreal in its mode of progression. The evidence from these two Miocene forms suggests that brachiation, as practised by the modern gibbon, had not yet developed in these early Primates (indeed *Proconsul* might well have been terrestrial). The evidence does suggest a very active type of quadrupedal locomotion, involving at least some of the structural modifications that, in later forms, resulted in the establishment of fully-developed brachiation. In view of these studies it therefore seemed desirable that our comparative series should include representatives of the following locomotor groups:

1. Arboreal quadrupedalism.
2. Terrestrial quadrupedalism.
3. Brachiation.

As well as indicating the locomotor habits of *P. africanus*, it was hoped that the morphology of the upper limb skeleton might throw some light on the manner by which the brachiating habit of the higher Primates had evolved from that of quadrupedalism. The factors considered in the selection of the representatives of the three locomotor groups are discussed below.

Arboreal Quadrupedalism.—The guenons were selected to represent this form of locomotion in the first instance, for these monkeys as a group are habitually arboreal, inhabiting the high gallery and the closed canopy type of rain forests in the equatorial belt of Africa.

Individual species of *Cercopithecus* vary considerably in the degree to which they pursue an arboreal or terrestrial life. *C. aethiops*, for instance, of which at least twenty sub-species are known, is equally at home in open savannah or in the trees (Sanderson, 1957). The *nictitans* group of guenons are mainly arboreal, while the closely-related *Erythrocebus* group including the patas monkeys are almost exclusively terrestrial; other guenons such as the sub-species *C. a. schmidti* are arboreal but are known to descend from the trees to raid native plantations (Haddow, 1952).

During the course of the present investigation, certain structural similarities were noted between *P. africanus* and the New World monkeys which made it imperative that further consideration should be given to these types. Subsequently it became clear that certain genera of New World monkeys, among which no extant ground living forms are known (Hill, 1957), have perhaps a stronger claim to represent arboreal quadrupedalism than *Cercopithecus*, in which a period of terrestrial life during the late Miocene and early Pliocene cannot be excluded. It is possible that *Cercopithecus* may have to be regarded as secondary arboreal in habitat (Napier—in preparation). The New World monkeys, on the other hand, are generally believed to have remained arboreal since their presumed independent evolution from the Paleocene and Eocene prosimian stock of North America (Simpson, 1945). Thus, it seemed advisable to include certain New World genera in the arboreal-quadrupedal group. The genera selected for study include the fully quadrupedal forms, *Cacajao*, *Pithecia* and *Saimiri*. The Alouattinae, the Atelinae and *Cebus* were excluded from this category in view of their known locomotor specialisations, associated in the main with the possession of a prehensile tail (Hill, 1957). The Hapalidae were also excluded since the clawed cheiridia of these genera profoundly modify their mode of locomotion.

Terrestrial Quadrupedalism.—*Papio* is the only genus of habitually terrestrial

Table I

DETAILED LIST OF SPECIMENS INCLUDED IN JUVENILE SERIES

Species	Ref.	Sex	Source	Status	Permanent Dentition	Upper Limb Epiphyses	Classification
Pan troglodytes . .	A	?	B.M. (N.H.) 1948.5.4.3	W.S.	Fully erupted	Not completely closed	Young adult
Pan troglodytes . .	B	♂	B.M. (N.H.) 1924.8.6.1	W.S.	Fully erupted	Not completely closed	Young adult
Pan troglodytes . .	C	♂	B.M. (N.H.) 1887.12.1.1	W.S.	Skull not available	Fully open except distal humerus	Juvenile 2
Pan troglodytes . .	D	♀	R.F.H. School of Medicine	C.	Fully erupted	Not completely closed	Young adult
Pan troglodytes . .	E	♀	Middlesex Hospital Medical School	C.	Fully erupted	Not completely closed	Young adult
Pan troglodytes . .	F	?	Duckworth Collection	?W.S.	3rd molars unerupted, upper and lower canines unerupted	Fully open except distal humerus	Juvenile 2
Papio ursinus . .	A	?♀	B.M. (N.H.) 1865.12.8.27	C.	3rd upper molars erupting	Fully open except distal humerus and proximal radius	Juvenile 2
Papio anubis . .	B	♂	B.M. (N.H.) 1940.1.20.21	W.S.	3rd molars erupting	Fully open except distal humerus, med. epicondyle and prox. radius	Juvenile 2
Papio anubis . .	C	?♀	B.M. (N.H.) 36d	W.S.	Skull not available	Not completely closed	Young adult
Papio hamadryas .	D	?	B.M. (N.H.) 985a	W.S.	Skull not available	Not completely closed	Young adult
Papio cynocephalus .	E	♀	B.M. (N.H.) 1948.3.30.1	C.	3rd upper molars unerupted, upper 4th premolar erupting	Fully open except distal humerus and proximal radius and ulna	Juvenile 2
Papio anubis . .	F	♀	Private Collection	C.	1st and 2nd molars in lower jaw only	All fully open	?Juvenile 1
Papio anubis . .	G	?	Private Collection	C.	Skull not available	Fully open except distal humerus	Juvenile 2

TABLE I (*contd.*)

Cercopithecus sp.	A	♂	B.M. (N.H.) 1958.8.14.3	W.S.	Skull not available	Fully open except distal humerus, proximal radius and ulna	Juvenile 2
Cercopithecus cephus	B	?	B.M. (N.H.) 783f	C.	Skull not available	Fully open except distal humerus, proximal radius and ulna	Juvenile 2
Cercopithecus petaurista	C	?	B.M. (N.H.) 1863.8.16.1	W.S.	1st and 2nd molars in lower jaw only	All fully open	Juvenile 1
Cercopithecus mona	D	♂	B.M. (N.H.) 1938.7.7.6	W.S.	All fully erupted	Distal humerus, proximal radius and ulna closed, others open	Young adult
Cercopithecus mona	E	♂	B.M. (N.H.) 1938.7.7.7	W.S.	All fully erupted	Distal humerus, proximal radius and ulna closed, others open	Young adult
Ateles paniscus	A	?	B.M. (N.H.) 38b	C.	1st and 2nd molars in lower jaw only	All open except distal humerus	Juvenile 2
Ateles ornatus	B	?	B.M. (N.H.) 1548a	?C.	3rd upper molars erupted	All open except distal humerus and proximal ulna	Young adult
Ateles belzebuth	C	?	B.M. (N.H.) 54.12.11.1. 39d	C.	3rd upper molars erupting	All open except distal humerus	Juvenile 2
Cacajao calvus	A	?	B.M. (N.H.) 806b	W.S.	Skull not available	All still open	Juvenile 1
Pithecia pithecia	B	♂	B.M. (N.H.) 52.852	W.S.	Fully erupted	Not completely closed	Young adult
Pithecia pithecia	C	♂	Private Collection W. Osman Hill	?W.S.	Skull not available	Fully closed	Adult
Saimiri	D	?	Private Collection W. Osman Hill	?W.S.	Skull not available	All open except distal humerus	Juvenile 2
Presbytis (*Kasi*) *senex*	A	♀	B.M. (N.H.) 1950.7.17.7	W.S.	3rd molars upper jaw erupting	All open except distal humerus	Juvenile 2
Presbytis (*Kasi*) *senex*	B	♀	B.M. (N.H.) 1950.7.17.8	W.S.	Lower 3rd molars erupting. Canines erupting	All open except distal humerus	Juvenile 2
Presbytis (*Kasi*) *senex*	C	?	Private Collection	?W.S.	Skull not available	All open except distal humerus and proximal ulna	Juvenile 2

W.S. = Wild shot. C. = Captive.

quadrupeds included in this group, although several species are considered (Table I). *Mandrillus* was omitted since it is a forest form and consequently its purely terrestrial status is suspect (Hill, personal communication).

Brachiation.—Pan was selected to represent this functional group in view of the probable affinities of this genus with *Proconsul* (Hopwood, 1933). The present authors believe that to be fully comprehensive the term brachiation should include all those forms in which the arms are raised above the head to grasp a handhold or in order to swing the body forward during locomotion. Thus the Atelinae come within this wide interpretation of the term; their mode of locomotion is a highly specialised one which combines arboreal quadrupedalism with a form of brachiation associated with the use of a prehensile tail. This combination is unique, as Washburn (1950) has pointed out, and may represent a transitional stage between arboreal quadrupedalism and true brachiation. It is also interesting to note that Le Gros Clark & Thomas (1951) pointed out the resemblance in certain details between the limb bones of *Limnopithecus* and those of the Atelinae. *Presbytis*, or the Purple-faced monkey of Ceylon, is also included on the grounds of its known propensity for arm-swinging which was so graphically recorded by Tennent (1860). Hill (personal communication) states that *Presbytis* differs from the more typical langurs such as *Semnopithecus* in its more robust build and in its habit of using the fore-limbs for reaching for handholds above its head, a habit recalling the pongid type of brachiation.

It is clear, therefore, that the term brachiation as interpreted here covers a wide variety of activities. These include the perfected brachiation of the Hylobatinae, the modified but habitual brachiation of *Pongo*, the modified and occasional brachiation of *Pan* and *Gorilla*, the special form of brachiation associated with the use of a prehensile tail employed by the Atelinae, and the occasional brachiation displayed by some of the Colobidae, particularly by the Asian langur *Presbytis* (*Kasi*) *senex* Erxleben, 1777.

The following families or genera were selected to represent the three locomotor groups:

1. Arboreal quadrupedalism—*Cercopithecus, Pithecia, Cacajao, Saimiri.*
2. Terrestrial quadrupedalism—*Papio.*
3. Brachiation—*Pan, Ateles, Presbytis.*

II. DETAILED DESCRIPTION OF MATERIAL

THE SKULL FRAGMENTS

Proconsul africanus Hopwood, Specimen Rs. 51/1499

The skull material consists of a right temporal bone (Pl. 1, figs. 6, 7), a right maxilla (Pl. 1, figs. 3–5; Pl. 2, fig.10) containing the posterior premolar and the first two molar teeth, part of the occiput, and a number of small fragments of the cranial vault (Pl. 1, figs. 8, 9). In addition, both upper lateral incisors and the right central incisor were present separately in the deposit.

The mandible (Pl. 1, figs. 1, 2; Pl. 2, fig. 11), is badly eroded behind the position of the unerupted third molars, but in front of them it is relatively intact with a complete dentition.

Comparison of the Gumba skull and mandible with the holotype of *Proconsul africanus* from Koru (Brit. Mus. No. M.14084) described by Hopwood (1933), and with the skull R.1948.50 (R.106) and other skull fragments of the same species described by Le Gros Clark & Leakey (1951), has shown that the Gumba specimens are definitely those of a young individual of the genus *Proconsul*, and of the species *P. africanus*. The Gumba skull is slightly smaller in most dimensions than specimen R.1948.50. The presence of an almost intact maxilla and of a fragment bearing the external occipital protuberance has added to our knowledge of the morphology of the skull in this species.

Upper Dentition.—(Pl. 1, figs. 3–5; Pl. 2, fig. 10). The spatulate *right central incisor* has a very sharp thin biting edge. The mesial margin of the crown joins the incisive edge abruptly at a right angle, whereas the lateral margin merges into it in a gradual curve, the two margins converging posteriorly on an ill-defined basal tubercle: from this tubercle a rounded central ridge passes down the posterior aspect. The width of the biting edge is 6 mm. The *lateral incisors*, much smaller than the central, have a greatly modified spatulate form. Both margins of the crown incline medially. The posterior vertical ridge which runs from a well-marked basal tubercle descends to join the incisive surface at a point where the lateral margin joins the latter, the basal tubercle being a thickening of a well-marked cingulum. The *upper canines* are missing but from the appearance of the sockets were obviously very stout teeth: the lateral margin of the alveolus of the right maxillary fragment is missing in the region of the canine, but sufficient is left to show that the dimensions of the root of the tooth where it borders on the crown were approximately 7 mm. antero-posteriorly and 8 mm. transversely. The depth of the socket from the alveolar margin is 16 mm., the rocket presenting a marked ridge in its antero-medial wall suggesting grooving of the canine root.

The *anterior premolar* is also missing, but the socket for its lingual root is intact, its dimensions on the alveolar surface being 3·5 mm. antero-posteriorly and 5 mm. transversely; the depth of the socket is 10 mm. The *posterior premolar* is intact and is in position in the maxillary fragment; it has a marked posterior cingulum. The two cusps and the central transverse ridge that connects them are closer to the anterior margin than the posterior. Le Gros Clark & Leakey (1951) believe that the labial cusp projects much more in males than in females; the labial cusp projects somewhat beyond the level of the lingual cusp in the Gumba specimen, but the difference is not marked, and suggests that the Gumba specimen may have been female.

The molar teeth correspond closely to those described in other specimens of *Proconsul.* In the *first molar* the hypocone and protocone are approximately the same size; the metacone is joined to the protocone by a sharp ridge. A small protoconule is present. The internal cingulum is well marked and is conspicuously beaded. The *second molar* differs slightly from the previous descriptions of *Proconsul* teeth in that the hypocone is somewhat smaller than the protocone; it is, however, continuous with the internal cingulum which again is well marked and beaded. In both molars the posterior cingulum is but weakly developed. Part of the root of the second molar is visible owing to erosion of the maxillary fragment, and the pulp canal is still widely open. The alveolar cavity for the unerupted *third molar* is also visible, but is filled with débris which includes part of the crown of the tooth.

The overall dimensions of the crowns of all the teeth from this specimen are given in Table II.

LOWER DENTITION.—(Pl. 1, figs. 1, 2; Pl. 2, fig. 11). The mandibular teeth are all present *in situ* in the mandible; the last molars are unerupted on either side. Unfortunately the anterior margin of the mandible has been crushed and the crowns of the two central incisors and of the left lateral incisor and left canine are extensively damaged.

The remains of the *central incisors* suggest that they were long, narrow, chisel-shaped teeth. The intact right *lateral incisor* has a sharp biting edge which joins the medial margin of the tooth at right angles: the lateral margin of the tooth joins the incisive edge in a broad curve. The intact *right canine* is relatively short and has a sharp point; it has a slight labial inclination but this is probably due to the crushing of the anterior part of the mandibular fragment. It possesses a convex labial surface with sharp anterior and posterior borders; the anterior margin continues into a much reduced internal cingulum. The lingual surface is flat.

The *anterior premolar* is sectorial, being compressed laterally and lying obliquely in the axis of the tooth row. The main cusp is markedly convex laterally and flattened medially. The crest separating these two surfaces anteriorly extends down from the apex to the anterior extremity of a well-marked internal cingulum. Posteriorly the two surfaces are separated by a deep groove which leads downwards to a very small talonid. The trigonid cusps of the *posterior premolar* are unequal, the labial cusp being much the larger; they are connected by a sharp low crest behind a small fovea. The low-lying talonid is well developed.

The proto-, meta- and hypoconids of the *first molar* are of approximately equal size, the metaconid and hypoconid having a broad area of contact owing to the small size of the entoconid. The hypoconulid is small and median in position; there is a small anterior fovea by the anterior margin of the crown. A reduced external cingulum is present anteriorly and has some beading; it also appears between the protoconid and hypoconid. The *second molar* has a much broader crown than the first; the features of its crown, however, are very similar to those of the first molar except that the hypoconulid is displaced somewhat laterally to the median axis of the tooth. Neither of the *third molars* has erupted, but the eroded surface of the left ascending mandibular ramus shows a small point of enamel from the unerupted crown of that

TABLE II

OVERALL CROWN MEASUREMENTS (mm.) OF THE DENTITION OF *P. AFRICANUS* Rs. 51/1499

	Condition	Ht.	A.P. diameter	Tr diameter	Index $\frac{\text{Tr.}\times 100}{\text{A.P.}}$	
		UPPER DENTITION				
Right side						
Central incisor	Free. Fractured but complete .	8·5	5·2 (at root)	5·5	105·8	
Lateral incisor	Free. Fractured but complete . .	6·5	5·1 (at root)	3·7	72·5	
Canine	Missing					
Ant. Premolar	Missing					
Post. Premolar	Intact in maxillary fragment . .	4·5	5·0	8·8	176·0	
1st Molar	Fully erupted . .	4·5	7·9	9·7	122·8	A.P. of $\frac{\text{M1}}{\text{M2}}=95\cdot2$
2nd Molar		4·5	8·3	10·2	122·9	
3rd Molar	Missing					
Left side						
Lateral incisor	Free. Fractured but complete . .	6·5	5·2 (at root)	3·5	67·3	
		LOWER DENTITION				
Left side						
Central incisor	Fractured root. Partly eroded Roots not clear of mandible	—	—	—		
Lateral incisor	Fractured root. Badly eroded	—	—	—		
Canine	Badly eroded . .	—	—	—		
Ant. Premolar	Intact	9·2	8·7	5·8	66·7	
Post. Premolar	Intact	5·2	5·7	6·1	107·0	
1st Molar	Intact	4·9	8·4	7·6	90·5	A.P. of $\frac{\text{M1}}{\text{M2}}=85\cdot7$
2nd Molar	Intact	5·0	9·8	8·3	84·7	
3rd Molar	Unerupted					
Right side						
Central incisor	Fractured root. Partly eroded Roots not clear of mandible	—	—	—		
Lateral incisor	Fractured root. Tip, slight erosion	10·0	5·2	4·7		
Canine	Intact	11·8	7·0	6·7	95·7	
Ant. Premolar	Intact	9·1	8·6	5·7	66·3	
Post. Premolar	Intact	5·0	5·4	6·3	116·7	
1st Molar	Intact	4·9	8·7	7·5	86·2	A.P. of $\frac{\text{M1}}{\text{M2}}=88\cdot8$
2nd Molar	Intact	4·9	9·8	8·3	84·7	
3rd Molar	Unerupted . .	—	—	—		

tooth on the left side. Radiography of the specimen shows the two mandibular teeth in position within the fossil material.

Since the specimen is immature the importance of the unerupted third molars is very great, for they give a clear indication of the developmental age of the specimen; as will be seen, an accurate assessment of age is an essential part of the analysis of the limb material.

THE MANDIBLE.—(Pl. 1, figs. 1, 2; Pl. 2, fig. 11). The mandibular fragment consists of the horizontal rami of both sides, the coronoid and condyloid processes having been broken off at about the level of the molar crowns. The left ramus is fractured between the two premolars, the fragments fitting perfectly when brought together. The outside of the right ramus had become distorted during fossilisation in the region of the premolar teeth, but the internal bone surface is intact: the anterior alveolar margin is slightly crushed.

The jaw is heavily built, and has the following dimensions:

	Lt.	Rt.
Mid-line anterior length of symphysis . . .	24 mm.	
Maximum antero-posterior thickness of symphysis .	11·5 mm.	
Height of body opposite first molar tooth . . .	18 mm.	19 mm.
Maximum thickness of body opposite first molar tooth	10 mm.	10 mm.
Total length of premolar-molar series (M3 added from radiographs)	42·5 mm.	42·5 mm.

There is no trace of a symphysial line, the symphysis having fused completely. The anterior surface of the symphysis slopes evenly downwards and backwards at about 60° from the horizontal and ends inferiorly in a very small tubercle for the mylohyoid raphe. The posterior aspect of the symphysis also slopes downwards and backwards in its upper part, but in its lower third it becomes almost vertical; it shows a small genial fossa 8 mm. above the lower border. There is no simian shelf.

The body of the mandible is robust and has a thick, rounded lower border, although in the region of the last molar tooth the inferior border narrows and is very thin behind the position of the molar teeth. The outer surface of the horizontal ramus exhibits a shallow concavity in its upper half opposite the posterior premolar and the first molar tooth. The mental foramen could not be identified on either side. Posteriorly the inner aspect of the horizontal ramus shows the lower end of a rounded ridge which ran down from the condylar process to the posterior alveolar border. The angle of the mandible is concave on the inner aspect in the region of attachment of the medial pterygoid muscle, the surface of the bone in this region being smooth.

The general appearance and relative dimensions compare closely with those of the mandible of *Proconsul africanus* described by Le Gros Clark & Leakey (1951:27).

THE RIGHT MAXILLA.—(Pl. 1, figs. 3–5; Pl. 2, fig. 10). This fragment consists of part of the body of the maxilla together with an almost intact pre-maxilla: the sutures are well shown.

The alveolar process shows some erosion anteriorly but is virtually intact posteriorly and contains the posterior premolar and first two molar teeth: behind the second molar the wall of the cavity which contained the developing crown of the third molar tooth has been eroded in part, and remnants of the third upper molar tooth crown are present in a matrix of débris. The body of the maxilla is deficient superiorly and posteriorly, but the root of the zygomatic process has been preserved; the central part of the palatine process is also present and terminates medially in the septal crest (Pl. 1, fig. 5); the frontal process is relatively intact and contains a single infra-orbital foramen.

The lateral surface of the specimen exhibits the premaxillo-maxillary suture running up from the anterior border of the socket for the canine tooth to the lateral margin of the nose, but its upper extremity cannot be defined. Behind the canine socket there is a shallow canine fossa, and behind this again the root of the zygomatic process joins the body opposite the first molar tooth and the anterior portion of the second. The frontal process curves medially in its upper part, and the single infra-orbital foramen faces downwards and a little forwards. On the medial aspect of the fragment the premaxillo-maxillary suture runs upwards and a little backwards from the incisive canal in front of the ridge for the attachment of the inferior turbinate, and superiorly it runs forwards. Unfortunately at this point the premaxilla had been slightly eroded and the suture lost; this erosion also involved the anterior margin of the frontal process of the maxilla and the exact point of junction cannot be defined. From the posterior end of the ridge for the attachment of the inferior turbinate, a ridge marking the anterior border of the naso-lachrymal groove ascends upwards close to the posterior margin of the medial aspect of the frontal process.

The floor of the relatively large antrum is smooth and rounded and lies opposite the posterior premolar and first two molar teeth. It exhibits small grooves for those branches of the palatine nerves and vessels which enter from behind. Anteriorly the canal for the anterior superior dental nerve is visible below the infra-orbital foramen.

The palate is arched slightly upwards; the incisive foramen is large and has an antero-posterior diameter of 4 mm. The width of the palate from the inner aspect of the first molar to the septal process in a horizontal plane is 9·5 mm., giving a probable total palatal width between the first molar teeth of 19 mm. Le Gros Clark & Leakey (1951) estimated the molar palatal width in R.1948.50 as 22 mm. The differences in palatal width may perhaps be explained by the greater overall size of the R.1948.50 skull, and the immaturity of the Gumba specimen.

The Occipital Bone.—(Pl. 1, figs. 8, 9). There are four major fragments of the occipital bone which fit together. Unfortunately they cannot be aligned with the rest of the skull fragments as there is no area of contact. The largest of the pieces consists of part of the post-occipital element behind the foramen magnum, but neither the foraminal border itself, nor either condyle, is present on the fragment. There is a well-marked groove for the superior sagittal sinus in the midline, terminating below in the confluence of the sinuses. The superior occipital fossae are well marked. On the outer surface the inferior part of the fragment exhibits a large external occipital protuberance, the small basal portion of the bone being at an angle of about 100° to the remainder of the external surface. The superior nuchal lines are prominent features and arch laterally to the margins of the specimen. From the external protuberance a low midline rounded ridge runs upwards for a distance of 22 mm.

and then fades into the rounded surface of the remainder of the vault. No parieto-occipital suture is visible, although it is possible that it ran along the fracture line between the basal fragment and the remainder of the specimen and is thus obscured.

The Right Temporal Bone.—(Pl. 1, figs. 6, 7). The temporal fragment consists of the main part of the petrous temporal bone, part of the tympanic plate, the condyloid fossa and the root of the zygomatic process, with small parts of the squamous temporal still attached.

The articular fossa is broad and deep and is slightly convex from side to side, having a maximum width of 13 mm. Behind the fossa is a well-marked post-glenoid process. The articular eminence is well marked and slightly convex from side to side. On its medial aspect there is a low crest, the lateral side of which is covered by articular bone which may have acted as a guide for the condyle as it slid forwards on to the articular eminence.

The external auditory meatus is round, and is 4 mm. in diameter; unfortunately its depth could not be plumbed since it is filled with matrix. The tympanic plate is broad, and measures 10 mm. antero-posteriorly. Behind the tympanic plate the root of the styloid process is visible within a small pit. The styloid process is a very slender piece of bone rather less than a millimetre in diameter. Behind, lateral, and very close to the styloid process, is the narrow stylo-mastoid foramen, less than a millimetre in diameter. Extending backwards from the stylo-mastoid foramen the suture between the pro-otic and epi-otic parts of the bone is still visible in part.

On the inferior surface the apex of the petrous temporal has been eroded beyond the region of the carotid canal, the canal itself being circular and 2·5 mm. in diameter at its inferior opening: behind it is a deep groove for the passage of the internal jugular vein and, between the two, a minute foramen is visible for the tympanic branch of the glossopharyngeal nerve.

The posterior aspect of the petrous temporal exhibits a large internal auditory meatus 3·5 mm. in diameter. In the depth of the meatus the crista falciformis is clearly visible, and below it the foramen centrale cochleae and the area cribrosa inferioris are well marked. Postero-lateral to the meatus lies the opening of the subarcuate fossa, which measures 2·5 mm. transversely and 4·5 mm. in the vertical diameter. It is deep, but, again, the full extent of its depth cannot be plumbed. There is scope for further work on the petrous temporal bone: preliminary radiographs have shown that the lateral canal can be visualised, and it is hoped that the orientation of this canal within the bone can be determined by further study.

The skull as a whole.—Apart from the occipital fragments, the various remains of the skull do not have areas of contact with each other, so that reconstruction is difficult, and has not, so far, been attempted. However, the maxillary and occipital fragments suggest that the previous reconstructions of the skull of *P. africanus* may require modification. Robinson (1952) in his reconstruction of the 1948 skull (R.1948.50), indicates a nasal aperture which slopes markedly backward, even though the marked prognathism shown in the first reconstruction (Le Gros Clark & Leakey, 1951) has been amended. The maxillary frontal process and premaxilla of the Gumba specimen lie nearly vertically, and even when allowance is made for the increasing prognathism that might have occurred during later development, it seems unlikely that the adult facial profile angle would have been as small as that shown in either of the two reconstructions.

The angle between the base and vault of the occipital fragment at the external occipital protuberance is relatively small: this provides evidence that Robinson's reconstruction of the posterior region of the vault is correct, and that the curvature of the vault was, as Le Gros Clark & Leakey (1951) intimated, cercopithecoid rather than pongid.

It is hoped that a fuller consideration of these points will be published at a later date.

THE BONES OF THE LEFT FORE-LIMB

A grossly fragmented portion of the distal end of the right humerus has been preserved, but does not merit separate description. Apart from this, all fore-limb material to be described is of the left side.

The bones of the left fore-limb are represented by the distal two-thirds of the humerus, a virtually complete radius, and the distal end of the ulna. Of the carpus only the trapezoid and the centrale are missing. The second, third, fourth and fifth metacarpals are virtually complete, as are several phalanges, including the proximal phalanx of the thumb.

THE HUMERUS (Pl. 3, figs. 12–14; Pl. 4, figs. 16, 17).

The left humerus is a well-preserved bone that has suffered some forward angulation and compression in the mid-shaft region during fossilisation. The proximal quarter of the shaft is missing, the fracture line passing just above the lowest part of the groove for the insertion of the tendon of latissimus dorsi. The upper part of the specimen is twisted laterally, relative to the distal part; this post-mortem torsion of the shaft was estimated at 10°. These various distortions have been allowed for in the reconstruction (Plate 4). The distal portion of the shaft including the articular surface is well preserved, lacking only the epiphysis for the medial epicondyle.

Reconstruction and comparison.—The length of the humerus was estimated by reference to the groove for the tendon of latissimus dorsi, the lower end of which is apparent at the proximal end of the fragment. This groove lies in the floor of the bicipital groove mid-way between the buttress for the lesser tuberosity medially and the delto-pectoral crest laterally. Its lower margin is well defined. The groove is readily apparent in most extant Primates (Text-fig. 2) and its lower margin can usually be defined precisely in *Cercopithecus* and *Papio*, where it forms a short, irregular scaphoid fossa. On the other hand the groove is broader and less sharply curved at its lower margin in *Pan*, *Ateles* and *Hylobates*.

The length of the humerus below the groove (Text-fig. 3 Lg) was measured in both juveniles and adults of a comparative series, and expressed as a percentage of the total length of the humerus (Text-fig. 3 Lc) by means of the index $\frac{Lg \times 100}{Lc}$. The mean values for the indices of 26 juvenile specimens of *Pan*, *Cercopithecus* and *Papio*

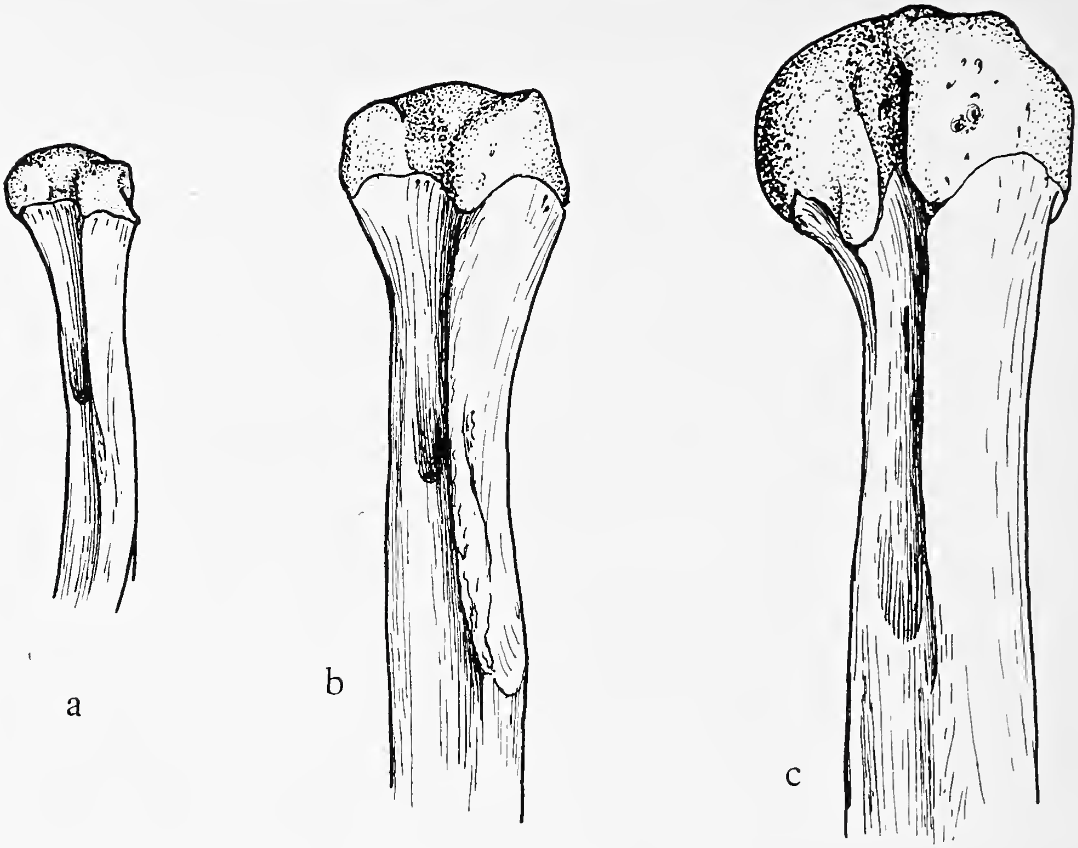


FIG. 2. Drawings of the upper end of the humerus of (*a*) *Cercopithecus*, (*b*) *Papio*, (*c*) *Pan*, showing the groove for the insertion of the tendon of latissimus dorsi. Natural size.

were calculated and the results are given in Table IV, the data being fully set out in Appendix 1 (Index 1). The index was also calculated for 42 adult specimens of the same three genera. There was no significant difference (Table III) between the adult and juvenile indices in any one genus or between the indices of the different genera. The indices of both the juvenile and adult series were very similar and consequently it was thought justifiable to sum them to provide a single mean.

TABLE III

RELATIONSHIP BETWEEN LENGTH OF HUMERUS BELOW GROOVE FOR LATISSIMUS DORSI (*Lg*) AND TOTAL LENGTH OF HUMERUS (*Lc*) IN OLD WORLD GENERA

Genus	Juvenile			Adult		
	Number of specimens	Mean value $\frac{Lg \times 100}{Lc.}$	S.D. (mm.)	Number of specimens	Mean value $\frac{Lg \times 100}{Lc.}$	S.D. (mm.)
Pan . .	6	72·9	1·4	10	72·2	1·6
Cercopithecus .	11	72·8	2·0	26	71·8	1·7
Papio . .	9	73·5	3·0	6	70·9	1·8

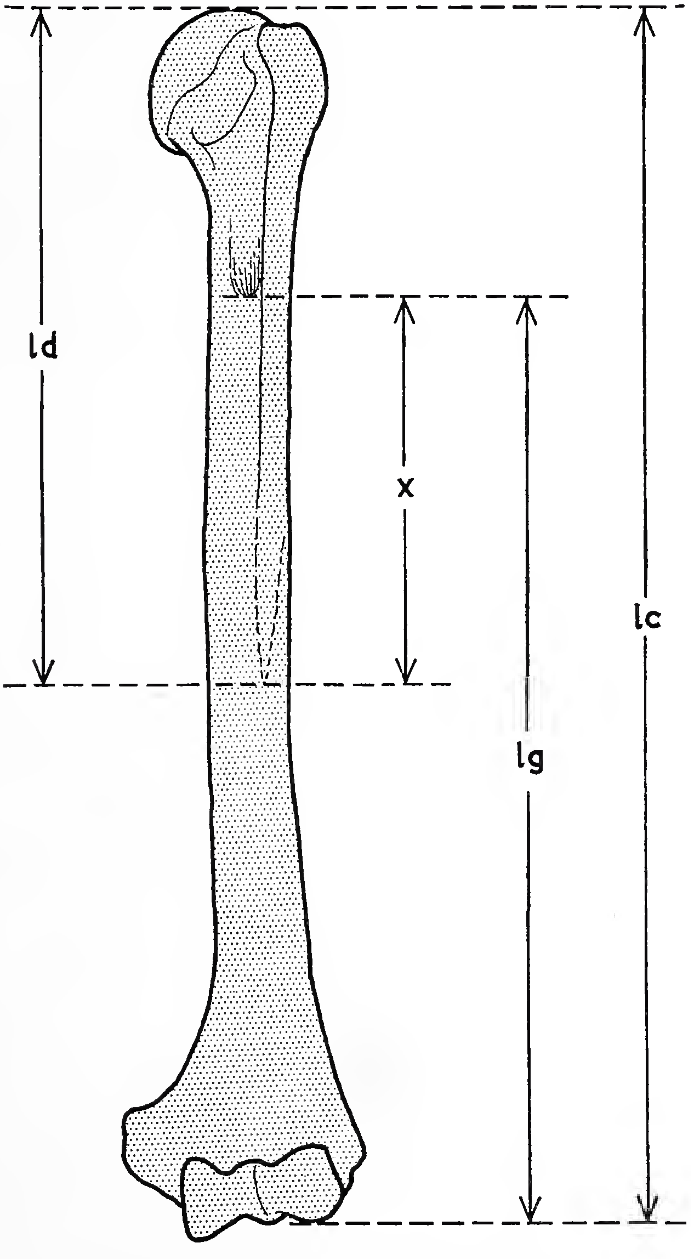


FIG. 3. Diagram to show measurements of the humerus employed in the construction of indices.

In the 68 specimens the mean value for $\frac{Lg \times 100}{Lc}$ was found to be 72·3 (Standard deviation = 1·95). Applying the mean figure to *P. africanus* the total length of the bone was calculated to be 182 mm. In view of the constant relationship between the length of the humerus below the groove (*Lg*) and the total length of the bone (*Lc*) in adult and juvenile Old World monkeys and apes, it seems reasonable to assume that the index in *P. africanus* lay within the range of one Standard deviation to either side of the mean, providing extremes of 177 mm. and 187 mm. The mean figure of 182 mm. was employed in the diagrammatic reconstruction.

The form of the proximal end of the humerus and the torsion of the head was determined by reference to the cross-sectional appearance of the humerus in *Papio*, *Pan*, *Cercopithecus* and *Presbytis*. Transverse sections of the bones were made through the lower end of the groove for the tendon of latissimus dorsi to allow a direct comparison with the fossil humerus, which was broken off at this level. The bones were orientated in the plane of the elbow joint and photographed in cross-section. From these photographs tracings were made (Text-fig. 4).

Sections of the humeri of *Papio*, *Cercopithecus* and *Pan* present a somewhat triangular appearance, while those of *Presbytis* and *P. africanus* are rhomboidal, the medial and posterior angles being formed by the buttresses for the lesser tuberosity

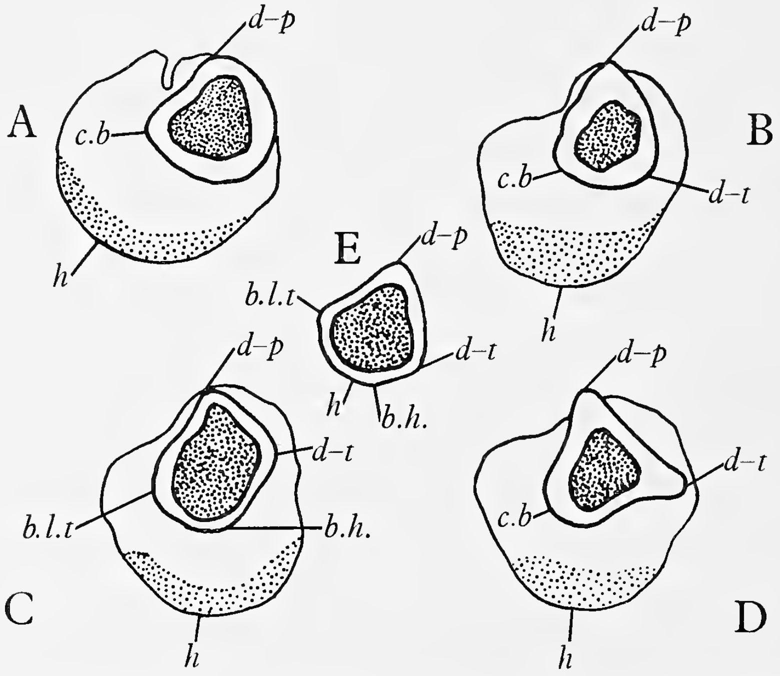


Fig. 4. Drawings of the upper ends of the humeri of four Primates after section through the upper part of the groove for latissimus dorsi, compared with the cross-sectional appearance of the upper end of the humeral fragment of *P. africanus*. × ⅔. (A) *Pan*, natural size; (B) *Papio*, × 2; (C) *Presbytis*, × 3; (D) *Cercopithecus*, × 2; (E) *P. Africanus*, × 2. In each case the plane of the lower end of the humerus lies transversely. Note thickness of cortex in each case. (*d-p*. Delto-pectoral crest. *d-t*. Delto-triceps crest. *b.l.t.* Buttress for lesser tuberosity. *bh.* Buttress for head. *c.b.* Combined buttress for head and lesser tuberosity. *h*. Direction of axis through centre of articular surface of head.)

and the head respectively. In *P. africanus* and *Presbytis* these buttresses are found as discrete elevations at this level. The two buttresses have already met and fused above this level in *Papio*, *Cercopithecus* and *Pan*, thus presenting a single instead of a double eminence in the cross-section. The manner in which this fusion takes place deserves mention in view of the importance attached to these buttresses for the determination of the torsion of the head (Le Gros Clark & Thomas, 1951). Immediately below the articular margin, the buttress for the head broadens out to form a bracket; below this level it narrows, forming a sharply curved ridge which is directed obliquely, winding forwards and laterally round the medial aspect of the shaft towards the buttress extending down from the lesser tuberosity. The two buttresses meet and fuse in the region of the neck in *Papio* and *Pan*, and at a somewhat lower level in *Cercopithecus*. In *P. africanus*, *Ateles* and *Presbytis* the buttresses remain discrete until they spread out and blend into the surface of the shaft above its middle third. The difference in the levels of fusion of the buttresses accounts mainly for the difference in the cross-sectional appearance (Text-fig. 4) of the various forms.

Le Gros Clark & Thomas (1951) were able to deduce the torsion of the humeral head of the Miocene hominoid *Limnopithecus macinnesi* by reference to the position of the head buttress, for only the articular region of their specimen was missing. As has already been discussed the two buttresses have fused at the level of the section in *Pan*, *Papio* and *Cercopithecus*, so that the torsion of the head of these forms could not have been deduced from the cross-sectional appearance. Fortunately, the discrete nature of the head buttress in *P. africanus* makes it reasonably certain that there was considerably less humeral torsion in the fossil bone than in modern *Pan*, where the head of the humerus is directed postero-medially. It is also clear that the torsion in *P. africanus* was greater than that in *Cercopithecus*, *Presbytis* or *Papio*, in which forms the head faces more nearly backwards: in the reconstruction the head has arbitrarily been placed midway between the position in these three forms and that of *Pan*.

The deltoid insertion.—The angularity of the lateral aspect in the cross-sections of the bone in *Cercopithecus* and *Papio* is due to the presence of the delto-triceps crest (Text-fig. 4). This crest, which is moderately well marked in *P. africanus* and *Presbytis*, is typical of terrestrial and arboreal quadrupeds. It is absent in the more specialised brachiators *Pan*, *Ateles* and *Hylobates*. The difference can presumably be related to the differences in locomotion and fore-limb posture in these adaptive types. It is of interest to note that, while *P. africanus* clearly possessed the backwardly directed head of *Papio*, *Cercopithecus* and *Presbytis*, the shaft lacked the sharp angularity of the former two genera: in this respect, and in respect of its quadrilateral shape, it bears a striking resemblance to *Presbytis*. In Text-fig. 4 it can be seen that the cortex of the fossil bone is thinner than that of *Papio* and *Cercopithecus* and is similar to that of *Presbytis*.

The delto-pectoral crest of the fossil humerus is well marked and is rough and irregular in its upper portion (Pl. 3, figs. 12, 14). Proximal to the insertion of deltoid it becomes a smooth, well-rounded ridge that extends as far as the insertion, below which it is lost. A crest having a similar appearance is seen in *Pan*, *Ateles* and *Presbytis* (Pl. 5, figs. 18, 19): in these forms the delto-pectoral crest provides attachment in its upper, rougher and more prominent portion for the tendon of pectoralis major and the anterior fibres of deltoid, while the lower and smoother portion below the insertion of pectoralis major receives the anterior fibres of deltoid alone. In *Papio* and *Cercopithecus* (Pl. 5, figs. 18, 19) on the other hand, the sharp or roughened portion extends to the lower limit of the insertion of deltoid and gives attachment to both deltoid and pectoralis major throughout its length. These findings, based on dissections of this region in *Papio*, *Pan* and *Cercopithecus*, are clearly related to the fact that the deltoid reaches further down the shaft of brachiators than of non-brachiators. In Table IV the mean deltoid indices for the Juvenile Series are given, these indices being calculated from the formula $\frac{Ld \times 100}{Lc}$ where $Ld =$ distance from the head of bone to the lower limit of the deltoid insertion and $Lc =$ the total length of the bone (Text-fig. 3). The data on which this Table is based are included in Appendix I (Index 2).

Table IV

MEAN DELTOID INDEX IN BRACHIATORS AND NON-BRACHIATORS

	Genus	No. of specimens	Mean deltoid index	Range
Brachiators	*Pan*	6	55·6	52·5–57·6
	Ateles	3	48·3	47·9–49·4
	Presbytis	3	47·5	46·9–48·5
Non-brachiators	*Cercopithecus*	5	43·7	41·7–46·3
	Papio	8	42·0	48·3–46·6
	New World monkeys	3	42·8	39·7–48·8

The deltoid index cannot be obtained in the fossil bone as the proximal portion of the shaft is missing. However, it is clear that the distance between the lowest point of insertion of deltoid and some other fixed point proximal to it would also provide an indication of the extent to which the deltoid reaches down the shaft. The lower margin of the groove for latissimus dorsi was selected as this proximal landmark since the level of insertion of this muscle is fairly constant in all genera under consideration (Table IV). The distance X (Text-fig. 3) between the lower margin of this groove and the most distal point of insertion of the deltoid was expressed as a percentage of the length (Lg) of the bone below the groove by means of the formula: $\frac{X \times 100}{Lg}$.

The values for X are given in Table V, and the data are set out in Appendix I (Index 3). The table shows that the value for X is greater in brachiators than in non-brachiators, due to the greater extension of the deltoid insertion in the former. In this respect, *P. africanus* shows an affinity with the brachiators, particularly *Pan*.

Robusticity of humerus.—The robusticity of bones varies not only with functional requirements of different species, but also with absolute size within the species. Thus, in comparing the robusticity of the fossil humerus with modern juvenile forms, only

TABLE V

THE MEAN VALUES OF $\frac{X \times 100}{Lg}$ IN BRACHIATORS AND NON-BRACHIATORS

	Genus	Number of specimens	Mean $\frac{X \times 100}{Lg}$	Range
Brachiators	*Pan* . .	6	39·6	32·5–44·3
	Ateles . .	3	30·9	30·4–31·9
	Presbytis .	3	29·7	27·3–31·2
Non-brachiators	*Cercopithecus*	5	23·5	20·0–26·0
	Papio . .	8	21·4	17·8–26·8
	Proconsul .	1	37·9	—

those forms have been selected that are of comparable size and weight. As there appeared to be no significant difference between the robusticity of juveniles and adults of any species, adults were also included in the series. The robusticity index of the fossil humerus is based on its mean calculated length. The index employed is equivalent to the "Stark-index" of Duerst and is based on the formula:

$$\frac{\textit{Circumference in mid-shaft} \times 100}{\text{Total length of bone}}$$

The robusticity of the fossil humerus is somewhat less than that of *L. macinnesi* and is intermediate between that of *Ateles* and *Papio*.

Curvature of the shaft.—The appearance of the humerus in antero-posterior and lateral views varies considerably in the three locomotor adaptive groups under consideration (Pl. 5, figs. 11, 12). In the lateral views the upper half of the bone in *Cercopithecus* has a well-marked anterior convexity which flattens out at a point corresponding to the insertion of deltoid; in the lower half, there is a shallow anterior concavity. In the terrestrial quadrupedal group, *Papio* has a similar appearance in profile, the anterior convexity of the upper half being a prominent feature. Among the brachiators, this anterior convexity is absent in *Pan* and *Ateles* and only moderately developed in *Presbytis* and the New World monkeys. It is apparent from the diagrammatic reconstruction of the fossil humerus (in which the distortions of the bone have been corrected) that the shaft had a moderately developed anterior convexity in its upper half, as in *Presbytis* and the New World monkeys.

In the antero-posterior view *Cercopithecus* has a very prominent lateral convexity affecting the whole shaft, the highest point of the curve corresponding approximately to the lowest point of insertion of deltoid. This lateral convexity is absent in *Papio*, *Pan* and *Ateles*. A lateral convexity appears in *Presbytis* and in New World monkeys but is less marked. A lateral convexity of the fossil bone cannot be entirely excluded in view of the absence of the proximal portion but, if present, it cannot have been marked. In general, therefore, the curvature of the shaft of *P. africanus* is neither typical of Old World terrestrial or arboreal quadrupeds nor yet of specialised brachiators such as *Pan* and *Ateles*. The curvatures more closely resemble those seen in *Presbytis*—an arboreal quadrupedal monkey with brachiating propensities.

Table VI

HUMERAL ROBUSTICITY INDICES IN MODERN AND FOSSIL PRIMATES

Genus	Number of specimens	Mean Robusticity Index	Range
Macaca . .	2	23·4	20·7–26·0
Papio . .	10	22·0	18·0–25·3
Cercocebus .	4	20·4	18·6–22·3
Limnopithecus .	1	19·3	—
Proconsul . .	1	17·2	—
Ateles . .	7	14·9	11·6–17·0

Lower end.—(Pl. 3, figs. 12–14; Pls. 4, 5). The lower half of the fossil humerus is complete except for the epiphysis for the medial epicondyle. Reconstruction of this epiphysis offered no special difficulties. It was important that some estimate should be reached of its probable size in view of the desirability of comparing the bi-epicondylar width of the fossil bone with that of modern forms. In Table VII, the width of the epiphysis is expressed as a proportion of the total bi-epicondylar width in a number of specimens in which the epiphysis is still unfused.

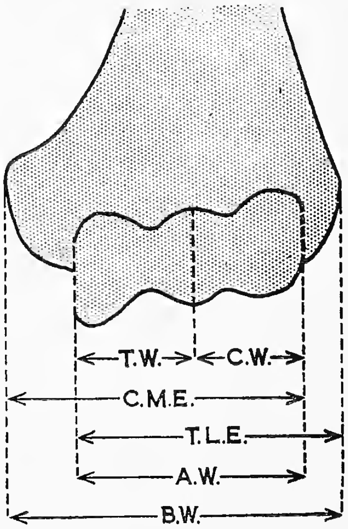


Fig. 5. Diagram to show measurements of lower end of humerus employed in the construction of indices.

TABLE VII

MEDIAL EPICONDYLAR INDICES IN SEVERAL MODERN FORMS

Genus	Reference Letter	E.W. (mm.)	B.W. (mm.)	$\frac{\text{E.W.} \times 100}{\text{B.W.}}$
Pan . .	F	3·0	60·0	5·0
Gorilla . .	—	4·0	89·5	4·5
Ateles . .	A	1·0	29·0	3·5
Ateles . .	B	1·0	26·0	4·8
Ateles . .	C	1·0	26·0	4·8
Papio . .	F	1·0	27·5	3·6
Papio . .	G	2·0	38·5	4·2
Cercopithecus .	A	1·0	21·0	4·7
Cercopithecus .	B	1·0	18·0	5·5

The size of the medial epicondyle constitutes a maximum of 5·5% and a minimum of 3·5% of total bi-epicondylar width in all genera investigated. By applying the mean value of these indices to the fossil humerus the width of the medial epicondyle in *P. africanus* has been estimated at 1·5 mm., and this figure has been employed in the reconstruction.

Projection of medial epicondyle.—The projection of the medial epicondyle in *P. africanus*, thus reconstructed, is compared in Table VIII with the projection found in the genera comprising the Juvenile Series. The index is obtained by expressing the medial epicondyle projection as a proportion of the total bi-epicondylar width thus: $\frac{(B.W.-T.L.E.)}{B.W.} \times 100$ where $B.W.$ = bi-epicondylar width (Straus, 1948) and $T.L.E.$ = distance from the medial margin of trochlear to lateral margin of lateral epicondyle (Text-fig. 5). The data on which this table is based are to be found in Appendix II (Index 3).

TABLE VIII

MEDIAL EPICONDYLAR PROJECTION INDICES

Genus	Number of specimens	Index $\frac{\text{(B.W.–T.L.E.)} \times 100}{\text{B.W.}}$	Range
Pan . . .	6	21·5	17·7–25·4
Ateles . . .	3	19·8	17·9–21·2
Presbytis . . .	3	13·6	11·6–15·6
Cercopithecus . .	5	18·7	14·3–20·9
Papio . . .	8	12·5	3·7–20·1
New World monkeys	4	17·7	10·8–24·0
Proconsul . .	1	15·9	— —

The indices show great variability in the Cercopithecidae, particularly in *Papio*. The indices in New World monkeys are also variable, that for *Saimiri* (Appendix II, Index 3) exceeding all but one of the *Pan* series. The high index found in *Saimiri* may probably be explained by the presence in this form of strongly curved and compressed nails or tegulae which would demand the presence of powerful superficial digital flexors and, therefore, of a prominent medial epicondyle. A prominent medial epicondyle is typical of New World monkeys (Hill, 1957). The indices for *Pan* and *Ateles* differ significantly from those for the Cercopithecidae but not from those for the New World monkeys. The table indicates that the medial epicondyle of *P. africanus* is proportionately narrower than that of *Pan* and *Ateles*, and more directly comparable with that of *Presbytis*, *Cercopithecus* and New World monkeys. It may be deduced from this and other evidence (p. 51) that the terminal phalanges of the fossil form were certainly not claw-bearing and that the nails, though probably tegulae and not ungulae, were of little functional significance in locomotion.

Bi-epicondylar width (Appendix II, Index 1). The epicondylar width (*B.W.*, Text-fig. 5) has been measured, and expressed as a proportion of the total length of the bone. The bi-epicondylar width of the fossil humerus is not as great proportionately as in *Pan*, and corresponds more closely with that found in *Cercopithecus* and *Papio*.

The indices for *Ateles* are uniformly lower, reflecting the elongation of the humeral shaft that has occurred in this genus without commensurate broadening of the lower articular surface. The indices for *Hylobates* (Le Gros Clark & Thomas, 1951: 10, table 4) show a similar trend to those for *Ateles*. The bi-epicondylar indices of the brachiating forms, *Pan* on the one hand, and *Ateles* and *Hylobates* on the other, indicate that the adaptive changes in the humerus associated with a brachiating mode of locomotion differ profoundly in the two groups. This point is further emphasised when the brachial index of these forms is considered.

Articular width (Appendix II, Index 2). The width of the articular surface (*A.W.*, Text-fig. 5) is expressed as a proportion of the total length of the bone. The index does not vary significantly between *Pan*, the Cercopithecidae and the New World monkeys. The low index in *Ateles* is another reflexion of the elongation of the shaft in this form. The relationship between the articular width and the shaft length in *P. africanus* does not differ significantly from any of the Juvenile Series, with the exception of *Ateles*.

Lateral epicondylar width.—This index was calculated by means of the following formula: $\frac{(B.-W.C.M.E.)\times 100}{B.W.}$ where $B.W.$ = bi-epicondylar width and $C.M.E.$ = distance from the lateral margin of capitulum to medial epicondyle (Text-fig. 5). The index proved to be somewhat variable and no deductions seemed permissible.

Supinator crest and flexor flange. The shaft of the fossil humerus is slender in its lower half, well-rounded anteriorly, and somewhat flattened posteriorly. There is no supracondylar foramen. The shaft expands symmetrically from just below the deltoid insertion, the lateral border forming the supinator crest which is sharp but not unduly prominent. Diagraphic sections through the shaft of the fossil bone immediately proximal to the olecranon fossa (Text-fig. 6) show considerable flattening in an antero-posterior plane, culminating in the supinator crest. The supinator crest is supported by a broad flange of bone which in modern forms gives attachment to the brachialis muscle. In the fossil form the flange is very similar to that seen in *Pan,* while in *Cercopithecus* and *Papio* it is narrower and more steeply inclined. It seems probable that the increased surface area of the bone provided by the flange is related to the importance of brachialis as a flexor of the elbow in brachiators.

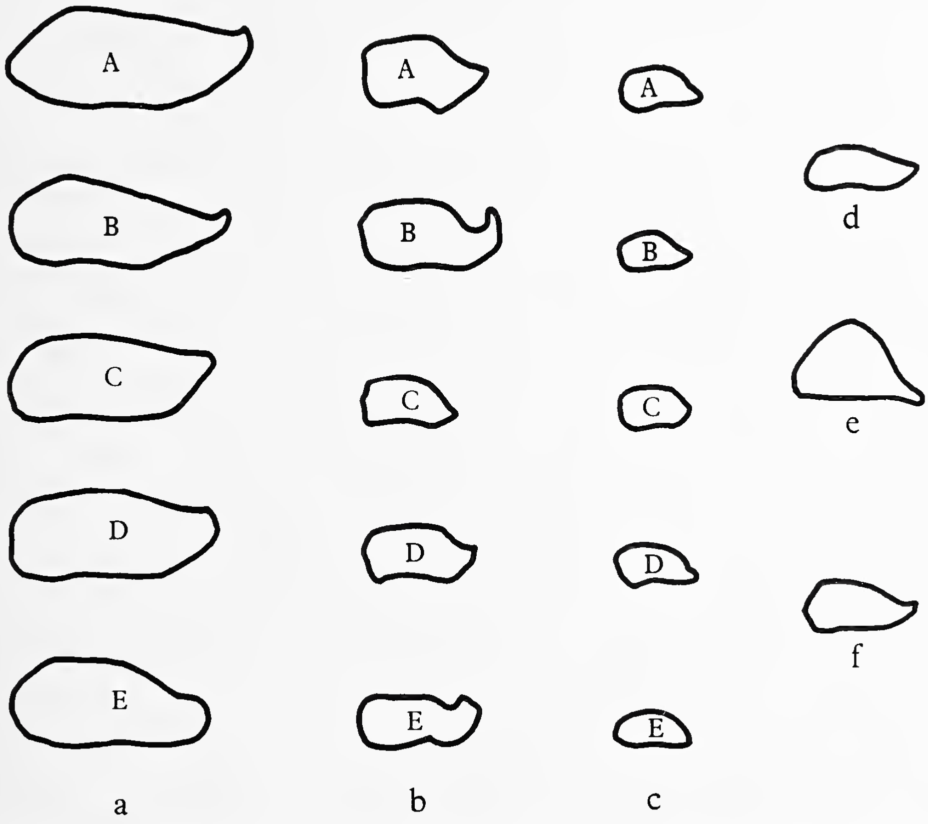


Fig. 6. Diagraph sections through the lower end of the humerus at a point just proximal to the upper margin of the olecranon fossa. (*a*) *Pan.* Juvenile Series A–E. (*b*) *Papio.* Juvenile Series A–E. (*c*) *Cercopithecus.* Juvenile Series A–E. (*d*) *P. africanus.* (*e*) *P. nyanzae* Moboko humerus. (*f*) *L. macinnesi.* $\frac{2}{3}$ natural size.

The supinator crest (which must be clearly distinguished from the flange) varies considerably in prominence within a single genus, but is generally somewhat better developed in *Papio* than in either *Pan* or *Cercopithecus.* Being a muscular ridge and subject to individual and ontogenetic variation, it would be fallacious to rely too greatly upon the supinator crest as a diagnostic feature in comparative studies involving animals of different sex and size. The extent of the crest in relation to the total length of the shaft has been calculated (Appendix I, Index 4) and shows little variation in *Pan, Papio, Cercopithecus, Presbytis* and New World monkeys, in which forms it extends for approximately one-third the length of the bone. Only in *Ateles* is this proportion significantly different. The length of the supinator crest of the fossil humerus constitutes one-third of the total length of the reconstruction. Thus, in this respect, the fossil bone cannot be distinguished from that of *Pan, Papio, Cercopithecus, Presbytis* or the New World genera. Following the precept of Milne-Edwards & Grandidier (1875) it can be deduced from the relative extent of the supinator crest that extension of the elbow in *P. africanus* is at least as great as it is in *Pan, Papio* and *Cercopithecus.*

Inferior articular surface.—The lower extremity of the fossil humerus resembles that of *Pan* (Text-fig. 7) in many ways. The trochlear surface is bounded laterally by a rounded and well-marked keel, which although not as large or as sharply defined as in *Pan,* is considerably more prominent than in either *Papio* or *Cercopithecus* (Text-fig. 7). As in *Pan* (Text-fig. 8*b*) the keel of the fossil humerus (Text-fig. 8*a*) follows a spiral course on the inferior aspect of the articular surface and ends by becoming continuous with the sharp ridge which forms the lateral margin of the olecranon fossa. In *Papio* and *Cercopithecus* the keel neither follows a spiral course, nor is there any continuity between it and the sharp lateral margin of the olecranon fossa found in these forms (Text-fig. 8*c, d*). This sharp lateral margin is very prominent in *Papio* and *Cercopithecus,* is less prominent in *Presbytis* and *Pan* and is entirely absent in *Ateles* and other New World genera in the Juvenile Series. In cercopithecoid monkeys the sharp lateral margin of the olecranon fossa and the

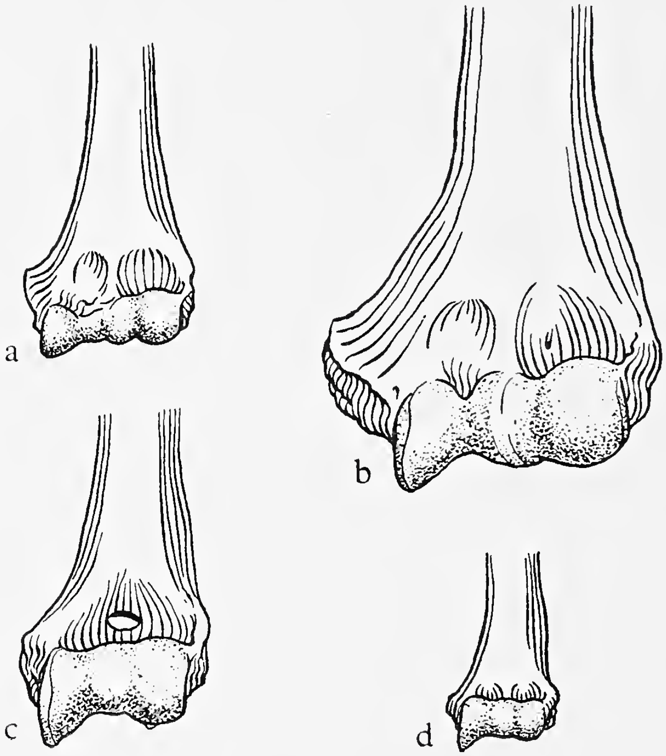


Fig. 7. Drawings of the anterior aspect of the lower end of the humerus in (*a*) *P. africanus,* (*b*) *Pan,* (*c*) *Papio,* (*d*) *Cercopithecus.* $\frac{2}{3}$ natural size.

prominent medial margin of the trochlea appear to provide stability for the humero-ulna articulation during pronograde, quadrupedal walking.

In *P. africanus* the medial border of the trochlea is well-rounded (Text-fig. 7*a*) and the articular surface extends for a short distance on to the medial surface of the trochlea (Text-fig. 9*a*). This rounded margin and medial extension of the articular surface are present in *Pan*, whereas in *Papio* and *Cercopithecus* the articular surface ends abruptly at the sharp and prominent medial lip of the trochlea (Text-fig. 9*c*, *d*). In *Presbytis*, *Ateles* and the New World genera the medial margin of the trochlea has a sharply defined edge, but is not so prominent as in *Papio* and *Cercopithecus*. Gregory (1920) has pointed out that the medial lip of the trochlea is prominent in those forms in which the forearm bones are habitually pronated. The rounded medial margin in *Pan* and *Proconsul africanus* appears to be concerned with stability of the elbow in all positions of the forearm and hand, rather than in pronation alone as in the pronograde forms. Considerable support is added to this view by the absence in *Pan* of the sharp medial border of the trochlea (Text-fig. 8) which, as mentioned above, appears to be functionally coupled with the form of the olecranon fossa. The medial border of the trochlea in *P. africanus* can be traced on to the posterior aspect of the lower articular surface, where it runs as a distinct low ridge towards the distal lip of the olecranon fossa (Text-fig. 9*a*). In *Pan* this posterior extension of the medial border is more clearly defined, although it has a similar relation to the olecranon fossa: in *Papio* and *Cercopithecus* the medial border of the trochlea flattens out on the inferior aspect of the bone and terminates some distance from the distal lip of the olecranon fossa (Text-fig. 9*c*, *d*). The appearance of the medial aspect of the lower end is shown in Text-fig. 9, where the backward extension of the medial trochlear margin in *P. africanus* can be seen to resemble that of *Pan* and is greater than in either of the cercopithecoid forms.

The capitulum of the fossil humerus is well-rounded as in *Pan*, and is more globular than in *Papio* or *Cercopithecus* (Text-fig. 7). The coronoid and radial fossae of *P. africanus* are shallow and resemble the condition in *Pan* and *Ateles*. The depth of these fossae depends largely upon the degree in which the distal articular surface faces downwards or is "extended" in relation to the shaft. This is illustrated in Text-fig. 10 by longitudinal diagraphic sections of the bone through the floor of the radial fossa. It can be seen from these tracings that "extension" of the articular end of the bone opens the angle between the articular margin and the shaft and thus reduces the depth of the radial fossa. The curved indicator line in Text-fig. 10 represents the extent of the articular surface in each diagraph section. In each bone the section passed through the most inferior point and followed the greatest curvature of the articular surface of the capitulum.

It can be seen from these tracings that the articular surface extends further posteriorly in *Pan* and *Ateles* than in *Cercopithecus* and *Papio*. In this plane of section, the posterior margin of the capitulum of *Cercopithecus* and *Papio* ends at a point which lies anterior to the morphological longitudinal axis of the bone; in *Pan* and *Ateles*, on the other hand, the posterior margin of the capitular surface ends at a point which lies in line with, or posterior to, the long axis of the bone. The backward extension of the articular surface in *Pan* and *Ateles* gives the lower end of the humerus the appearance of having been unrolled or extended. The posterior margin

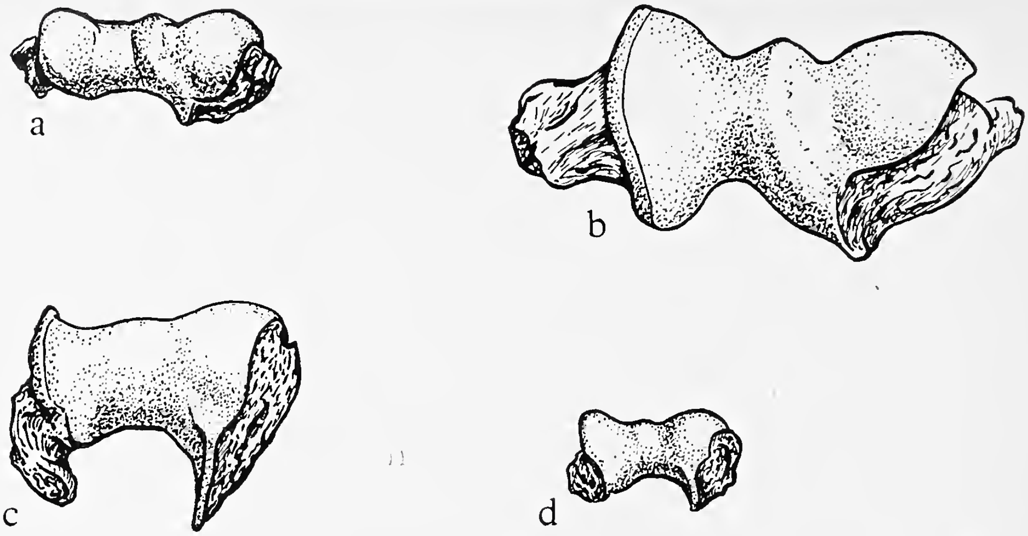


Fig. 8. Drawings of the inferior articular surface of the humerus in (*a*) *P. africanus*, (*b*) *Pan*, (*c*) *Papio*, (*d*) *Cercopithecus*. Natural size.

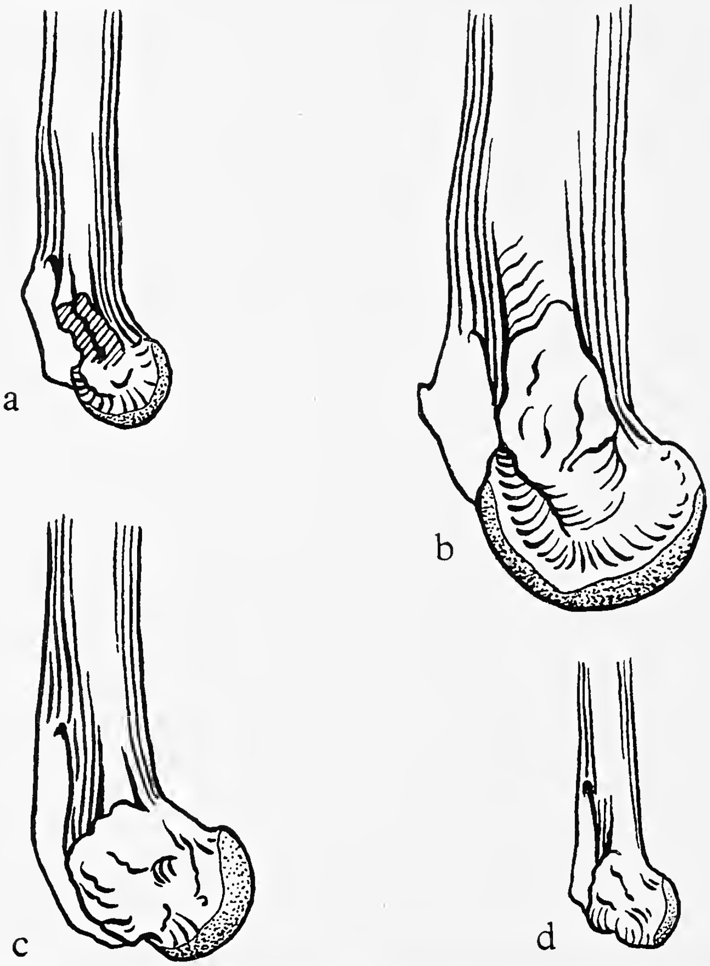


Fig. 9. Drawings of the lateral view of the lower end of the humerus in (*a*) *P. africanus*, (*b*) *Pan*, (*c*) *Papio*, (*d*) *Cercopithecus*. Natural size.

of the capitular surface, though considerably narrower than the anterior margin, is still fairly broad in *Pan* (Text-fig. 8*b*). This is in marked contrast with the appearance in *Papio* and *Cercopithecus* where a posterior margin cannot be said to exist since the lateral margin of the capitulum inclines sharply to meet the lateral margin of the trochlea at an acute angle (Text-fig. 8*c*, *d*).

The backward extension of the articular surface (Text-fig. 10) and the rounded posterior capitular margin (Text-fig. 8*a*) of the fossil humerus bear a marked similarity to *Pan* and *Ateles* and are in complete contrast to *Papio* and *Cercopithecus*.

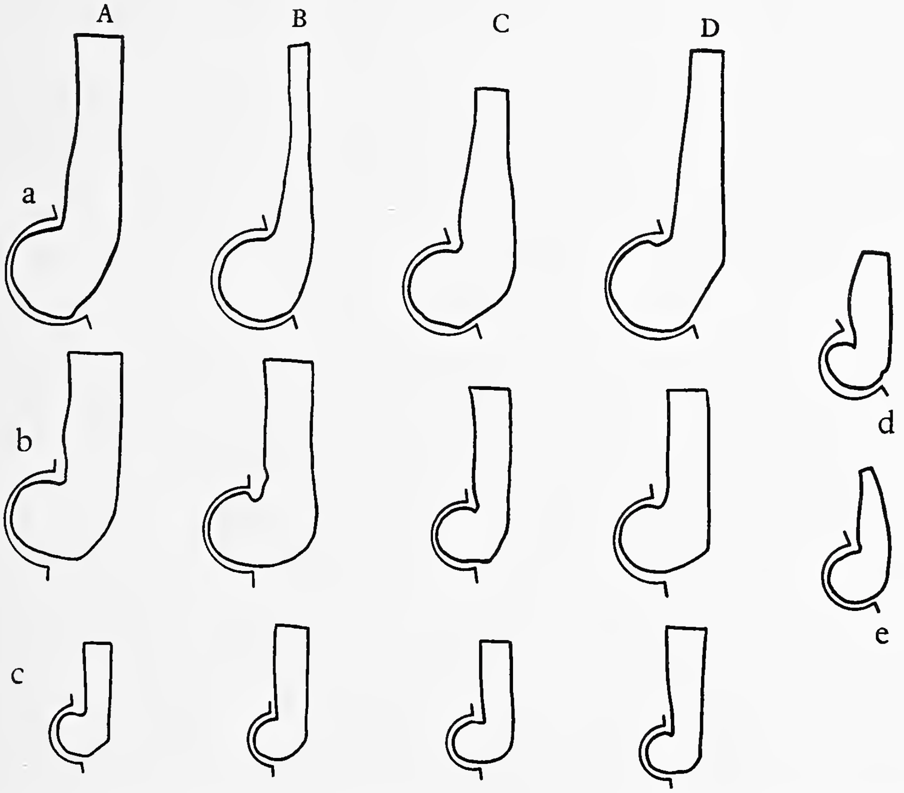


FIG. 10. Sagittal diagraph sections through the maximum curvature of the capitulum of the humerus in (*a*) *Pan*, Juvenile Series A–D; (*b*) *Papio*, Juvenile Series A–D; (*c*) *Cercopithecus*, Juvenile Series A–D; (*d*) *Ateles*, Juvenile Series A; (*e*) *P. africanus*. The curved lines mark the extent of the articular surfaces. ½ natural size.

It seems likely that the difference in the degree of backward extension of the articular surface between *Pan* and *Ateles*, representing brachiators, and *Papio* and *Cercopithecus*, representing quadrupedal forms, is related to the degree of extension of the elbow in these two locomotor groups. The degree of extension at the elbow was estimated in the comparative series by articulating the humerus and the ulna and extending the joint until further movement was prevented by contact between the olecranon and the floor of the olecranon fossa. The angle between the distal one-third of the humerus and the proximal one-third of the ulna was then measured with a goniometer, the centre of the arc formed by the medial part of the trochlea being taken as the centre of motion. The measurements thus indicate the maximum degree of extension possible between the two bones. Table IX indicates the maximum degree of elbow extension in the genera comprising the Juvenile Series.

TABLE IX

THE MEAN EXTENSION OF THE HUMERO-ULNAR JOINT IN DRY BONE PREPARATIONS OF DIFFERENT GENERA

Genus	Number of observations	Mean extension of elbow-joint
Pan . .	7	182°
Ateles . .	3	177°
Papio . .	7	156°
Cercopithecus .	5	150°
Presbytis .	3	142°

In view of the striking similarity in form of the articular surface of *P. africanus* to that of *Pan*, particularly in respect of the backward extension of the capitulum, it is justifiable to assume that *P. africanus* could extend the elbow nearly as much as *Pan* and *Ateles* and had more extension than have *Papio*, *Cercopithecus* and *Presbytis*.

Washburn (1950) has pointed out a fundamental difference of function in the elbow joints of quadrupedal monkeys and brachiators.* He points out that when the annular ligament holding the head of the radius in place is divided in the former, the elbow joint is deprived of its side-to-side stability. If, however, the same ligament is divided in brachiators the stability of the joint is unimpaired. This greater stability in brachiators is due to the form of the articular surface, the keel between the trochlea and the capitulum providing a stabilising element for the ulna in both flexion and extension. It has been suggested that the radius, thus emancipated, is free to undergo a greater range of pronation-supination. It would seem likely that emancipation of the radius from pure weight transmission is of particular significance during brachiation. In the suspended position, the radius can contribute little towards transmitting the body weight to the hands except through its ligamentous and capsular attachments and indirectly through the interosseus membrane, the greater part of weight transmission clearly being played by the ulna. The radius is thus free to undergo a certain amount of coincidental axial rotation during brachiation. To compensate in some measure for the loss of the radius as a weight-transmitting surface, the ulnar or trochlear element of the distal humeral articulation might be expected to increase in relative size and the capitular element to decrease. The two parts of the articular surface were measured in the Juvenile Series and also in *P. africanus*, and the trochlear width ($T.W.$) was expressed as a proportion of the capitular width ($C.W.$) thus: $\frac{T.W. \times 100}{C.W.}$ = Trochlear index. The results are tabulated in Table X (for data see Appendix II, Index 4).

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* Washburn includes *Pan, Gorilla, Pongo, Hylobates* and *Symphalangus* among the brachiators, and thus uses the term in a more limited sense than that employed in this text.

Table X

THE MEAN TROCHLEAR INDEX IN SERIES OF MODERN AND FOSSIL BONES

Genus	No. of specimens	Mean trochlear index
Pan	6	93·9
Ateles	3	67·8
Papio	7	67·8
Cercopithecus	5	74·7
Presbytis	3	72·9
New World monkeys	4	80·2
Proconsul	1	104·0

It can be seen that the trochlear index is higher in *Pan* and *Proconsul africanus* than in *Cercopithecus, Papio, Presbytis* and the New World monkeys. The apparent difference between *Pan* on the one hand, and the remaining groups of modern genera considered together, on the other, is statistically significant ($p < 0·001$). As might well have been expected from the prominence of the keel in the fossil humerus, the trochlear index of *P. africanus* is very high.

Summary.—The proximal extremity of the fossil humerus in many ways resembles that of quadrupedal monkeys, particularly in the angularity of the upper third of the shaft in cross-section, the general direction of the head, and the anterior bowing of the bone. On the contrary the extent to which the deltoid muscle reaches down the shaft is typical of brachiators (Washburn, 1950). The absence of a prominent delto-triceps crest in the fossil similarly suggests a functional affinity with the arboreal monkeys, particularly with *Presbytis*; this crest forms a striking feature of the shaft of *Papio* and *Cercopithecus* and is in part responsible for the marked angularity of the cross-sectional appearance. In this particular combination of quadrupedal and brachiating features, the fossil humerus approaches most closely to the condition seen in the quadrupedal-brachiator, *Presbytis*. In the distal extremity of the shaft the proportion of quadrupedal to brachiating characteristics is reversed. In both form and appearance the lower articular surface closely approaches the condition seen in *Pan*. This is particularly evident in the increased surface of origin for brachialis, 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. These morphological observations, considered together, constitute a functional complex that provides the mechanical basis for full extension of the elbow and, at one and the same time, for the freedom with which the forearm can be pronated and supinated during over-arm swinging.

The Radius (Pl. 6, fig. 20*g*; Pl. 7, figs. 22–24).

The several fragments of the radius of *P. africanus* from Gumba, when brought together, form a complete bone except for the epiphysis for the head, a small portion of the posterior aspect of the proximal metaphysis, and a shaving from the anterior aspect of the distal extremity of the diaphysis. The shaft and distal epiphysis measure 154 mm. from the centre of the proximal metaphysis to the tip of the styloid process. By allowing 2 mm. for the thickness of the missing proximal epiphysis, the full length of the bone has been assessed as 156 mm. The diagrammatic reconstruction is shown in Plate 7, fig. 22.

The fossil radius thus reconstructed is a slender bone that has few strong muscular markings. The anterior surface is flat, and in section the posterior surface curves gently to reach the posterior crest, which is low and well-rounded. The interosseous border, well-marked in the upper half of the bone, becomes less well-marked inferiorly. A small protuberant flattened crest is apparent on the interosseous margin just distal to the tuberosity.

The shaft curves medially for a short distance below the metaphysis: at the level of the radial tuberosity the shaft changes direction and curves laterally. The convexity of this lower curve is directed laterally and reaches its highest point well proximal to the middle of the shaft. At the apex of the curve the muscular marking of pronator teres is seen.

The appearance of the shaft in cross-section (Text-fig. 11*f*) is in immediate and obvious contrast to the triangular, scalloped appearance of the cercopithecoid radius (Text-fig. 11*c*). It is considerably less grooved on its anterior surface and less sharp at its interosseous border than *Papio* (Text-fig. 11*a*). The smaller members of the baboon series, e.g. *P. anubis* (*Papio* C) and *P. hamadryas* (*Papio* D), have less muscular moulding of the shaft and in section more closely resemble *Proconsul africanus*. Even in these forms, however, the cross-sectional appearance of the mid-shaft region remains triangular, whereas the section of the radius in *P. africanus* has the appearance of an ovoid flattened on its anterior surface. The radius in *Pan* is somewhat stouter than that of *Papio*, but also appears triangular in sections through the mid-shaft region (Text-fig. 11*b*). The appearance in *P. africanus* most closely resembles that in *Presbytis* and *Capuchin* (Text-fig. 11*d*, *e*) which both have long, rather slender bones with an anterior surface which is flattened in *C. capuchinus* and convex in *Presbytis* (*Kasi*) *senex*.

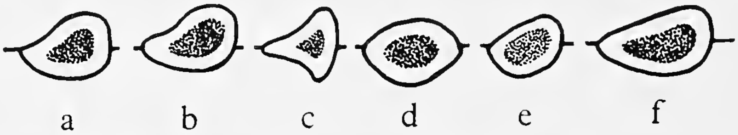

FIG. 11. Drawings showing the appearance of cross-sections of the radius at mid-shaft in (*a*) *Papio*, (*b*) *Pan*, (*c*) *Cercopithecus*, (*d*) *Presbyteris*, (*e*) *Cebus*, (*f*) *P. africanus*. The lines indicate the transverse plane of the lower ends of the radii, the anterior surface facing upwards. Not to scale.

When examined from the anterior aspect, the shaft of the fossil radius appears to be more curved than that of *Papio* (Pl. 6, fig. 20*a*, *g*). From the lateral aspect, however, *Papio* appears to be more curved than *P. africanus*. The explanation of this apparent paradox lies in the plane of maximum curvature in the two forms. In *P. africanus* the curvature is directed mainly laterally and is therefore most apparent in an anterior view. In *Papio* the curvature is directed mainly posteriorly and is apparent only when the bone is examined from the lateral view. The direction of the curvature is somewhat variable in *Pan*: in four specimens (Juvenile Series C, D, E, F), it is directed laterally and in two specimens (Juvenile Series A, B), postero-laterally. In *Cercopithecus, Ateles, Presbytis* and New World monkeys (Plate 6) the direction of the curve is postero-lateral. It would seem that the backwardly directed curve is a specialisation of *Papio* and may be related to the habitual pronation of the forearm during quadrupedal locomotion. Clearly the curvature of long bones is subject to considerable ontogenetic variation and therefore, in view of the smallness of the population under study, this observation must be viewed with caution.

Much of the radial tuberosity in the fossil specimen has been lost by erosion, but its limits are clearly defined. The posterior margin of the process corresponds to the upward prolongation of the interosseous border, a relationship that is seen in *Papio, Cercopithecus, Ateles* and other New World genera. In *Pan* on the other hand the tuberosity is displaced relatively backward, and its posterior margin usually extends well dorsal to the plane of the interosseous border.

The small flange projecting from the interosseous border of the fossil radius, 12 mm. from the lowest point of the tuberosity, is present in most specimens of *Papio* and *Cercopithecus* in the Juvenile Series, and is considerably more prominent than it is in *P. africanus*. In *Presbytis, Ateles, Pan* and New World genera, the flange is absent, but there is usually a small roughened area on the medial surface of the bone which corresponds in position to the flange in catarrhine monkeys (Plate 6). The flange has been shown by dissection in modern catarrhines to provide the origin for the radial head of abductor pollicis longus (Extensor ossis metacarpi pollicis).

The neck of the fossil radius is relatively long compared with that of *Papio*; it is slightly longer than that of *Presbytis* and *Cercopithecus* but shorter than in *Pan*. In Table XI, a summary is given of the comparative data fully set out in Appendix III, Index 2. The neck of the radius, measured between the epiphysial line of the upper margin of the radial tuberosity, is expressed as a proportion of the widest diameter of the metaphysis. This radial neck index is a modification of that used by Le Gros Clark & Thomas (1951) in which the length of the neck is expressed as a proportion of the greatest diameter of the radial head. Since the radial head is absent in *P. africanus*, the greatest diameter of the metaphysis has been employed in its stead.

Elongation of the neck of the radius is most pronounced among brachiators, e.g. *Pan* and *Ateles* (Table XI) and *Hylobates* and *Symphalangus* (Le Gros Clark & Thomas, 1951:13). It is least marked in the terrestrial quadrupedal group, e.g. *Papio*. In this respect *P. africanus* lies midway between the arboreal quadrupedal group represented by *Cercopithecus* and the brachiators represented by *Pan*. The index of the fossil bone most closely approaches that of *Presbytis*.

The metaphysial surface in *P. africanus* is roughly oval, the long axis of the metaphysis being directed medially and slightly posteriorly. The shape of the head of the fossil bone thus appears to have been similar to that of *Cercopithecus, Presbytis, Cacajao* and *Saimiri*, and dissimilar to that of *Pan* and *Ateles*, in which the epiphysial surface is more nearly circular. On the other hand the metaphysial surface of the radius of *P. africanus* is placed horizontally (Plate 6) as in the brachiators, whereas that of the cercopithecoid radius is tilted downwards and laterally in relation to the long axis of the shaft. Since the plane of the metaphysis reflects the plane of the radial head in all cases in this series, it may be deduced that the articular surface of *P. africanus* was also horizontal.

TABLE XI

RADIAL NECK INDICES IN DIFFERENT GENERA

Genus	No. of specimens	Mean length of neck of radius (mm.) (*a*)	Mean maximum width of metaphysis (mm.) (*b*)	Index = $\frac{a}{b}$
Pan	6	21·3	20·3	1·06
Papio	5	6·0	14·5	0·41
Cercopithecus	5	5·3	7·7	0·69
Presbytis	3	6·6	8·8	0·75
Ateles	3	14·5	9·5	1·53
Pithecia	2	6·5	6·5	1·0
Proconsul	1	8·0	10·0	0·8

The distal extremity of the shaft of the fossil radius is expanded (Pl. 7, figs. 22, 23). A similar appearance is observed in *Presbytis, Ateles, Pan* and the New World genera, but not in *Cercopithecus* or *Papio* (Plate 6). The effect of lateral expansion of the lower end is to displace the insertions of brachioradialis and pronator quadratus laterally relative to the inferior radio-ulnar articulation, and thus to increase the moment of these muscles about the joint.

The distal articular surface of the fossil radius is morphologically indistinguishable from that of all cercopithecoids except for the styloid process, which is relatively bulkier as a result of the greater expansion of the distal extremity in the fossil form. The lower articular surface of the fossil bone is flat, as in *Cercopithecus, Presbytis* and *Papio,* and differs profoundly from the deeply concave surface in *Pan.*

The plane of the distal articular surface in *Pan* is directed slightly anteriorly as it is in *Hylobates* and, to a lesser degree, in *Ateles.* In all other genera of the Juvenile Series, the articular surfaces point directly distally in the long axis of the bone. The inclination of the surface in *Pan* (Pl. 7, fig. 24) appears to have resulted from an increase in length of the posterior lip, a state of affairs which also accounts for the depth of the concavity. The effect of this anterior tilt of the articular surface is to permit a greater range of flexion of the radio-carpal joint—clearly an adaptation to brachiation. In *P. africanus* the articular surface faces directly inferiorly as it does in all the arboreal and terrestrial quadrupeds.

Summary.—As in the humerus, so in the fossil radius there are morphological characteristics of both brachiators and arboreal quadrupeds in one and the same bone. The neck of the fossil bone has neither the extreme shortness of the terrestrial quadrupeds nor the very marked elongation shown by certain brachiators, notably *Ateles.* The proportional length of the neck is greater than in *Cercopithecus* and less than in *Pan,* and corresponds most closely to that found in the quadrupedal brachiator *Presbytis.* It is interesting to note that the condition of the neck found in the primitive arboreal quadruped, *Pithecia,* corresponds closely with that seen in modern *Pan.*

With regard to the convexity of the shaft little can be deduced of a positive nature. It is clear that the direction of the curvature in the fossil form was quite unlike that of the terrestrial quadruped *Papio*. The markedly posterior direction of the convexity of this latter genus must be regarded as an adaptation for the habitual pronation associated with terrestrial quadrupedalism. The generalised Primate condition is probably similar to that seen in the arboreal quadrupeds, in which the convexity is directed postero-laterally. The presence of a more directly lateral convexity in certain specimens of *Pan* may perhaps be regarded as a brachiating specialisation associated with the increase in the range of supination found in these forms: the lateral direction of the convexity in *P. africanus* may thus well be a brachiating specialisation.

The principal features of the distal extremity of the fossil radius are indistinguishable from those of aboreal and terrestrial quadrupeds and the quadrupedal brachiators (*Presbytis* and *Ateles*). That this should be so is not surprising, for the form of the radio-carpal joint is ultimately related to the position of the wrist and hand during quadrupedal walking. In all quadrupeds the hand is palmigrade, or digitigrade in the case of terrestrial quadrupeds, while in *Pan* the wrist is held in the neutral position or slight flexion and the weight of the body is transmitted through the flexed middle phalanges. It would be indeed surprising to find a *Pan*-like radiocarpal joint in a fossil form so clearly quadrupedal in locomotor habit.

THE ULNA (Pl. 7, fig. 21).

The fragment of the ulna of *P. africanus* from Gumba consists of slightly less than the distal quarter of the bone. The portion of the shaft and the epiphysis of the head were found lying separately in the block of matrix containing the hand bones (Plate 8), the fragment of shaft being complete except for some erosion at the metaphysis. The epiphysis is not yet fully grown.

The shaft is roughly circular in section, the anterior surface being slightly flattened and exhibiting a well-marked groove for pronator quadratus. The epiphysis bears a long styloid process which is deeply grooved on its posterior aspect. Inferiorly a smooth rounded facet for the pisiform can be seen, and on the radial side, at the extreme tip, there is a flattened facet for articulation with the triquetral. The articular surface for the radius is circumferential and extends on to both anterior and posterior surfaces of the bone.

The styloid process is relatively longer in the fossil bone than in *Pan* (Table XII), and corresponds closely with most specimens of *Papio*, *Cercopithecus*, *Presbytis*, *Ateles* and the New World monkey group.

The styloid index is calculated by taking the distance from the tip of the ulna styloid to the epiphysial line, and expressing this as a proportion of greatest epiphysial width, measured at the metaphysis, thus: $\frac{\text{Styloid length} \times 100}{\text{Epiphysial width}}$. The data are given in Appendix III, Index 3, and are summarised in Table XII.

The articular portion of the lower end of the ulna in *P. africanus* corresponds in extent and definition to that in catarrhine monkeys. It is not so clearly defined, nor so extensive, as it is in *Pan*. The fossil bone differs also from *Pan* in the absence of the fossa for attachment of the intra-articular disc, which leaves a deep, highly vascular pit in this genus.

Table XII

THE MEAN ULNAR STYLOID INDEX

Genus	No. of specimens	Mean styloid length (mm.)	Mean epiphyseal width (mm.)	Mean index
Pan	5	10·9	19·6	55·6
Papio	6	10·5	13·3	79·0
Cercopithecus	5	6·0	7·5	80·0
Ateles	2	7·5	9·3	80·7
Presbytis	2	6·0	7·5	80·0
New World monkeys	4	4·4	5·25	83·8
Proconsul	1	10·0	11·0	83·3

Brachial index.—The length of the fossil humerus has been estimated at 182 mm. with a confidence range of 177–187 mm. (p. 17). After correction of the angulation between the fragments, and an allowance of 2 mm. for the missing proximal epiphysis, the length of the radius was estimated at 156 mm. It is thus possible to estimate the brachial index. The method employed was figured by Mollison (1911), and later defined and used by Schultz (1930). The long bones were measured according to the following particulars (Schultz):

Humerus length. Greatest distance between *head of humerus* and *capitulum* parallel to longitudinal axis of the bone.

Radial length. Greatest distance between *head of radius* and *styloid process* parallel to longitudinal axis of the bone.

The length of the radius is expressed as a percentage of the length of the humerus thus: $\frac{\text{Length of radius} \times 100}{\text{Length of humerus}} = \text{Brachial index.}$

The results of the brachial index calculations in *P. africanus* are:

		Brachial Index
"Shortest" Humerus	(177 mm.)	88
"Mean" Humerus	(182 mm.)	86
"Longest" Humerus	(187 mm.)	83

The "shortest" and "longest" humeri represent the lower and upper limits of the confidence range respectively. It is important that the immaturity of the fossil specimen should be taken into account. Schultz (1926) has shown that the brachial index increases with age in all higher Primates, excluding the lowland gorilla but including Man. He has also shown that the greatest ontogenetic change occurs in those forms which have relatively the longest radii in adult life.

Table XIII sets out the differences in the brachial index between the juvenile and adult forms of certain higher Primates, catarrhines and platyrrhines. The data on which this table is based are partly derived from our own Juvenile and Adult Series (Appendix III, Index 1), partly from Schultz (1930) and partly from Mollison (1911).

Table XIII

COMPARISON OF THE BRACHIAL INDICES OF JUVENILE AND ADULT PRIMATES

Genus	Mean brachial index		p	Mean brachial Index
	Juvenile	Adult		All ages
Pan	90·9 (12)	92·6 (29)	·05	92·1
Pongo	98·9 (10)	100·6 (66)	·03	—
Hylobates	105·9 (9)	112·7 (39)	·01	—
Papio	108·8 (7)	108·3 (10)	·05	108·4
Cercopithecus	100·6 (5)	100·4 (27)	·05	100·4
Presbytis	103·0 (3)	101·7 (3)	—	—
Pithecia	92·5 (2)	95·5 (2)	—	—
Ateles	102·7 (3)	— —	—	—

The difference between the juvenile and adult indices in each of the three genera *Papio, Pan* and *Cercopithecus* is not statistically significant. In *Pongo* the difference may be significant and is clearly significant in *Hylobates*. In *Presbytis, Ateles* and *Pithecia* the specimens were too few in number to be treated statistically. Thus, although it is probable that the proportionate length of the radius increases ontogenetically between infant and adult life in *Pan, Papio* and *Cercopithecus* (relevant figures unfortunately are not available), there is clearly no large increase between juvenile and adult stages in the same three genera, and it has thus been possible to calculate the combined mean brachial index of both the juvenile and the adult series in these forms (Table XIII, last column). The findings that there is no significant difference in the brachial index between the Juvenile 2 and adult forms in *Pan, Papio* and *Cercopithecus,* and that there is little apparent difference in other genera (apart from *Hylobates*) makes it unlikely that the brachial index of *P. africanus* would have changed significantly had bone growth been completed.

The brachial index of *P. africanus,* based on the "mean" humeral length, is well below that of all modern Primates* except the gorilla (Lowland gorilla, 81, Highland gorilla, 85 (Schultz, 1930)) and Man (Negro, 76, White, 75 (Schultz, 1930)). Even were the "shortest" humeral length employed the resulting index for *P. africanus* of 88 would still be below the common Primate level.

Table XIV shows a comparison between the brachial indices of fossil forms and forms that are generally considered to be their modern descendants. The proportions of the Lower Pliocene *Mesopithecus* from Pikermi are derived from measurements given by Gaudry (1862) of a female specimen; those of *Cebupithecia* from Stirton (1951); those of the Miocene *Limnopithecus macinnesi* were derived from Le Gros Clark & Thomas (1951) and based on their reconstruction of the humerus and the radius.

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* Individual specimens with low brachial indices have been recorded; for instance: *Callicebus* 85 (Erikson, personal communication); *Cacajao calvus* 80.6 (Juvenile Series, New World monkey A).

TABLE XIV

COMPARISON OF THE BRACHIAL INDICES OF SEVERAL FOSSIL PRIMATES WITH THOSE OF THEIR PROBABLE MODERN DESCENDANTS

Tertiary form		Modern form	
	Brachial index		Brachial index
Cebupithecia (Miocene)	85	*Pithecia*	95
Limnopithecus macinnesi (Miocene)	104	*Hylobates*	113
Mesopithecus (Pliocene)	97·8	*Semnopithecus*	101
**P. africanus* (Miocene)	86	*Pan troglodytes*	92

* Based on "mean" humeral length.

In all instances the modern form has a larger brachial index than its fossil counterpart, which lends support to Schultz's (1930) view that "a radius somewhat shorter than the humerus is ontogenetically, and in all likelihood phylogenetically, the original condition".*

In summary, therefore, the brachial index of *P. africanus* is considerably lower than that found in most modern catarrhines and platyrrhines, and in the Juvenile Series is closest to that of *Pan*.

THE HAND (Pl. 3, fig. 15; Pl. 8, fig. 25; Pl. 9, fig. 26).

Plate 8 shows the bones of the left hand and right foot in the block of limestone after preliminary development. Some of the fragments were still buried within the block and their position and identity have been indicated in the key diagram. The bones were numbered *in situ* and their relative positions were recorded when they were developed from the matrix. Identification of the bones and reconstruction of the hand were based primarily on morphology but the relative position of the bones within the block provided valuable confirmatory evidence.

The position of the lower extremities of the radius (1) and ulna (2) at the extreme right of the block suggested that at death the hand had lain palm uppermost. Some of the carpal bones were lying in their expected positions, for example: the capitate (10), the lunate (5) and the scaphoid (4). The trapezium (11) was markedly displaced towards the ulna side of the hand; the hamate (9) was somewhat distally displaced. Radiating from the region of the carpus were four metacarpals (13, 15, 17, 19) and in the same region four metacarpal epiphyses (14, 16, 18, 20).

Intruding into the block from the ulna side was a bone, the head of which is

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* When compared with those of modern genera (Table XIV), the brachial index of *L. macinnesi* does not indicate the extent to which this form, at the time of the Early Miocene, had evolved in the direction of modern gibbons. It is only when this index is considered in terms of the other contemporary genera that the considerable relative increase in radial length, which suggests brachiating affinities, becomes apparent.

directed towards the wrist; this bone was identified as the metatarsal of the right hallux. Associated with it, and indicated by stippling in the key diagram, were several bones belonging to the right foot including the medial cuneiform and the phalanges of the hallux.

The proximal phalanges of the manus (21, 22, 24) lay just distal to the heads of the metacarpals. The heads of the proximal phalanges were directed *towards* the carpus, as were those of the middle phalanges (27, 29, 30, 31). This inverted position of the phalanges was presumably due to the fact that, at death, the hand assumed a position in which the metacarpo-phalangeal and interphalangeal joints were acutely flexed—a posture frequently to be observed in cadavers of modern Primates.

Identification.—The carpal bones present were readily recognisable, the os centrale and the trapezoid being absent. The epiphysis of the pisiform (8) was not in the main block but was identified at a much later date from associated débris. The metacarpals were distinguished from the metatarsals partly by their position in the block and partly because of their relative shortness, the shortest metatarsal of the Old World monkeys being invariably longer than the longest metacarpal. Allocation of the metacarpals to their correct digit was carried out on morphological grounds. The first metacarpal is missing but a fragment of the epiphysis (12) was identified.

The identification of the proximal phalanges as those of the manus was based partly on their relative position in the block and partly by comparision with bones of the pes and the manus of extant forms. The final positioning of these bones in the reconstruction (Pl. 9, fig. 26) was made on comparative morphological grounds. It was observed in modern Old World monkeys that, while the shaft of the proximal phalanx of the third digit is symmetrical, the shafts of the second, fourth and fifth digits are more curved on one side than the other; this curvature is directed laterally in the second proximal phalanx and medially in the fourth and fifth. This asymmetry doubtless results from the manner in which the muscles are inserted into the digits; the third digit, receiving the insertion of a dorsal interosseus muscle on either side, is symmetrical; the second and fourth, receiving an insertion on one side only, are asymmetrical. The fifth proximal phalanx is asymmetrical owing to the attachmant to its base of the abductor digiti minimi. The asymmetry of the proximal phalanx of the second digit is apparent in Pl. 3, fig. 15. The remaining proximal phalanx is to all intents and purposes symmetrical at its base and would therefore appear to belong to the third digit: its epiphysis (25) is, however, too small to have articulated with the head of the third metacarpal bone, and thus it has been assigned to the fourth digit, where, as comparative studies have shown, asymmetry is not always well marked.

Six middle phalanges were found in the block, of which two were allotted to the foot, partly because of their position in the block (lying between radius and ulna) and partly on comparative morphological grounds. The remaining four middle phalanges (27, 29, 30, 31) were placed in the reconstruction in accordance with their lengths and widths; the stoutest and longest being attributed to the third digit, the second longest to the fourth digit, the third longest to the second digit and the shortest and most slender to the fifth digit. This order is in accordance with the formulae most commonly met with in Old World monkeys, i.e. length $3 > 4 > 2 > 5$, width $3 > 4 > 2 > 5$.

A single terminal phalanx (32) was present in the block, and in view of its close proximity to the middle phalanx of the third digit (29) it has been assigned to this digit in the reconstruction.

All the digital epiphyses were lying separately in the matrix and the only criterion used in allotting them to their appropriate diaphyses was that the two should articulate perfectly.

Bone 21 in the block was considered to be the proximal phalanx of the thumb for the following reasons:

1. The bone, which is clearly a proximal phalanx, is too short to be that of digits 2 to 5 of either hand or foot.
2. A cup-shaped distal extremity, related to two large sesamoids in close contact in the mid-line, is characteristic of this bone in modern Old World monkeys and apes.

Plate 3, fig. 15 shows the final assembly of the existing fragments. A reconstruction of the complete hand is illustrated in Pl. 9, fig. 26. The missing fragments are shown in outline.

Reconstruction of the thumb.—It is by no means easy to determine the length of the thumb of *P. africanus*. The overall proportions of the three main parts of the hand are almost identical with those of *Pan* (Table XV), yet to make the thumb in *P. africanus* as short relative to the hand as it is in *Pan* is to assume that in the early stage of evolution of brachiators the specialisations of the hand associated with the brachiating habit were already fully developed. Such an assumption would be at complete variance with the total morphological and functional picture of *P. africanus* as a whole. More specific evidence that the thumb of *P. africanus* was not as short as that of *Pan* is provided by the relationship between the length of the proximal phalanx of the thumb and that of the third metacarpal in the fossil form and in the modern genera comprising the Juvenile Series (Table XVIII). These observations indicate that the proximal phalanx of *P. africanus* was proportionately considerably longer than in *Pan* or *Papio*, and somewhat longer than in *Cercopithecus*; it can also be seen that the index corresponds most closely with that of the New World monkeys. It therefore seems not unlikely that the proportion of the proximal phalanx of the thumb to the first metacarpal would have a similar value in *P. africanus* to that found in New World monkeys. Calculations based on this assumption provide a possible length for the first metacarpal, of the order of 25 mm. This figure, which has been used in the reconstruction, must clearly be regarded as tentative.

Proportions of the Hand.—The material employed in the measurement of proportions and in the comparative morphological study of the carpus and metacarpus of *P. africanus* consisted of the Juvenile Series, less *Pan* B, C and D, *Papio* B, D and F, *Ateles* A, *Presbytis* C and New World monkey B, in which forms the hand was not available. Additional material was used for this part of the study (Appendix IV).

The proportions are based on the reconstructed length of the middle digit of the fossil hand. In the reconstruction of this digit the proximal phalanx, which was missing, has been drawn to the same scale as the proximal phalanx of the fourth digit, a relationship which holds true in the majority of modern monkeys and apes.

The digital projection formula of the reconstructed hand is $3 > 4 > 2 > 5 > 1$ and corresponds with that generally found in modern monkeys and apes (Midlo, 1934; Wood Jones, 1942). In view of the post-mortem fracture through the terminal half of the shaft of the second metacarpal of the fossil bone, the metacarpal projection formula is somewhat equivocal. A minute portion of the epiphysial surface of the shaft is apparent at the disto-lateral margin of the smaller fragment, and it can be stated with confidence that the second metacarpal did not project beyond the third metacarpal, but it is impossible to determine whether the formula was $3 > 2 > 4 > 5 > 1$ or $3 = 2 > 4 > 5 > 1$.

The relative thickness of the metacarpals in mid-shaft (the metacarpal thickness formula) provides a more useful guide to function than does the metacarpal projection formula. In *P. africanus* the metacarpal thickness formula is $3 > 2 > 4 > 5 > 1$. The following formulae were observed in the Juvenile Series (Appendix IV):

$$\left.\begin{array}{l}\textit{Pan}\\ \text{New World}\\ \quad\text{monkeys}\end{array}\right\} 3 > 2 > 4 > 5 > 1 \quad \left.\begin{array}{l}\textit{Papio}\\ \textit{Cercopithecus}\\ \textit{Presbytis}\end{array}\right\} 3 > 4 > 2 > 5 > 1 \quad \textit{Ateles}\ 4 > 3 > 2 > 5$$

The formula of the fossil hand is like that of *Pan* and of all the New World monkeys except *Ateles,* in which the unusual formula of $4 > 3 > 2 > 5$ is found.

The proportionate lengths of the carpus, the metacarpus and the phalanges provide a valuable guide to the different structural adaptations of the hand in the main locomotor types of monkeys and apes (Table XV). The figures given represent the mean dimensions of the different genera calculated from data presented in Appendix IV (Indices 1, 2 and 3).

TABLE XV

THE PROPORTIONS OF THE DIFFERENT PARTS OF THE HAND IN DIFFERENT GENERA

Genus	Number of specimens	Percentage of total length of the hand of:		
		Carpus	Metacarpus	Phalanges
Pan	5	14	36	50
Papio	5	17	38	45
Cercopithecus	5	15	33	52
Ateles	2	12	34	54
New World genera	4	14	31	55
Notharctus	1	15	22	63
Tarsius	1	9	26	65
Proconsul	1	15	36	49

From this table it can be seen that the fossil hand is remarkably similar to that of *Pan* in the proportions of its main parts. It shows neither the specialised condition of the long metacarpals and short phalanges as in *Papio,* nor the short metacarpals and long phalanges of the New World genera. Even in the long-handed New World brachiators (e.g. *Ateles*) a relatively short metacarpal segment is found.

TABLE XVI

THE PROPORTIONS OF THE DIFFERENT PARTS OF THE FORE-LIMB IN DIFFERENT GENERA

Genus	Number of specimens	Percentage of total length of the fore-limb of: Hand	Forearm	Arm
Pan	5	29·3	33·9	36·8
Papio	4	23·7	39·7	36·6
Cercopithecus	5	26·5	36·5	37·0
Presbytis	2	28·1	36·3	36·0
Ateles	2	26·2	36·6	37·2
New World genera	4	28·4	33·6	38·0
**Notharctus*	1	29·0	34·5	36·5
†*Proconsul*	1	25·5	34·4	40·1

* Measurements taken from life-size diagrams of the fore-limb bones of *Notharctus osborni* (Gregory, 1920).

† Based on mean estimated length of humerus.

While the proportions of the three segments of the hand are similar in *Pan* and *P. africanus*, the proportions of the three parts of the limb show some difference (Table XVI, Appendix IV, Indices 4, 5, 6). The fossil hand is relatively short and the humerus relatively long compared with that of *Pan*. The high value of the arm length in *P. africanus*, based on the "mean" humeral length, constitutes the highest in the series. This finding is somewhat surprising and may possibly indicate that the length of the humerus has been overestimated in the reconstruction of this bone. However, reference to the Colombian Miocene form *Cebupithecia* (Stirton, 1951) indicates that the estimated mean humeral length of *P. africanus*, relative to the radial length, is not unduly high (p. 38).

THE CARPUS

The carpus is complete except for the trapezoid and the os centrale. There can be no doubt that the latter bone was present and separate, and occupied the typical position found in Anthropoidea, separated from the hamate bone by the capitate and articulating with the trapezium, trapezoid, scaphoid and capitate. The free os centrale distinguishes the fossil hand from that of modern *Pan*, in which fusion between the centrale and the scaphoid occurs at or just after birth (Schultz, 1936).

The anterior concavity of the carpus, which forms the osseous portion of the carpal tunnel, can best be observed by studying the distal articular surface of the distal row in a fresh or ligamentous preparation. The greater the curvature of the carpus, the deeper is the fibro-osseous carpal tunnel. In modern forms an increased curvature is brought about mainly by "wedging" of the bones, particularly of the capitate, from dorsal to volar surface (cf. *Cacajao* with *Pan*, Text-fig. 12*e*, *a*). The greater the curvature of the carpus as a whole, the more nearly does the set of the trapezium approach a right angle with the plane formed by the posterior margin of the capitate.

In Text-fig. 12 it is apparent that *Pan* (*a*) shows the greatest curvature, and in this genus the trapezium is set at an angle of 90° or more to the plane of the posterior margin of the capitate. At the other extreme, the trapezium in *Cacajao* (*e*) is set at approximately 45° to this plane. In *Cercopithecus* (*c*) the angle approximates to 60° and in *Papio* (*b*) it is less than 90°. In *Ateles* (*f*) the set of the trapezium more nearly approaches 90° than in other New World genera.

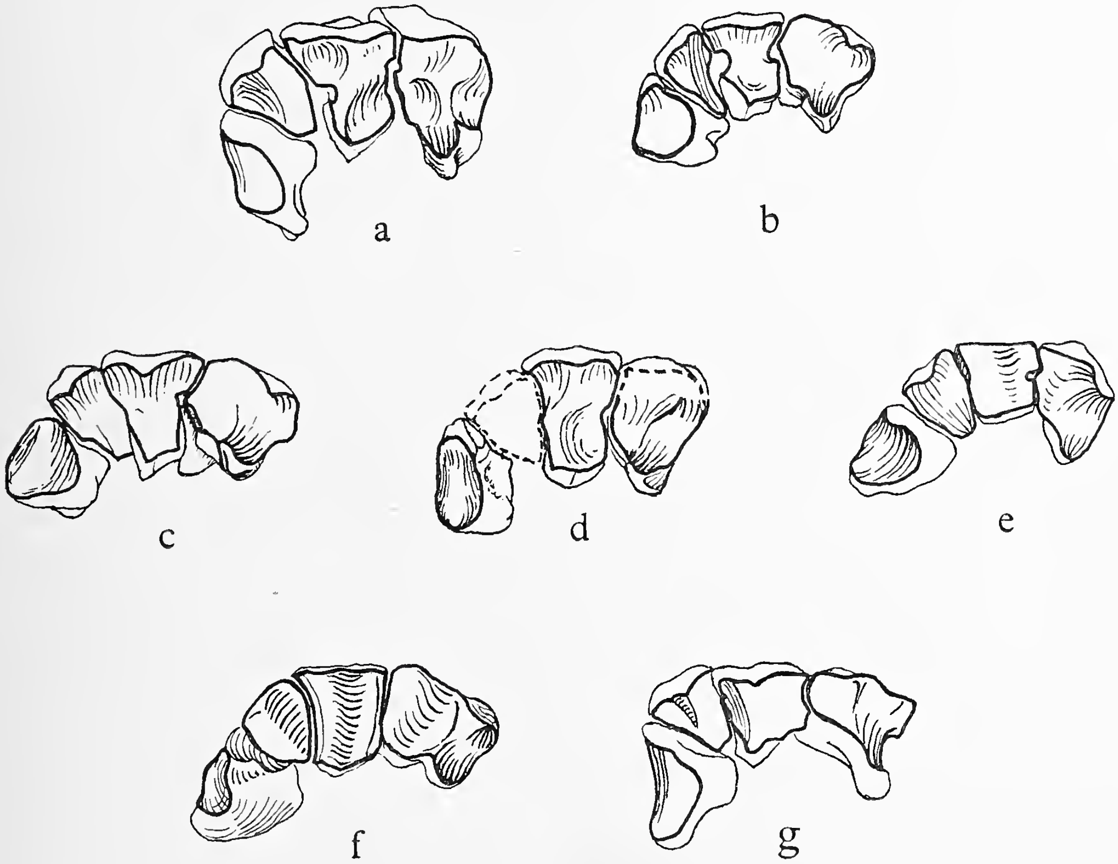

FIG. 12. Drawings of the distal aspect of the carpus in (*a*) *Pan*, natural size; (*b*) *Papio*, natural size; (*c*) *Cercopithecus*, × 2; (*d*) *P. africanus*, × 1½; (*e*) *Cacajao*, × 2; (*f*) *Ateles*, × 2; (*g*) *Cebus*, × 2. Note the differences in obliquity of the trapezium and depth of the carpal tunnel in the different forms.

This observation in *Ateles*, together with the finding in *Pan*, suggests that medial rotation of the trapezium about a vertical axis in association with an increase in depth of the carpal tunnel is a structural adaptation for brachiation. Furthermore, the marked degree of medial rotation in *Ateles* (in which a free thumb is absent), when compared with other New World genera, strengthens the view that the significance of medial rotation of the trapezium in brachiators is related to the depth of the carpal tunnel rather than to a functional specialisation of the thumb itself. *Cebus* (Text-fig. 12*g*), a New World form possessing a prehensile tail and indulging in occasional brachiation, shows a greater degree of medial rotation of the trapezium than do *Cacajao* and

Pithecia, genera in which the tail is non-prehensile and which are therefore considerably less acrobatic. The considerable medial rotation in *Papio* is accompanied by a shallow carpal tunnel, and this rotation may be looked upon as an adaptation to terrestrial quadrupedalism and, in particular, to the digitigrade gait of the genus.

In *P. africanus* (Text-fig. 12*d*) the set of the trapezium has been evaluated by reference to the articular facet for the second metacarpal (p. 47), and is estimated to have been 90°. This degree of rotation more closely approaches the condition in *Pan* than that in any other genus studied. The general shape of the articulated carpus in the fossil specimen suggests that the anterior concavity was fairly deep, approximating to that of the arboreal quadrupeds, but was not as marked as in *Pan*.

Although the degree of medial rotation of the trapezium appears to be associated primarily with the depth of the carpal tunnel, it also affects the amount of medial rotation of the first metacarpal. In *Pan* the thumb lies at an angle of 90° or greater to the plane of the palm, and even at rest it is in a favourable position to oppose the remaining digits. This position of the thumb, owing nothing to muscular activity, might well be termed "passive opposition". The marked degree of passive opposition that must have been present in *P. africanus* is of significance when considered in the light of the shape of the distal articular surface of the trapezium, which will be discussed later (p. 46).

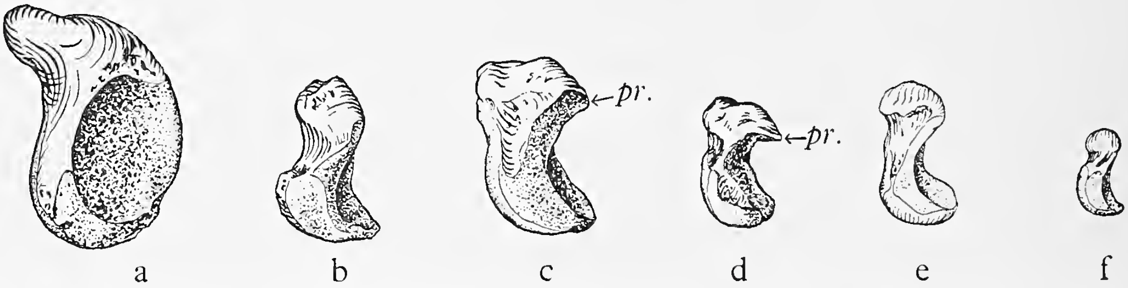

Fig. 13. Drawings of the medial aspect of the scaphoid in (*a*) *Pan*, (*b*) *P. africanus*, (*c*) *Papio*, (*d*) *Cercopithecus*, (*e*) *Ateles*, (*f*) *Cacajao*: pr. = the beak-like process present in *Papio* and *Cercopithecus*, but absent in the other forms. × $1\frac{1}{3}$.

Scaphoid.—The fossil bone is complete and differs profoundly from that of *Pan* (Text-fig. 13*a*), for in the chimpanzee the os centrale fuses with the scaphoid late in foetal or early in post-natal life (Schultz, 1936). Macalister (unpublished MS.) from a study of the irregularities of the bone and the occurrence of extra ossicles in this region of Man, considered that the os centrale element constitutes a large part of the scaphoid in the region of the postero-medial angle, whereas the late Professor Wood Jones (1949) considered that the bone was composed of the primitive scaphoid in its proximal part and a preaxially displaced os centrale in its distal part. *P. africanus* clearly possessed a separate os centrale, and in this respect was similar to all catarrhine and platyrrhine monkeys.

The scaphoid of *P. africanus* (Text-fig. 13*b*), however, shows a striking difference from catarrhines in the absence of an unnamed beak-like process (Text-fig. 13, *pr.*) forming an outstanding feature of the scaphoid of *Papio* and *Cercopithecus* (Text-fig. 13*c*, *d*): this beak lies in a direction diametrically opposite to that of the tuberosity, and extends towards the angle between the trapezoid and the capitate. In these genera the process articulates with the facet on the proximal surface of the trapezium. In *Pan* (Text-fig. 13*a*) the process is obscured by the fusion of the os centrale with the scaphoid; it is apparent, though poorly developed, in *Hylobates*, in which form the os centrale usually forms a separate entity; it is absent in platyrrhine monkeys. Its absence in *Ateles* and *Lagothrix* and its relatively poor development in *Hylobates*, suggests that it is not specifically a brachiating feature. Equally, its absence in the generalised arboreal New World monkeys (i.e. *Cacajao* and *Pithecia*) and its presence in Old World arboreal monkeys (e.g. *Cercopithecus*, Text-fig. 13*d*) suggests that it bears little direct relation to the functional demands of an arboreal environment.

The size and prominence of the tuberosity (Text-fig. 13) may well be related to the necessity for a deep carpal tunnel in brachiating forms. This structure is prominent in *Pan* and *Hylobates* and, to a slightly lesser extent, in *Ateles;* it is relatively small in *Papio* and *Cercopithecus*. The tuberosity in *P. africanus* is more stoutly built and somewhat more prominent than in *Ateles*, but not so large or prominent as in *Pan*.

Lunate.—The fossil specimen is complete. It cannot be distinguished from that of *Cercopithecus* or *Papio*. The bone is somewhat elongated in New World genera in a proximo-distal direction, a feature not displayed in *P. africanus*. The lunate of *Pan* bears a crescentic articular surface for the scaphoid which is not apparent in *P. africanus* or any catarrhine or platyrrhine monkey examined by us.

Triquetral.—The fossil bone is incomplete in its radial portion where it articulates with the lunate. The fragment cannot be distinguished from corresponding portions of the bone in *Papio*, *Cercopithecus* or the New World genera including *Ateles*.

Pisiform.—The pisiform in *P. africanus* is a large squat bone bearing an open epiphysis at its free extremity. The articular surface bears two facets set at 60° to each other which articulate with the triquetral and the styloid process of the ulna. The triquetral facet, which is somewhat rectangular, is convex, while the ulna facet is concave. While having the same general shape as in *Papio* the fossil pisiform clearly takes a considerably greater part in the wrist joint than it does in modern baboons, in which only a single facet for the triquetral is present on the base of the bone, the facet for the ulnar styloid being inconspicuously situated on the ulnar aspect of the shaft. It is completely unlike that of *Pan*, which is a slender elongated bone articulating only with the carpus. Indeed an exactly similar articular surface could not be found in any Primate of the Juvenile Series. Among the few mammals examined the fossil bone bears perhaps the greatest similarity with that of the dog. In view of the tendency for the pisiform to migrate distally, and thus to lose contact with the ulnar styloid in the specialised conditions, e.g. *Pan*, *Homo* and Lorisinae (Nayak, 1933), the intimate relation of the pisiform in *P. africanus* to the ulnar styloid may be regarded as the persistence of a generalised character in a hand that is clearly showing indications of specialisation in other features.

Hamate.—The fossil bone is slightly eroded on its distal and radial surfaces, its distal articular surface being virtually intact. The articular facet for the fifth metacarpal faces slightly medially, being set at a small angle to that for the fourth metacarpal: this appearance is seen to a somewhat greater degree in *Papio* and *Cercopithecus* but not in *Pan* where the two facets lie in the same plane. The medial tilt of the facet for the fifth metacarpal in catarrhine monkeys is related to the presence of a styloid process on the fifth metacarpal, a process absent in *Pan* and *Ateles*, and poorly developed in *P. africanus*. The fossil bone bears a "hook" of moderate proportions, similar to that seen in *Papio*, somewhat smaller than in *Cercopithecus*, and considerably smaller than that of *Pan* or *Ateles*.

In general the fossil bone is more typical of catarrhine monkeys than of *Pan* or *Ateles*.

Capitate.—The fossil capitate is complete. There is little to distinguish it in general from the capitate in *Pan*, *Cercopithecus* or *Papio*, except that the distal articular surface in *P. africanus* does not appear to be as markedly wedge-shaped (Text-fig. 12) as it is in *Papio* or *Pan*. In this respect it corresponds more closely with that of *Cercopithecus*.

Trapezium.*—Of all the carpal bones the trapezium shows the greatest variety of shape in a comparative series. In *Pan* (Text-fig. 14*a*) the bone has the appearance of a vertically compressed rhomboid: in *Papio* and *Cercopithecus* (Text-fig. 14*b*, *c*), it is rectangular, being longer in the proximo-distal diameter than in the radio-ulnar diameter: in New World monkeys the trapezium is triangular. The shape of the trapezium of *P. africanus* (Text-fig. 14*d*) is unlike that seen in any other form in the Juvenile Series. It is rectangular in outline, but unlike *Papio* and *Cercopithecus* the greatest diameter is in the dorsi-ventral plane as it lies in its articulated position.

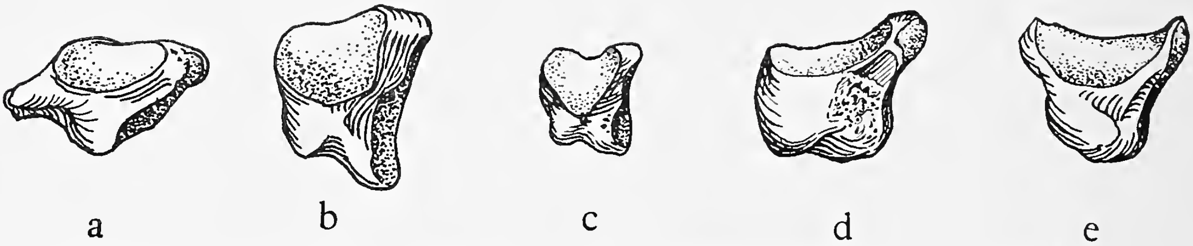

Fig. 14. Drawings of the oblique medial aspect of the trapezium in (*a*) *Pan*, $\times 1\frac{1}{2}$; (*b*) *Papio*, $\times 2$; (*c*) *Cercopithecus*, $\times 2$; (*d*) *P. africanus*, $\times 2$; (*e*) *Cebus*, $\times 2\frac{1}{2}$.

The distal articular surface also shows considerable variation throughout the series. That of *Pan* is restricted to the distal surface of the bone as in Man, but unlike Man it is usually only slightly saddle-shaped. There is considerable variation in the degree to which the saddle-shaped articular surface is present in chimpanzees (Mivart, 1867), and Huxley (1864) noted that the saddle formation was sometimes absent, as it is in three of the five Juvenile 2 chimpanzees in the present series. The articular surface in *Papio* extends well on to the ventral aspect of the bone. The articular surface in *Cercopithecus* extends, as in *Papio*, on to the ventral surface of the bone, but forms a much more pronounced saddle than is seen in the latter form. As noted by Lucae (1865), the surface in *Ateles* is convex, being similar to but not identical with the appearance shown in *Hylobates*. With the exception of *Ateles* the distal articular surface in the New World genera is restricted to the distal aspect,

---

* For the sake of uniformity, it has been assumed that the trapezium is medially rotated about a vertical axis, and the articular surface thus orientated at right angles to the plane of the distal carpal row in all genera, as it is in *Pan* (Text-fig. 14*a*). Thus, this surface will have a dorsi-ventral diameter (morphologically analogous with the radio-ulnar diameter of, for example, the capitate), and a radio-ulnar diameter.

and forms a saddle which is considerably longer in the dorsi-ventral than in the radio-ulnar diameter (Text-fig. 14*e*): the surface is thus somewhat cylindrical and bears a marked resemblance to the distal articular surface of the medial cuneiform of the pes of Old World monkeys and apes. The articular surface of New World genera, however, is concave in its longest diameter, while that of the medial cuneiform is flat or slightly concave. In *P. africanus* the distal articular surface of the trapezium is also of the cylindrical type, having the dimensions 4·0 × 7·5 mm. The dimensions in *Pan* G. are 8·0 × 9·5 mm., in *Pan* F. 6·5 × 10·0 mm., in *Papio* A. 6·5 × 6·5 mm.

The size and prominence of the tuberosity of the trapezium varies in the different genera (Text-fig. 14). It is well-developed in *Pan*, and is present, although small, in *Papio*, *Cercopithecus*, and the New World genera. In *P. africanus* the tuberosity is relatively large. In this respect the fossil bone shows some degree of functional affinity with *Pan*. In the shape of the articular surface, however, *P. africanus* shows a marked similarity to the Pithecinae and the Cebinae. It is interesting to observe the striking resemblance between the fossil bone and that of an adult *Cebus* that would result were the prominent tuberosity of the former reduced in size.

In the reconstruction of the hand the fossil trapezium was orientated by articulating the small, flat, triangular-shaped facet on the prominent tubercle of the trapezium, which extends from the articular surface in a dorsal direction, with the correspondingly shaped facet on the radial side of the base of the second metacarpal. When so articulated the trapezium lies in a plane approximately at right angles to the plane of the carpus as judged by the dorsal surface of the capitate bone.

A cylindrical type of articular surface reduces the degree of rotatory movements possible at this joint. In the case of the fossil thumb the only movements that might be expected would be those usually associated with a condyloid joint, i.e. flexion and extension, abduction and adduction. In view of the cylindrical type of articular surface and the "set" of the fossil trapezium at right angles to the rest of the carpus, it would be justifiable to deduce that *P. africanus* was capable of opposition, though not in the sense of an active rotatory movement as in Man. Such opposition might be described as "passive opposition" occurring by virtue of the "set" of the thumb. It must be remembered, however, that the effectiveness of opposition in prehensile function of the hand depends on other factors, particularly on the relative lengths of the digits and of the thumb. Unfortunately in *P. africanus* the true length of the thumb is at present unknown and therefore the effectiveness of its pollecial opposition must remain in doubt.

THE METACARPUS (Table XVII).

Second Metacarpal.—The second metacarpal is a rather stout, cylindrical bone, circular in cross-section, that in general shape resembles the cercopithecoid type. In *Pan* and *Ateles* the bone has a narrow waist, is expanded at its distal end, and is triangular in cross-section.

Seen from the front the distal epiphysis is asymmetrical, the flattest part of the curve being on the lateral aspect. This appearance is typical of the second metacarpals of the Primates including Man. Seen from above, the epiphysis is heart-shaped, ending posteriorly in a blunt apex. This shape is typical of the cercopithecoid monkeys and ceboids. The appearance of the epiphysis in *Pan*, and to some extent in *Ateles*, is quadrilateral with a well-rounded posterior margin.

The general smoothness of the contour of the epiphysis of the fossil bone, however, bears a closer resemblance to *Pan* and *Ateles* than to *Papio*, *Cercopithecus* or the New World monkeys. In many Primates, the anterior surface of the digital metacarpal epiphyses exhibit deep grooves on either side of the centre line, grooves which extend downwards and gradually fade out on the distal aspect: between the grooves the bone is raised to form a central eminence or keel. The grooves articulate with sesamoid bones, and the extent to which they pass towards the posterior surface of the epiphysis indicates the degree of hyperextension employed at the metacarpo-phalangeal joint during weight-bearing. In *Papio*, the grooves are deep and extend posteriorly for a considerable distance, a condition clearly related to the metacarpo-phalangeal hyperextension associated with the habitual digitigrade posture adopted by these forms. In the Cercopithecoidea and the New World monkeys the grooves are less deep, and extend less far posteriorly. In *Pan* and *Ateles* sesamoid grooves are not usually apparent, the central keel being absent. In *P. africanus* the epiphysis of the second metacarpal bears a faint shallow groove on its lateral side alone, and has a barely discernible keel.

The proximal end of the fossil bone shows a well-marked notch in an antero-posterior direction. This notch, which is typical of all Primates, varies considerably in depth in different forms. In *Pan* and *Proconsul africanus* it is deep, due to the presence of a well-developed lateral buttress for the trapezoid. The notch is shallow and the buttress poorly developed in *Papio* and *Cercopithecus*; in New World monkeys the buttress is atypical and bears the articular facet for the trapezium on its proximal surface. The buttress in *Ateles* and *Presbytis* is intermediate in size between that of *Pan* and the cercopithecoids.

The lateral profile of the lower end of the second metacarpal in *P. africanus*, *Pan* and *Ateles* is in contrast with the contour seen in the Cercopithecidae where it is distinctly "boat-shaped".

In summary, the absence of marked sesamoid grooves on the epiphysis, the depth of the notch, and the relative shortness of the antero-posterior diameter at the proximal extremity indicate a clear structural affinity of the fossil metacarpal with those of the brachiators. On the other hand the "heart-shaped" epiphysis is typical of the quadrupeds of both the arboreal and terrestrial groups.

Third Metacarpal.—The shaft of the fossil bone expands gently proximo-distally, the bone bearing a slight waist in the mid-shaft region. This appearance is similar to, though much less marked than, that seen in *Pan* and *Ateles*, in which forms the taper is clearly apparent. On the other hand the Cercopithecidae show no taper; in this family the shaft has practically the same diameter at the proximal and distal ends and thus might be described as cylindrical. The degree of taper seen in *P. africanus* corresponds more closely to that seen in most New World monkeys. In cross-section the shaft is circular and contrasts with the somewhat triangular cross-sectional appearance of *Pan* and with the rectangular appearance of *Papio*.

The epiphysis of the fossil bone is somewhat elongated and heart-shaped and is slightly asymmetrical, the flatter portion of the curve being directed laterally. The sesamoid gutters and the central keel are barely apparent. In the corresponding bone of *Papio* and *Cercopithecus* the gutter and keel are well marked. They are absent in *Pan* and practically so in *Ateles*. Seen from above the epiphysis is totally unlike that of *Pan* and is more typically cercopithecoid.

The proximal extremity of the fossil bone is fractured on the medial side and a small fragment is missing. Of the portion that remains it is clear that the styloid process characteristic of *Pan* is absent in *P. africanus*.

In summary the third metacarpal of the fossil specimen bears some structural resemblance to *Pan* in the absence of a keel and sesamoid gutters for the epiphysis. The slightly tapering shaft is somewhat reminiscent of *Pan* and *Ateles*, but is perhaps more directly comparable with that found in some New World monkeys, e.g. *Cacajao calvus* and *Pithecia pithecia*.

Fourth Metacarpal.—Although the shaft is fractured in several places the fossil bone is complete. The disto-proximal taper is apparent. A keel and sesamoid gutters are absent. The contour of the proximal extremity is indistinguishable from the cercopithecoid pattern and is distinct from that of *Pan* and New World monkeys including *Ateles*.

Fifth Metacarpal.—The proximal two-thirds of the shaft are complete as is the epiphysis. The distal one-third of the shaft is missing. The proximal extremity is club-shaped and is conspicuously devoid of a styloid process, in which feature the fossil bone bears a marked resemblance to *Pan*. The styloid process, which is most prominent in *Papio*, is represented to a greater or lesser extent in all Old and New World monkeys studied. Hill (1957), however, states that the styloid process is absent in New World monkeys. The existing portion of the shaft is roughly cylindrical and lacks the side-to-side compression typical of the fifth metacarpal of modern *Papio*. The epiphysis is similar to that of the second and fourth metacarpals, being elongated and heart-shaped. Sesamoid gutters and median keel are absent. The epiphysis is asymmetrical, being flattened on its medial aspect.

THE PHALANGES (Pl. 3, fig. 15; Pls. 8–10, Table XVII).

Proximal Phalanges.—Three proximal phalanges of the fore-limb were present in the block containing the hand and foot bones. The shortest was identified as belonging to the thumb, and the remaining two were allotted to the second and fourth digits respectively. In addition, two separate epiphyses were identified and allotted to the third and fifth digits.

Proximal Phalanx of the Thumb (Pl. 10, fig. 28).—The shaft of this bone is nearly cylindrical, showing neither the conical shape characteristic of *Pan* nor the waisted appearance seen in *Papio*, *Cercopithecus* and *Presbytis*. The shaft is asymmetrical, the side with the greater curvature being directed laterally as in most catarrhine and platyrrhine monkeys. The head of the bone is slightly narrower than its neck. This appearance is in marked contrast to *Pan*, *Papio*, *Cercopithecus* and *Presbytis*, in which forms the head is considerably wider than the neck. The flexor aspect of the distal extremity is somewhat cup-shaped, having concave facets for paired sesamoid bones lying between the condyles. Again, this appearance is typical of most catarrhine and platyrrhine monkeys. The plane of the articular surface inclines slightly laterally as in *Pan*: in *Cercopithecus* and *Papio* the surface tilts markedly towards the lateral side. New World monkeys either show a complete absence of tilt as in *Cacajao*, or a slight tilt as in *Saimiri*.

TABLE XVII

MEASUREMENTS OF THE METACARPAL AND PHALANGEAL FRAGMENTS OF *P. AFRICANUS*

Metacarpal	Length (mm.)	Width of distal epiphysis (mm.)	
2	36·0	7·5	
3	38·0	7·0	
4	38·5	7·0	
5	—	6·5	
Phalanx	**Length (mm.)**	**Width of proximal epiphysis (mm.)**	**Width of distal articular surface (mm.)**
Proximal phalanx			
1	18·0*	—	6·0
3	—	8·0	—
4	30·0	—	5·0
5	—	8·0	—
Middle phalanx			
2	15·0	5·5	5·0
3	17·5*	—	—
4	17·0	—	5·0
5	—	—	4·5
Distal phalanx			
3	6·0	—	2·25

* Epiphysis missing.

Without its epiphysis, the bone is 18·0 mm. in length. The thickness of the missing epiphysis has been estimated at 1·5 mm., giving a total length for the bone of 19·5 mm. In the comparative series the length of the first proximal phalanx has been compared with that of the third metacarpal and expressed as an index. The findings are summarised in Table XVIII.

TABLE XVIII

COMPARISON OF THE LENGTHS OF THE FIRST PROXIMAL PHALANX AND THE THIRD METACARPAL IN DIFFERENT GENERA

Genus	No. of specimens	Mean L. 1st proximal phalanx (mm.) (*a*)	Mean L. 3rd metacarpal (mm.) (*b*)	$\frac{a \times 100}{b}$
Pan	5	24·8	77·2	32·1
Papio	4	14·5	44·5	32·6
Cercopithecus	4	12·5	28·2	44·3
New World monkeys	4	10·75	20·0	53·75
Proconsul	1	19·5	38·0	51·3

It can be seen that the fossil bone is relatively long and is only surpassed in relative length by the New World monkeys. The significance of these measurements in respect of the determination of total thumb length is discussed on p. 40.

Proximal Phalanges of the second and fourth digits (Pl. 10, fig. 29). The phalanx for the second digit is incomplete, lacking the distal one-third of the shaft and the posterior portion of the base.

The fourth proximal phalanx is complete except for a small part of the dorsal surface of the head and the lateral half of the epiphysis. This phalanx is slender for its length but does not differ in robusticity from the similar phalanx in *Cercopithecus*, *Pan* or *Presbytis*. The shaft of the bone has an inconspicuous waist at the junction of the middle and proximal thirds, and a dilatation in the distal half. In cross-section the bone appears oval, the anterior aspect being somewhat flattened. In none of these features can the fossil bone be distinguished from that of *Cercopithecus*, *Pan*, *Presbytis* or *Pithecia*. The phalanx of *Papio* is generally more cylindrical and shows an irregular dilatation in the middle third of the shaft, the site of muscular insertion in this form being at a lower level on the bone than it is inferred to be in *P. africanus*.

The distal extremity of the fossil bone narrows at the junction of the shaft and the head, the articular surface being somewhat compressed from side to side. The condition is similar to that seen in the proximal phalanx of the thumb. This narrowing is not found in any other form to the same extent. The articular surface bears two distinct condyles separated by a deep notch; in this respect it is similar to most catarrhine and platyrrhine monkeys and differs only from *Pan*, in which form the intercondylar notch, though present, is shallow.

Middle Phalanges (Pl. 10, fig. 30).—Four middle phalanges were recovered from the block containing the hand bones but only one epiphysis belonging to these bones was recovered; this was allocated to the second digit for the reasons discussed on p. 39.

Fourth Middle Phalanx.—This bone is complete except for its epiphysis. The bone is moderately robust, being in this respect intermediate between the corresponding phalanx of *Papio* (Pl. 10, fig. 30*b*) which is short and stout and that of *Pan* (Pl. 10, fig. 30*a*) which is long and rather slender. The fossil phalanx has a gentle taper from base to head, an appearance also seen in cercopithecoid monkeys (Pl. 10, fig 30*c*). The phalanx can be distinguished from that of *Pan* by the absence in the fossil form of strong projecting flanges situated on either side of the shaft. The presence of these flanges, which provide attachment for the flexor digitorum sublimis muscle, gives the chimpanzee phalanx a characteristic piriform shape.

Terminal Phalanx.—A single terminal phalanx, without an epiphysis, was recovered from the block. It is piriform in shape, bearing a slight terminal dilatation; it is somewhat flattened dorsi-ventrally and lacks the side-to-side compression seen in claw-bearing Primates (e.g. *Callithrix*). In view of the absence of spatulation of the phalanx, the absence of a fully formed ungula can be inferred. It seems likely that the slight dilatation of the distal end indicates a nail which was compressed from side to side and had a pronounced longitudinal curve, a nail form described by Le Gros Clark (1936) as a tegula.

Summary.—The fossil hand embodies some structural characteristics which are typical of arboreal quadrupedal monkeys, and some which are typical of brachiators. Terrestrial quadrupedal specialisations such as the characteristic proportions of the three main parts of the hand and the cylindrical form of the metacarpals are not found in *P. africanus*. In addition there are certain features, particularly in the carpus, which are found in the hands of most New World monkeys. The scaphoid is such an example; the absence of the beak-like process in *P. africanus* must be looked on as a primitive feature of the carpus that had been lost in the Old World genera but retained in the New World forms. The trapezium, too, is a bone of considerable interest. Once again the characteristic shape of the distal articular surface in certain modern New World monkeys is found in the fossil form but has apparently been lost in the modern representatives of the catarrhines: it is of particular interest that this primitive feature should be combined in the fossil form with a trapezium that is set in the carpus in a manner typical of certain modern brachiators (*Pan* and *Ateles*). The presence of both primitive and specialised features in this particular bone, however, are not irreconcilable if it is appreciated that two different aspects of function are involved. The distal articular surface is related entirely to function of the thumb, while the set of the bone in the carpus is related to the action of the long flexors of the digits during brachiation and, consequently, the need for a deep carpal tunnel.

The arboreal quadrupedal features of the fossil hand are most evident in the carpus, while those structural characteristics which suggest adaptation to a brachiating mode of locomotion are most evident in the metacarpus and phalanges. This partition is well shown by the metacarpal series, in which the proximal ends retain arboreal quadrupedal features while the distal extremities, with their somewhat globular heads with ill-developed sesamoid grooves, betoken a functional affinity with the brachiators. The partition in *P. africanus* is not, however, complete, as testified by markedly heart-shaped metacarpal epiphyses characteristic of quadrupeds and the absence of a styloid process typical of brachiators on the fifth metacarpal.

THE BONES OF THE FOOT

(Plates 8, 9)

Within the block containing the hand bones were a number of fragments of the bones of the right foot. These fragments consist of the medial cuneiform, the metatarsal and phalanges of the hallux complete with their epiphyses, one sesamoid bone possibly attributable to the hallux, fragments of the shafts of two other metatarsals, parts of the shafts of four phalanges and five phalangeal epiphyses.

The medial cuneiform.—The medial cuneiform is complete and intact apart from slight erosion of the plantar aspect of the distal surface. Its greatest width in the plane of the axis of the metatarso-phalangeal joint is 15·5 mm., and its greatest length at right angles to the plane is 13·0 mm., the bone having a maximum thickness of 8·0 mm. Seen from the medial aspect (Pl. 9, fig. 27; Text-fig. 15) the bone is roughly triangular in shape, the distal and planter margins being approximately at right angles to each other and the dorsal and navicular margins being nearly in a straight line to form the third side of the triangle.

The articular surface for the navicular is small, pear-shaped and concave, the apex of the surface leading into the sharp dorsal margin of the bone. There are two articular surfaces for the intermediate cuneiform, the proximal surface being relatively large and continuous with that for the navicular, whereas the distal one is very small and triangular in shape. This distal facet is continuous with the small square articular surface for the medial aspect of the base of the second metatarsal. The plantar surface is broad and rounded.

The distal articular surface (Text-fig. 15) resembles the shape of the surface of a segment of a curved cylinder, the concavity of the curve facing laterally. The most lateral parts of the surface face distally: the articular surface is rolled over well on to the medial aspect.

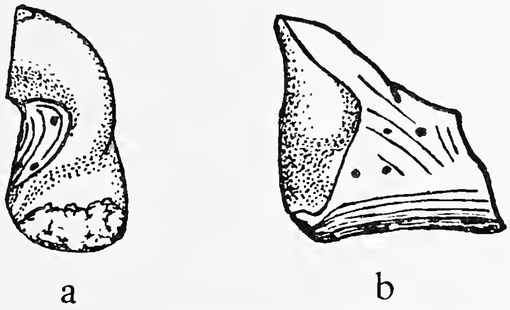

FIG. 15. (*a*) Distal and (*b*) medial views of the right medial cuneiform of *P. africanus*. × 2.

In its general form the medial cuneiform resembles the condition in *Cercopithecus* much more closely than it resembles *Pan*, particularly in its triangular outline, its small navicular facet and the shape of the articular surface for the metatarsal. The relative shortness of the bone (Text-fig. 16) is, however, more like the condition seen in *Pan* than in *Cercopithecus*. This shortening may indicate a shortening of the whole of the anterior tarsal segment, a finding associated by Morton (1924) with extreme arboreal specialisation. The medial extension of the distal articular surface is evidence that the hallux could be widely abducted, and the set of the bone in relation to the plane of the tarsus is such that the hallux would have passively opposed the digits in a manner similar to that described for the fossil pollex (p. 47). Such wide abduction is clearly an arboreal specialisation.

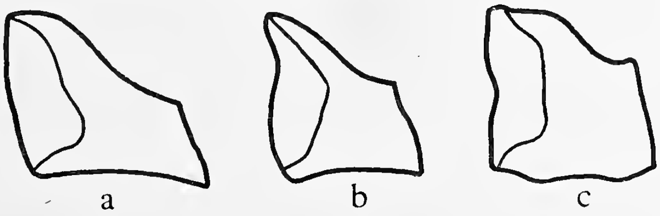

FIG. 16. Diagrams of the medial aspect of the medial cuneiform in (*a*) *Cercopithecus*, (*b*) *P. africanus* and (*c*) *Pan*. Note the relative shortness of the bone in the two latter forms. (Drawn to the same vertical diameter.)

The first metatarsal.—The first metatarsal is complete apart from some slight erosion of the plantar surface of its distal extremity. With its epiphysis *in situ* its principal dimensions are: length 38·5 mm., width of basal epiphysis 11·5 mm., width of distal end 8 mm., mid-shaft width 6 mm. The proximal articular surface is deeply concave in an oblique axis, the plantar portion being extended on to a marked ventral beak projecting from the epiphysis. The shaft of the bone appears robust when compared with the Cercopithecidae, but is somewhat more slender than in *Pan*, having a definite "waist" in the mid-shaft region.

The distal articular surface resembles that of *Pan* in its possession of a well-rounded central keel. The sesamoid grooves extend farther on to the dorsal surface than they do in *Papio* and *Cercopithecus*, but not so far dorsal as in *Pan*, and suggest that some degree of hyperextension was possible.

The hallux (Pl. 9, fig. 27).—The phalanges of the hallux are robust. The proximal phalanx is 22 mm. in length, its mid-shaft width being 6·0 mm.; the width of the proximal epiphysis is 9·0 mm., the distal end being 7·5 mm. wide. The distal phalanx is 12 mm. in length and 8·5 mm. wide at the base, being a stout flattened bone indistinguishable in shape from those of *Pan*, *Papio* and *Cercopithecus*; thus, it may be inferred that it bore a flattened nail.

The proximal articular surface of the proximal phalanx is deeply concave from side to side, and flattened in a dorsi-plantar direction. In *Pan* and *Cercopithecus* this surface is deeply concave in both directions; the metacarpo-phalangeal joint in *P. africanus* is thus of a more simple form in which side-to-side movements and rotation were clearly not possible. The remaining articular surfaces of the hallux are similar in *Pan*, *Cercopithecus*, *Papio* and *P. africanus*.

Table XIX

THE DIMENSIONS (in mm.) OF THE PHALANGEAL FRAGMENTS FROM THE RIGHT FOOT

Fragment	Condition	Length	Width of proximal epiphysis	Width of distal end
Proximal phalanx a	Intact . . .	26	7	4·5
Proximal phalanx b	Distal half missing .	—	7	—
Distal phalanx c	Intact . . .	17	5·5	4·5
Distal phalanx d	Intact . . .	13·5	5·0	4·5
Distal phalanx e	Epiphysis only .	—	6·0	—

Other metatarsal fragments.—The basal third of the fifth metatarsal can be identified since part of the buttress for the styloid process is present, but the fragment is too badly eroded for deductions to be drawn. The remaining metatarsal fragment consists of the distal third of the shaft of a metatarsal, the fragment being too small to allow a more precise identification. The side-to-side flattening of the epiphysial surface of this fragment is similar to that seen in *Pan*: the metatarsals of *Cercopithecus* and *Papio* are flattened in a reverse direction.

The pedal phalanges.—The phalangeal fragments consist of one complete and one incomplete proximal phalanx, and two complete middle phalanges. There are two epiphyses from the proximal row which fit the phalangeal fragments, and three from the middle row, two of which can be fitted to the existing phalanges. With the available material, there is no absolute method of allotting any of these phalanges to particular digits.

The dimensions of the various phalanges are given in Table XIX. All exhibit a gentle curvature of the shaft with a plantar concavity. All are flattened in a dorsi-plantar direction, and in each the expansion of the shaft as it approaches the distal extremity is small. In this respect the bones are similar to the pedal phalanges of *Pan*, and contrast with those of *Cercopithecus* and *Papio*, in which forms the distal extremities of the phalanges are expanded. In view of the widely divergent hallux, the shortness of the medial cuneiform, the side-to-side compression of the metatarsal fragments, the flattening and the lack of expansion of the distal ends of the middle phalanges, the foot must be regarded as that of an arboreal form.

III. DISCUSSION

It is apparent from the foregoing account of the Gumba specimen that the limb material provides considerable scope for determining the locomotor habits of this species of *Proconsul*, hitherto known only from the dentition, jaws and skull. Furthermore there appears to be much to be derived from a study of the evolutionary trends apparent in this individual that can be applied to the wider problem of brachiation in the Pongidae. Finally, the material constitutes a second determinant by which the family status of this fossil hominoid may be confirmed.

Locomotor Habit

The upper limb bone of *P. africanus* shows many primitive and generalised features that provide evidence of a quadrupedal arboreal heritage; associated with these characters are others that appear to be adaptive for a brachiating mode of life. Specialisations of the fore-limb bones towards a terrestrial and cursorial life are entirely absent.

The basic adaptive type for placental mammals, represented by the smaller Paleocene creodonts and insectivores, possessed limbs of medium length, mobile and adaptable. The hands were pentadactylous, having long, slender and well-separated digits, a "semi-opposable" (Matthew, 1917) thumb and metacarpals with globular heads. The elongation of the digits characteristic of the Primate hand is already apparent in the Upper Paleocene form *Plesiadapis* (Matthew, 1917), in *Pelycodus*, a notharctine of the Lower Eocene (Matthew, 1937), and is fully apparent in *Notharctus* (Gregory, 1920) of the Lower and Middle Eocene (Bridger formation) of North America. Although the limb bones of *Notharctus* present more generalised mammalian characters than do modern lemurs (Hill, 1953), Primate affinities are shown particularly at the lower end of the humerus, where evidence of free rotatory movements of radius and ulna are apparent. In the hand of *Notharctus* many of the modern lemuroid specialisations of the carpus, the thumb, and the phalanges are absent. Thus, though it is no longer doubted that the Notharctinae must be looked upon as primitive and aberrant lemuroids and, therefore, as not directly relevant to any discussion of ancestry of the catarrhine and platyrrhine grades, nevertheless the upper limb skeleton is not too specialised to provide evidence of the stage of arboreal adaptation reached by the Primates in the Middle Eocene.

The generalised features of the fore-limb of *P. africanus* include the shape of the upper end of the humerus and the direction of the humeral head, the rounded capitulum, the moderate length of the radius with its somewhat flattened oval shaft and terminal expansion, the low brachial index, the relatively short hand with a long thumb, the free os centrale, and the general shape of the scaphoid and the trapezium. The adaptive features of the humerus include the low deltoid insertion, the form of the humero-ulnar articulation, the horizontal set of the head and the lateral direction of the convexity of the shaft of the radius, the relative proportions of the carpus, metacarpus and phalanges, the set of the trapezium, the relative depth of the carpal tunnel, and the form of the articular extremities of the metacarpals.

The upper end of the humeral fragment of *P. africanus*, as inferred from the reconstruction, is typically that of a quadrupedal monkey. The pattern is modified, firstly, by the presence of a deltoid muscle extending further down the shaft than is usual in purely quadrupedal monkeys and, secondly, by the absence of a strong delto-triceps crest. While in both these respects the fossil humerus approaches the condition seen in fully developed brachiators, it resembles most closely that of the quadrupedal brachiating form *Presbytis*.

A strong deltoid is characteristic of both arboreal and terrestrial quadrupedal monkeys. In *Notharctus* it extended over only the proximal one-third of the shaft (Gregory, 1920). In modern non-brachiating forms the deltoid occupies at least the proximal two-fifths of the humerus, while in the brachiating forms it extends well below the mid-point of the shaft. Thus, elongation of the deltoid muscle may be considered to be a progressive feature in arboreal life and probably one that is pre-adaptive for brachiation. On the other hand, a strong delto-triceps crest is clearly an adaptation to terrestrial quadrupedalism. This crest is absent from the humerus of both *Notharctus* and the fully arboreal quadrupedal monkeys of today.*

The lower extremity of the fossil humerus is unequivocally that of an arboreal brachiating form. The features which may be regarded as adaptive for brachiation include the prominent keel separating the trochlea and capitulum, the high trochlear index and the extension of the articular surface on to the posterior aspect of the lower extremity of the bone. The generalised characteristics include the rounded capitulum, the absence of a marked medial lip to the trochlea, and the absence of a sharp lateral edge to the olecranon fossa; these characters are found in the Eocene lemuroid *Notharctus* as well as in the modern arboreal monkeys of the New World. Thus one may assume that the sharp-edged capitulum and the prominent margins of the trochlear and olecranon fossae of *Papio* and *Cercopithecus* are adaptations to terrestrial life.

With regard to the fossil radius the generalised arboreal features include a neck of moderate length, a somewhat flattened shaft which is oval in section, and a slight terminal expansion of the distal extremity with a moderately developed styloid process. All these features are well shown by the genera of New World monkeys. *Notharctus*, however, while possessing a radial neck of moderate length and an oval contour of the shaft, had a small styloid process and no expansion at the lower end of the radius (Gregory, 1920). The adaptive (brachiating) features of the radius of *P. africanus* include the horizontal plane of the head of the radius relative to the shaft and the laterally directed convexity of the shaft itself. Terrestrial features of the radius of *Papio*, which are absent from the fossil bone, include the short radial neck and the posterior direction of the convexity of the shaft.

Since Miocene times there appears to have been a tendency among certain Primates to increase the length of the forearm at the expense of the upper arm. In modern forms the brachial index is higher than that of their Tertiary counterparts (Table XIV), an observation that adds support to Schultz's view (1930), based on his ontogenetic studies of modern Primates, that elongation of the radius occurs late in phylogeny.

In all representatives of Mesozoic amphibians, reptiles and proto-mammals, the

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* The presence of a delto-triceps crest in *Cercopithecus*, as in *Macaca* and other semi-terrestrial Cercopithecidae, can probably be explained by assuming that this modern arboreal form has been evolved from an ancestral form terrestrial in habitat and cursorial in habit (Napier—in preparation).

humerus far exceeds the radius in length. It is not until the Lower Eocene that examples are found among mammalian fauna in which the radius equals or exceeds the length of the humerus. In *Notharctus* a relative elongation of the forearm is already apparent.

Among modern mammals the radius exceeds the humerus in length in a variety of forms, including horses, camels, giraffes, bats, kangaroos, jerboas and flying squirrels. Among pithecoids a radius longer than the humerus is found in gibbons, orang-utans, spider monkeys and baboons, and it is also found in lemuroids. This list is clearly not exhaustive, but it would appear to indicate that a high brachial index occurs in many mammals in which a marked degree of lengthening of the whole fore-limb has taken place as part of an overall locomotor specialisation.

Arboreal life *per se* does not appear to give rise to either excessive growth of the fore-limb or a disproportionate growth of the middle segment. A radius shorter than the humerus is typical of the New World monkeys, only *Ateles* (102) and *Leontocebus* (101) showing high brachial indices. The majority of New World forms have indices which lie between 85 (*Callicebus*) and 95 (*Cebus*) (Erikson, personal communication). Brachiation on the other hand tends to be associated with excessive relative growth of the arm as a whole and of the middle segment in particular, with consequently a high inter-membral index and a high brachial index. This is true of gibbons and spider monkeys. Both chimpanzees and gorillas have high inter-membral indices compared with generalised arboreal quadrupedal monkeys and low brachial indices compared with other brachiators [adult chimpanzee = 92·2; adult lowland gorilla = 80·7 (Schultz, 1930)]. It is possible in both these pongid forms that some *secondary* shortening of the middle segment has occurred since they assumed a mainly terrestrial habitat and became quadrupedal in locomotor habit. This seems to be the most likely explanation of the relatively low brachial index in *Pan* and, particularly, in *Gorilla*. In support of this is the fact that chimpanzees, which are more arboreal and therefore the more competent brachiators, have a higher average index than do the gorillas. Furthermore, Schultz's studies of post-natal growth in *Gorilla gorilla* indicate that in the lowland species the total limb length relative to trunk height, the inter-membral index, and the brachial index itself, all decrease with age (1930). The only alternative assumption is that in both *Pan* and *Gorilla* extensive elongation of the fore-limb has taken place by means of disproportionate lengthening of the humerus; such a pattern of growth would be at complete variance with the fundamental evolutionary trend in mammals to lengthen the limb mainly by means of a relative growth in length of the forearm.

The low brachial index of *P. africanus* must probably be regarded as a primitive arboreal feature, since the elongation of the fore-limb as a whole and the forearm in particular, which are characteristic of modern arboreal brachiators, had not yet developed in the fossil form. It is interesting to note that the brachial index for *P. africanus* is almost identical with that of the single individual of the Miocene genus *Cebupithecia* recovered by Stirton.

The hand of *P. africanus* once again demonstrates a combination of generalised arboreal and specialised brachiating characters. The comparative shortness of the fossil hand compared with the total length of the limb is a generalised condition: this is in contrast with most modern Old World monkeys and apes (with the exception of the terrestrial forms) and with the Eocene form *Notharctus*, in which the typical lemuroid specialisation was already apparent. In its relative hand length *P. africanus* corresponds most closely to the arboreal monkeys of the New World. In contrast, the relative proportions of the three main segments of the fossil hand indicate that the specialised condition of long metacarpals and long phalanges found in brachiators is already apparent. Fossil evidence (Gregory, 1920, Matthew, 1937) suggests that the primitive mammalian hand had short metacarpals and short fingers, and that a pursuance of arboreal life brought about a lengthening of the phalanges while the metacarpals remained short. This trend, already well developed in *Notharctus* of the Lower Eocene and *Cebupithecia* of the Upper Miocene, is apparent today in the long phalanges and short metacarpals of the tarsier, the lemuroids and the New World monkeys, all thoroughly arboreal Primates. From the generalised arboreal hand at least two other specialised hand forms have evolved in modern Primates. Firstly, the brachiating hand with long metacarpals and long phalanges, and, secondly, the terrestrial quadrupedal hand with long metacarpals and short phalanges. Proportions of the three main segments of the hand of *P. africanus* correspond more closely with those of modern *Pan* than with modern arboreal quadrupedal forms. It should be remembered, however, that while the proportions of the segments of the hand of *P. africanus* must be regarded as adaptive, the relative shortness of the hand in relation to the whole upper limb is a primitive arboreal feature.

Unfortunately it has proved impossible to reconstruct the length of the fossil thumb with any assurance. The proximal phalanx of the thumb is of a greater absolute length than that found in any of the specimens of the Juvenile Series except *Pan*, and of a greater relative length (Table XVII) than any group in the Juvenile Series with the exception of the New World monkeys. Clearly it would be unjustifiable to draw any definite conclusion regarding the total thumb length from these observations, but they suggest, at least, that the thumb in the fossil form was not relatively as short as it is in modern *Pan*. Relative shortness of the thumb must be regarded as a characteristic associated with extreme brachiation. Anthony (1912) pointed out that some monkeys, including *Colobus*, *Ateles* and certain unspecified semnopitheques, by reducing the thumb are becoming transformed from arboreal "prehenseurs" to arboreal "suspendus". The relative length of the thumb of *P. africanus* must be regarded as being nearer to the generalised arboreal type than to the specialised brachiating type.

The digital projection formula of *P. africanus* (based on the authors' reconstruction) is of the generalised simian type common to both arboreal and terrestrial forms. The metacarpal-thickness formula in *P. africanus* conforms to the pattern seen in the primitive Paleocene Insectivore, *Onychodectes* (Matthew, 1937), in which the order of stoutness at mid-shaft level can be demonstrated by the formula: $3 > 2 > 4 > 5 > 1$. This formula is seen today among the generalised arboreal New World monkeys as well as in the specialised brachiator *Pan*. In baboons, the relative stoutness of the fourth metacarpal, apparent from the formula: $3 > 4 > 2 > 5 > 1$, can be regarded as a terrestrial adaptation and reflects the manner in which the weight of the body is carried on the ulnar side of the forefoot.

It has been inferred that the fossil form had a free os centrale, occupying a position in the carpus corresponding to that found in all Anthropoidea in which the bone is separate. The evidence provided by the carpus of certain of the Paleocene St. Juan Basin fauna (*Ectoconus*, *Onychodectes*) indicates that the position of the centrale on the radial side of the capitate is the primitive mammalian arrangement and that the ulnar migration in the lemuriforms is the specialised condition. Gregory (1920) inferred that the centrale in *Notharctus* occupied a primitive mammalian position in spite of the lemuroid affinities of the limb as a whole.

Certain of the carpal bones of the fossil hand are of particular interest, notably the scaphoid and the trapezium. The scaphoid can clearly be distinguished from that of *Pan* and from the Old World genera including *Papio*, *Cercopithecus* and *Presbytis*, but it is remarkably similar in appearance to that of the New World genera including the brachiating form *Ateles*. This similarity is due to the absence in both the fossil form and the New World monkeys of the beak-like process which extends towards the angle between trapezoid and capitate in Old World genera. This beak-like process is particularly prominent in *Papio* and *Cercopithecus*, an observation which suggests that the structure in some way (possibly related to stability) constitutes an adaptation for terrestrial quadrupedalism. *Presbytis*, however, which lacks the terrestrial adaptations of the limb bones seen in *Papio* and *Cercopithecus*, also shows a moderately well-developed process. The apparent absence of this process from the carpus of *Onychodectes tisonensis* figured by Matthew (1937) suggests that the process is an adaptive feature in Old World monkeys which had not yet appeared in *P. africanus*. The prominence of the tuberosity of the scaphoid, which approaches that of *Pan* in relative size, must also be regarded as adaptive in the fossil hand and related to the development of a deep carpal tunnel.*

The trapezium of the fossil carpus is characterised by a crest or tuberosity of relatively large proportions approaching those of *Pan*. The primitive mammalian trapezium found in the earlier creodonts, taligrades and condylarthra (Matthew, 1937) was typically trihedral in shape, as it is in modern *Cebus*. It might be supposed that a primitive trihedral trapezium could achieve a quadrilateral appearance similar to that found in *P. africanus* by the addition of a prominent tuberosity resulting from adaptive change towards a brachiating type of hand function. On the other hand the fossil trapezium possesses an articular surface cylindrical in shape that clearly did not permit of axial rotatory movements of the first metacarpal—a primitive type of articular surface present in the New World arboreal forms. Thus, both adaptive and generalised primitive features are apparent in the same bone. The set of the trapezium in the carpus has already been discussed in relation to function of the thumb (p. 47) and must also be regarded as adaptive in nature.

The arboreal quadrupedal features of the fossil hand, which are *ipso facto* primitive and generalised Primate features, are most evident in the carpus; those structural characteristics which are adaptive to brachiation are for the most part limited to the metacarpus and phalanges. The metacarpals of the generalised primitive creodonts and insectivores of the Lower Paleocene or Puerco formation of New Mexico were somewhat slender and possessed the rounded ball-like heads with little or no keel. This type of metacarpal can be traced through the Upper Paleocene or Torrejon

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* A prominent tuberosity is also seen in *Perodicticus potto*, a lorisoid in which strong digital flexion constitutes an essential part of the locomotor habit. Mivart (1867) notes that the tuberosity of the scaphoid is enlarged in *Gorilla*, *Indris* and *Nycticebus*.

(*Plesiadapis*), and the Middle Eocene (*Notharctus*). Among modern Anthropoidea the primitive metacarpal pattern is seen only in certain advanced brachiators, e.g. *Pan* and *Ateles*. Among the quadrupedal monkeys, the shafts of the metacarpals are stout, particularly in *Cercopithecus* and *Papio*, and the metacarpal heads are heart-shaped with the apex directed dorsally, being deeply channelled by sesamoid bones on either side of the central keel.

The metacarpal heads in *P. africanus* are rounded and smooth in contour and show little evidence of sesamoid impressions or of keel formation. Such an appearance could be interpreted as indicating the persistence in the fossil of primitive mammalian features. Alternatively the fact that a similar smoothness of contour is found in both *Pan* and *Ateles* could suggest that this appearance in *P. africanus* indicates a secondary adaptation towards a brachiating mode of locomotion; the fact that in the arboreal monkeys of the New World the sesamoid grooves and median keel are well marked gives some support to the view that these features in *P. africanus* are adaptive in nature rather than primitive.

Certain characteristics of the proximal extremity of the metacarpal bones, including a well-marked notch at a proximal articulation of the second metacarpal and absence of a well-developed styloid process at the base of the fifth metacarpal, provide support for the interpretation, for these features are characteristic of brachiators. Hill (1957) states that the styloid process is absent from the base of the fifth metacarpal in New World monkeys. In the present series of juvenile forms it was found that the styloid in New World genera, though not nearly so well developed as in *Papio* and *Cercopithecus*, was nevertheless present. Thus, it is possible that the absence of a styloid process in the fossil form may represent a primitive arboreal condition rather than an adaptive one. The depth of the notch at the base of the second metacarpal, observed only in *Pan* and *Ateles* in the Juvenile Series, is, however, unequivocally a brachiating specialisation.

The phalanges cannot be easily distinguished from those of catarrhine and platyrrhine quadrupedal monkeys. They lack the marked dorsal longitudinal convexity of the phalanges of advanced brachiators as well as the characteristic shape, particularly of the middle phalanges, brought about by the presence of well-developed finger flexors. The proximal phalanx of the thumb is quite unlike that of a modern brachiating form both in shape and relative proportion.

The fore-limb of *P. africanus* indicates that in Early Miocene times there existed fossil Primates having the bodily size of a medium-sized baboon with a pongid type of dentition and a fore-limb of a primitive and generalised arboreal nature, but in which certain structural adaptations towards a more specialised form of arboreal life were already apparent. There is no denying the quadrupedal habit of *P. africanus*, nor is it possible to aver that the fossil form was entirely arboreal in habitat on morphological grounds alone. It can only be said that there is no evidence of any specialised adaptation towards a terrestrial life.

Le Gros Clark (1954) has stressed the importance of considering "total morphological pattern" in palaeo-anthropological studies rather than relying overmuch on the separate comparison of individual characters. It has been found more helpful in the present study to extend the conception of "pattern" to a point where it ceases to be a purely morphological concept and becomes a functional or dynamic one. More regard has therefore been given to combinations of characters which form a "total functional pattern" than those constituting a "total morphological" one. Closely bound up with this concept of functional pattern is the need for a precise knowledge of the nature of the environment and for an analysis of the opportunities it offers for exploitation by a particular group of animals. The recent studies of Carpenter (1934, 1940), Sanderson (1940, 1957) and Haddow (1952), and the accounts of older naturalists such as Hose, Bates, Belt and Shelford make it apparent that the territories of Primates are as varying as they are numerous, and that preferences of different species and sub-species have regard not only to latitude and altitude, but to particular regions of forest growth and even to precise vegetational levels in the trees. Such ecological differences are reflected by divergences in functional specialisation which in turn lead to further speciation, for not only major but minor habitats constitute what Simpson (1949) has referred to as the "non-random or anti-chance factor" in adaptive change.

There is every reason to suppose that the environment of *Proconsul* was closely linked with its pattern of locomotion. It is therefore of particular interest to note that what is known of this environment correlates well with the type of quadrupedal brachiating mode of locomotion envisaged for *P. africanus*. Chesters (1957) has reconstructed the environment of the main fossiliferous horizons of Rusinga from the botanical fossils recovered from the different sites; she has demonstrated the existence of a gallery type forest, heavily festooned with lianas, which would provide then, as it does today, the type of habitat in which active, agile, arboreal forms could flourish. It is possible that the forest floor in a lacustrine region fed by numerous water-courses would become seasonally flooded, restricting the animals to the closed canopy regions in the high galleries; during the drier seasons, the forest floor would, by providing a source of water and food, attract animals from the trees. Most of the completely arboreal monkeys of the Old and New World descend from the trees in search of water, that in the drier seasons disappears from the bowls and niches of the trees. There is palaeontological evidence to support this pattern of behaviour in *Proconsul*: large collections of fossil remains of this genus were recovered from shallow-water lacustrine deposits on Rusinga. Le Gros Clark & Leakey (1951) suggest that these sites were habitual watering-places where *Proconsul*, coming down to drink, was particularly prone to attack by carnivores.

The occurrence of endocarps of *Odina* and fruits of *Cnestis* among the fossil flora suggests the presence of forest clearings which may well have provided for *P. major* and *P. nyanzae* the type of terrain suited to the larger size of these forms.

Although at present our knowledge of the forests of Miocene East Africa is very incomplete, there is every expectation that further work on the extensive material from the Rusinga and Mfwanganu sites may yield information which will permit a closer correlation between the functional locomotor patterns of *Proconsul* and its environment.

Significance of Brachiation

The importance of the conclusion that *P. africanus* was a quadrupedal-brachiating form with a pongid type of dentition rests entirely on the interpretation of the term brachiation. If the onset of this mode of locomotion is regarded as having been an occurrence unique in evolution—a radical change in direction involving far-reaching consequences—then this fossil Primate may justifiably be regarded as the long anticipated annectant form between quadrupedal monkeys and brachiating apes. On the other hand if, as we believe, brachiation is looked upon merely as an inevitable oft-repeated outcome of arboreal life, then the recovery from the East African Miocene of limb-bones demonstrating both quadrupedal and brachiating features should occasion little surprise.

Brachiation has undoubtedly acquired a somewhat pongid connotation, but it seems to us that it should by no means be limited to the Pongidae. The use of the fore-limbs as a means of grasping hand-holds above the head or of swinging the body forward in arboreal progression is widely practised throughout the catarrhine and platyrrhine series. The gibbons—perfectionists in this capacity—form, in this sense, the extreme of the range; certain Old and New World monkeys, mere neophytes in the pursuit, constitute the other. Brachiation in its perfected form may be regarded as the ultimate expression of success in arboreal life; once perfection is achieved, arboreal adaptation in this particular direction is complete. The gibbons, including the siamangs, represent in the Old World near perfection as brachiators, while in the New World, through evolutionary parallelism, the spider monkeys have reached much the same point in their own particular way.

The modern chimpanzees, though structurally brachiators and capable of this form of locomotion, are not truly arboreal, and spend much of their time on the ground where they progress in a quadrupedal manner. The gorillas, while adapted for brachiation, are even less arboreal than the chimpanzees. The orang-utans, on the other hand, have remained arboreal in spite of their great weight. Among platyrrhines and catarrhines there are many examples of essentially quadrupedal arboreal monkeys in which brachiation constitutes an occasional part of the locomotor pattern. The capuchins and woolly monkeys of South America, certain langurs of Asia, and the Colobus monkeys of Africa, are examples of "part-time" brachiators. All these forms are habitually arboreal monkeys that, in their natural state, spend little if any time on the ground; in spite of this, and perhaps because of the example of the larger Ponginae, there is a tendency to forget that brachiation is essentially an arboreal pursuit. Indeed, it is regarded by some as a sort of physiological apprenticeship for terrestrial bipedalism. Clearly, to limit the use of the term brachiation to the type of advanced arm-swinging found in the Pongidae, and to regard it as a new adaptational characteristic of anthropoid apes rather than as a fundamental trend of Primate evolution, is to ignore the many examples of this mode of locomotion practised with varying degrees of success throughout the modern pithecoid world.

Viewed in this light, the brachiating characteristics of *P. africanus* cannot be regarded as evidence of a "new" adaptive trend appearing suddenly and for the first time in the Lower Miocene of East Africa, but as the inevitable outcome of a long and uninterrupted arboreal lineage. This hypothesis in no way invalidates the conclusion that *P. africanus* is to be regarded as a primitive hominoid, a conclusion reached by Hopwood (1931) and Le Gros Clark & Leakey (1951) mainly on the basis of the dentition. The fossil form may well have been a representative of the stock from which arose the more specialised pongid brachiators of later times: equally

P. africanus may represent a slightly aberrant type in which brachiation never advanced much beyond the level shown by some modern arboreal quadrupedal monkeys. In this context it is of interest to examine our present knowledge regarding the locomotor skeleton of the fossil hominoids of the Miocene and Pliocene.

The limb-bones of *Limnopithecus* were discovered by Dr. L. S. B. Leakey in 1948 on Rusinga Island associated closely with jaw fragments and isolated teeth which in their morphology corresponded closely with the species *L. macinnesi* (Le Gros Clark & Leakey, 1951). These bones, which were fully described by Le Gros Clark & Thomas (1951), consist of an incomplete humerus, the proximal portion of a radius and ulna, several incomplete portions of femora, a tibia, a fragment of fibula, an incomplete calcaneum and part of a talus, and they show in many features resemblances to the modern gibbon. Associated with these characters, however, were features which reflected a ". . . more primitive (cercopithecoid) phase of evolution associated with a quadrupedal type of activity". Le Gros Clark & Thomas concluded that *Limnopithecus* was not a brachiating form like modern gibbons but much more akin in its arboreal habits to modern cercopithecoid monkeys. Our own studies of the fore-limb bones of *L. macinnesi*, however, incline us to the belief that in their proportions (p. 38) and their morphology they may well be regarded as those of a quadrupedal form in which brachiation, in the most liberal sense of the word as discussed above, formed part of the locomotor habit. It is particularly relevant in this respect that, as Le Gros Clark & Thomas have stressed, there are many striking resemblances between *Ateles* and *L. macinnesi*. While broadly speaking both *P. africanus* and *L. macinnesi* are arboreal quadrupeds in which brachiating adaptations are becoming apparent, it is clear that the pattern of structural adaptation is not identical in the two forms.

There is insufficient evidence at present to indicate whether the Dryopithecinae of the Upper Miocene and Lower Pliocene of Europe and India had advanced much beyond the level of brachiation observed in *P. africanus*. Indeed, Schlosser (1901) has suggested from the evidence of the Eppelsheim femur that *Dryopithecus* may still have been largely quadrupedal, a view held, on general grounds, by others, e.g. Patterson (1954). This small assembly of fossil forms, in all of which quadrupedalism, whether terrestrial or arboreal, appears to be combined in some measure with brachiation, provides evidence that the extreme specialisations of locomotor habit, exemplified by the modern Pongidae, occurred late in their history.

The larger members of the genus *Proconsul*, *P. nyanzae* and *P. major*, were large forms approximating to the size of a chimpanzee and a gorilla respectively (Le Gros Clark & Leakey, 1951), although of lighter build. From modern analogy it would appear that they were too heavy to be wholly arboreal in habitat. The upper end of the femur and a portion of the humeral shaft which have been provisionally attributed to *P. nyanzae* are the only limb bones of the larger species of *Proconsul* available. These fragments serve only to indicate a quadrupedal mode of locomotion. Le Gros Clark & Leakey (1951) expressed a view that neither bone provided evidence for a brachiating mode of life; this opinion was based mainly on the anterior curvature of the shaft of the humerus in its upper one-half. A further consideration which suggests that *P. nyanzae* was not so advanced a brachiator as *P. africanus* is the absence from the humeral fragment of a broad flexor flange culminating in a well-defined supinator ridge; this ridge is a prominent feature of the humeri of advanced modern brachiators and is moderately well developed in *P. africanus*.* The comparison of locomotor habits of the smallest with the larger species of *Pronconsul* will clearly have to await the recovery of further limb material; but as a purely tentative hypothesis it is suggested that both *P. nyanzae* and *P. major* were less arboreal than *P. africanus* and, for this reason, less advanced as brachiators.

Taxonomic Status of *Proconsul africanus*

Le Gros Clark & Leakey (1951) concluded from their comprehensive study of the *Proconsul* material available in 1951 that this fossil genus must "... certainly be regarded as an anthropoid ape, albeit of a very primitive type". In view of the many "cercopithecoid" features apparent in the skull, brain, and limb bones, these authors rightly discussed the propriety of including the genus *Proconsul* in the Hominoidea. They concluded that such a classification was justified on the grounds that in the Early Miocene the Hominoidea might well have been expected to retain many primitive features indicative of their recent separation from the Cercopithecoidea. With regard to the limb-bone fragments then available they concluded that there was no evidence that *Proconsul* had adopted a brachiating mode of life. The evidence of brachiation that has emerged from the present study of the Gumba limb-bones would appear to support the inclusion of the genus within the family Pongidae.

It is clear that many of the features of the limbs of *Proconsul* are adaptive in nature and thus by themselves of limited taxonomic relevance. However, adaptive characters are not without value where they are related to what are regarded as the main trends in evolution. Washburn (1950) observed that "... the critical primary adaptation responsible for the origin of Man as a distinct group ..." was in the pelvis: thus in the case of the Australopithecinae and their earlier representatives the skeletal characters of the bones of the pelvis and the lower extremity are of profound taxonomic significance. Of the Pongidae it may be said with equal truth that the "critical primary adaptation" responsible for their origin as a distinct group was in the upper limb, and that therefore the brachiating features of *P. africanus* have an equal value in taxonomy to the bipedal features of the pelvis and lower limb in the Australopithecinae.

We have already indicated that the habit of brachiation is widespread in the modern pithecoid world, and that many of the adaptations towards this mode of locomotion apparent in the fossil bones are found in modern forms as distantly related as *Ateles*, *Pan* and *Presbytis*. These morphological resemblances are, for the most part, attributable to a functional parallelism dependent primarily on a common arboreal ancestry and secondarily on a similar environment and way of life. There are, however, certain features of the fossil fore-limb bones which more closely resemble those of *Pan* than those of any other genus. This is especially true of the form of the distal end of the fossil humerus, where the increased surface of origin for brachialis, the prominence of the keel and the high trochlear index are seen only in *Pan* in the comparative series. Other features of the lower articular surface observed

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* We have been able to examine the Moboko humeral fragment through the courtesy of the Keeper of Palaeontology, British Museum (Natural History).

both in the fossil bone and in *Pan*, such as the absence of a sharp lateral border to the olecranon fossa and a well-rounded, backwardly extended capitulum, are also found in *Ateles* and *Presbytis*, and must therefore be regarded as "generalised" brachiating features and of little taxonomic relevance. Again with regard to the radius, the relatively long neck which distinguishes *P. africanus* from the purely quadrupedal catarrhines is a feature shared with *Pan*, *Presbytis* and *Ateles*, and must also be looked upon as a "generalised" brachiating feature attributable to a common arboreal ancestry. On the other hand the laterally directed curve of the shaft of the fossil radius is a feature found only in *Pan*: taken in conjunction with the evidence for a large range of supination provided by the inferior articular surface in both *P. africanus* and *Pan*, this feature is probably of taxonomic relevance.

The morphological similarities between the fossil hand and that of modern *Pan* have little value taxonomically, for many of these features are also found in *Ateles* and to some extent in *Presbytis*, showing that while these particular characters are of value in indicating a common mode of locomotion they are useless for the determination of zoological affinity.

Thus it can be seen that in but few instances are the adaptive features of the fossil fore-limb bones of value in determining the relationship of *Proconsul* to Recent *Pan*. In the absence of *a priori* evidence as to the probable nature of the fossil remains provided by the associated jaw fragments, it is to be doubted whether there would have been sufficient evidence from the fore-limb bones alone to postulate the pongid affinities of *P. africanus*, although there is no doubt that the brachiating propensities of the form would have been recognised.

As Oakley (1951) has pointed out with reference to *Australopithecus*, at least two determinants are necessary to place this form in the family Hominidae—a dentition of essentially human form and a pelvis which permits of upright walking. The problem of the classification of *P. africanus* would seem to be analogous, at least two determinants being necessary to place this species in the family Pongidae—a dentition of essentially pongid form and fore-limbs that are adapted for brachiation.

In the sense of these criteria, there seems little doubt that *P. africanus* may be regarded as a pongid, though a very primitive one. The brain, so far as can be inferred from the skull, and the skull itself have advanced little beyond a "cercopithecoid" level of development (Le Gros Clark & Leakey, 1951); the dentition, though possessing primitive features, bears a marked resemblance to that of the modern African anthropoid apes (Hopwood, 1933, Le Gros Clark & Leakey, 1951); the foot indicates the arboreal habitat of the animal; and the upper limb, though relatively slender and lightly built, shows in the critical region of the elbow a degree of extensibility and a freedom of forearm rotation that foreshadows the extreme degree of mobility necessary for brachiation of the pongid type.

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APPENDIX I

Data and Indices relating to certain Measurements of the Humerus

Lc = Capitular length of humerus
Lg = Length of humerus below lower limit of groove for latissimus dorsi
Ld = Length of deltoid insertion
X = Distance between lower limit of groove for latissimus dorsi and the insertion of deltoid
$L.S.$ = Length of supinator crest

$$\text{Index } 1 = \frac{Lg \times 100}{Lc}. \quad \text{(Groove index)}$$

$$\text{Index } 2 = \frac{Ld \times 100}{Lc}. \quad \text{(Deltoid index)}$$

$$\text{Index } 3 = \frac{X \times 100}{Lg}$$

$$\text{Index } 4 = \frac{L.S. \times 100}{Lc}. \quad \text{(Supinator crest index)}$$

APPENDIX I

Species	Ref.	*Lc*	*Lg*	*Ld*	*X*	*L.S.*	Indices			
							1	2	3	4
Pan troglodytes . .	A	309	230	178	102	114	74·4	57·6	44·3	36·9
Pan troglodytes . .	B	315	232	167	85	104	73·7	53·3	36·6	33·1
Pan troglodytes . .	C	291	206	153	67	102	70·8	52·5	32·5	35·1
Pan troglodytes . .	D	277	200	155	80	100	73·3	56·0	40·0	36·1
Pan troglodytes . .	E	285	215	164	94	105	73·6	57·5	43·7	36·8
Pan troglodytes . .	F	265	189	145	69	98	71·3	54·7	36·5	37·0
Ateles paniscus . .	A	194	148	94	45	51·5	76·3	48·5	30·4	26·5
Ateles ornatus . .	B	166	125	78	38	44·5	75·3	47·9	30·4	26·8
Ateles belzebuth . .	C	182	138	90	46	48	75·8	49·4	31·9	26·4
Presbytis (*Kasi*) *senex* .	A	130	95	61	26	49	73·1	46·9	27·3	37·7
Presbytis (*Kasi*) *senex* .	B	134	101	63	31	52	75·4	47·0	30·7	38·8
Presbytis (*Kasi*) *senex* .	C	132	103	64	33	46	78·0	48·5	31·2	34·9
Papio ursinus . .	A	198	149	83	35	81	75·3	42·2	23·5	41·4
Papio anubis . .	B	225	162	93	33	77	72·0	41·3	20·7	34·2
Papio anubis . .	C	162	125	62	23	50	77·2	38·3	18·4	30·9
Papio hamadryas . .	D	174	122	81	29	57	70·1	46·6	23·8	32·8
Papio cynocephalus .	E	183	131	77	27	63	71·6	42·1	20·6	34·4
Papio anubis . .	G	141	102	60	20	53·5	71·8	42·2	19·6	37·9
Papio anubis . .	H	195	141	80	25	64	72·3	41·0	17·8	32·8
Papio anubis . .	J	151	119	64	32	53·5	78·8	42·4	26·8	35·4
Cercopithecus speciosa .	A	123	90	54	19	38·5	73·2	43·9	21·1	31·3
Cercopithecus cephus .	B	103	75	43	15	31	72·8	41·7	20·0	30·1
Cercopithecus petaurista .	C	86·5	61·5	37·5	13·5	31	71·1	43·4	21·9	28·3
Cercopithecus mona .	D	134	96	62	25	38	71·6	46·3	26·0	30·6
Cercopithecus mona .	E	129	96	55	22	38	74·4	42·6	22·9	29·4
Cacajao calvus . .	A	103	79	41	17	37·5	76·7	39·8	21·5	36·4
Pithecia pithecia . .	B	97	73	47	22	26	75·3	48·5	30·1	26·8
Pithecia pithecia . .	C	—	—	—	—	—	—	—	—	—
Saimiri . . .	D	63	51	25	12	19·5	80·1	39·7	23·5	31·2
Proconsul africanus .	—	182	132	—	50	60	72·5	54·7	37·9	33·3

APPENDIX II

DATA AND INDICES RELATING TO CERTAIN MEASUREMENTS OF THE HUMERUS

Lc = Capitular length of humerus
B.W. = Bi-epicondylar width
A.W. = Articular width
C.M.E. = Capitular—medial epicondylar width
T.L.E. = Trochlea—lateral epicondylar width
C.W. = Capitular width
T.W. = Trochlear width

$$\text{Index } 1 = \frac{B.W. \times 100}{Lc}. \quad \text{(Bi-epicondylar index)}$$

$$\text{Index } 2 = \frac{A.W. \times 100}{Lc}. \quad \text{(Articular width index)}$$

$$\text{Index } 3 = \frac{(B.W. - T.L.E.) \times 100}{B.W.}. \quad \text{(Medial epicondylar index)}$$

$$\text{Index } 4 = \frac{T.W. \times 100}{C.W.}. \quad \text{(Trochlear index)}$$

APPENDIX II

Species	Ref.	*Lc*	*B.W.*	*A.W.*	*C.M.E.*	*T.L.E.*	*C.W.*	*T.W.*	Indices			
									1	2	3	4
Pan troglodytes .	A	309	64	44	61	51	25·0	20·5	20·7	14·2	20·3	82·0
Pan troglodytes .	B	315	67	45	61·5	50	22·5	22·5	21·3	14·3	25·4	100·0
Pan troglodytes .	C	291	61	42	57·5	47	21·0	21·0	21·0	14·4	23·0	100·0
Pan troglodytes .	D	277	62	44·5	57	51	23·0	22·0	22·4	16·1	17·7	95·6
Pan troglodytes .	E	285	53	38	49	42	20·0	18·0	18·6	13·3	20·8	90·0
Pan troglodytes .	F	265	60	42	55	47	19·5	22·5	22·6	15·8	21·7	115·4
Ateles paniscus .	A	194	28	19	25·5	23	11·0	8·0	14·4	9·8	17·9	72·7
Ateles ornatus . .	B	166	26	18	24·0	20·5	11·5	6·25	15·7	10·8	21·2	54·4
Ateles belzebuth .	C	182	27	18	23·5	21·5	10·5	8·0	14·8	9·9	20·4	76·2
Presbytis (*Kasi*) *senex*	A	130	22	17·5	21·0	19·0	9·5	7·0	16·9	13·5	13·6	73·7
Presbytis (*Kasi*) *senex*	B	134	22·5	16	19·5	19·0	9·5	7·0	16·8	11·9	15·6	73·7
Presbytis (*Kasi*) *senex*	C	132	21·5	15·5	20·0	19·0	8·75	6·25	16·3	11·7	11·6	71·4
Papio ursinus . .	A	198	37	29	33·0	32·0	17·5	10·25	18·7	14·7	13·5	58·6
Papio anubis . .	B	225	40	28	35·0	32·0	16·0	11·5	18·7	12·4	20·0	71·9
Papio anubis . .	C	162	27	21	24·0	26·0	12·0	9·0	16·7	13·0	3·7	75·0
Papio hamadryas .	D	174	32·5	23·5	29·0	28·0	14·5	9·0	18·7	13·5	13·9	62·0
Papio cynocephalus .	E	183	34	22·0	30·0	28·5	12·5	9·5	18·6	12·0	16·2	76·0
Papio anubis . .	H	195	40	29·5	35·0	34·0	16·5	12·5	20·5	15·1	15·0	75·8
Papio anubis . .	J	151	29·5	23·0	26·5	28·0	14·5	8·0	19·5	15·2	5·1	55·2
Cercopithecus speciosa	A	123	21·5	14·5	19·5	17·0	8·0	6·5	17·5	11·8	20·9	81·3
Cercopithecus cephus .	B	103	18·0	12·5	16·0	14·5	7·0	5·5	17·5	12·1	19·4	78·6
Cercopithecus petaurista	C	86·5	17·5	12·5	16·0	15·0	7·5	5·5	20·2	14·5	14·3	73·3
Cercopithecus mona .	D	134	22·0	16·0	20·5	17·5	9·9	6·75	16·4	11·9	20·5	68·2
Cercopithecus mona .	E	129	22·0	15·0	20·0	18·0	9·0	6·5	17·1	11·6	18·2	72·2
Cacajao calvus . .	A	103	18·5	13·0	14·0	16·5	8·0	6·0	18·0	12·6	10·8	75·0
Pithecia pithecia .	B	97	16·5	10·5	14·5	14·0	6·0	5·5	17·0	10·8	15·2	91·0
Pithecia pithecia .	C	97	15·5	11·0	14·5	13·0	6·5	5·0	16·0	11·3	16·1	77·0
Saimiri . . .	D	63	12·5	8·0	10·5	9·5	4·5	3·5	20·0	12·8	24·0	77·7
Proconsul africanus .		182	35·0	26·0	33·0	29·0	12·5	13·0	19·2	14·3	17·1	104·0

APPENDIX III

DATA AND INDICES RELATING TO CERTAIN MEASUREMENTS OF THE RADIUS AND ULNA

R.L. = Length of radius
Lc = Capitular length of humerus
L.N.R. = Length of the neck of the radius
W.R.M. = Width of proximal radial metaphysis
L.S.U. = Length of ulnar styloid process
W.U.E. = Width of distal ulnar epiphysis

$$\text{Index } 1 = \frac{R.L. \times 100}{Lc}. \quad \text{(Brachial index)}$$

$$\text{Index } 2 = \frac{L.N.R. \times 100}{W.R.M.}. \quad \text{(Neck of radius index)}$$

$$\text{Index } 3 = \frac{L.S.U. \times 100}{W.U.E.}. \quad \text{(Ulnar styloid index)}$$

APPENDIX III

Species	Ref.	*R.L.*	*Lc*	*L.N.R.*	*W.R.M.*	*L.S.U.*	*W.U.E.*	Indices		
								1	2	3
Pan troglodytes	A	286	309	20·0	23·0	12·0	20·5	92·6	0·87	58·5
Pan troglodytes	B	279	315	23·0	20·0	—	—	88·6	1·15	—
Pan troglodytes	C	265	291	20·0	19·0	10·5	19·0	91·1	1·05	55·3
Pan troglodytes	D	248	277	21·0	21·0	12·0	21·0	89·5	1·00	57·1
Pan troglodytes	E	240	285	22·5	20·0	10·0	19·0	84·2	1·12	52·6
Pan troglodytes	F	247	265	—	—	10·0	18·5	93·2	—	54·1
Ateles paniscus	A	188	194	18·0	9·5	8·0	9·5	96·9	1·90	84·2
Ateles ornatus	B	161	166	15·0	10·0	7·0	9·0	97·0	1·50	77·8
Ateles belzebuth	C	180	182	10·5	9·5	—	—	98·9	1·10	—
Kasi senex vetulus	A	134	130	6·5	9·0	—	—	97·0	0·72	—
Kasi senex vetulus	B	136	134	7·0	8·5	6·0	7·5	98·5	0·82	80·0
Kasi senex vetulus	C	135	132	6·5	9·0	6·0	7·5	97·8	0·72	80·0
Papio ursinus	A	221	198	5·0	16·0	12·0	17·0	111·6	0·31	70·6
Papio anubis	B	246	225	9·0	17·0	13·0	13·0	109·3	0·53	100·0
Papio anubis	C	175	162	4·5	13·5	8·0	12·5	108·0	0·33	64·0
Papio hamadryas	D	175	174	8·5	13·0	11·5	13·0	100·6	0·65	88·5
Papio cynocephalus	E	198	183	6·0	13·0	9·5	11·25	108·2	0·46	84·4
Papio anubis	G	212	195	6·0	16·5	—	—	108·7	0·36	—
Papio anubis	H	159	151	3·0	12·5	9·0	13·0	105·3	0·24	69·2
Cercopithecus speciosa	A	122	123	5·5	8·0	7·0	8·0	99·2	0·70	87·6
Cercopithecus cephus	B	101	103	5·5	6·5	5·0	6·5	98·1	0·85	76·9
Cercopithecus petaurista	C	84	86·5	3·5	7·0	5·5	7·0	97·1	0·50	78.6
Cercopithecus mona	D	129	134	6·0	8·5	6·0	8·0	96·3	0·71	75·0
Cercopithecus mona	E	131	129	6·0	8·5	6·5	8·0	101·6	0·71	81·0
Cacajao calvus	A	83	103	5·5	6·0	6·0	6·5	80·6	0·92	92·3
Pithecia pithecia	B	90	97	6·5	6·5	4·5	6·0	92·8	1·00	75·0
Pithecia pithecia	C	89·5	97	6·5	6·5	3·5	4·5	92·3	1·00	77·7
Saimiri	D	55	63	4·0	4·5	3·5	4·0	87·3	0·88	87·5
Proconsul africanus		156	182	8·0	10·0	10·0	11·0	85·7	0·80	83·3

APPENDIX IV

DATA AND INDICES RELATING TO CERTAIN MEASUREMENTS OF THE HAND

C.L. = Maximum length of carpus
M.L. = Length of third metacarpal
P.L. = Length of phalanges of third digit
Lc = Length of humerus
R.L. = Length of radius
M.P.F. = Metacarpal projection formula
M.T.F. = Metacarpal thickness formula

$$\text{Index } 1 = \frac{M.L. \times 100}{\text{Total length of hand}}$$

$$\text{Index } 2 = \frac{P.L. \times 100}{\text{Total length of hand}}$$

$$\text{Index } 3 = \frac{C.L. \times 100}{\text{Total length of hand}}$$

$$\text{Index } 4 = \frac{\text{Total length of hand} \times 100}{\text{Total length of upper limb}}$$

$$\text{Index } 5 = \frac{Lc \times 100}{\text{Total length of upper limb}}$$

$$\text{Index } 6 = \frac{R.L. \times 100}{\text{Total length of upper limb}}$$

APPENDIX IV

Specimen	Ref.	*C.L.*	*M.L.*	*P.L.*	Total length of hand	*Lc*	*R.L.*	Total length upper limb	*M.P.F.*	*M.T.F.*	Indices					
											1	2	3	4	5	6
Pan . .	A	35	86	124	245	309	286	840	3245	3245	35·1	50·6	14·3	29·2	36·3	34·5
Pan . .	E	31	75	104	210	285	240	735	3245	3245	36·0	50·0	14·0	28·6	38·7	32·7
Pan . .	F	29	73	109	211	265	247	723	2345	2345	34·6	51·7	13·7	29·2	36·6	34·2
Pan . .	G	25	67	95	187	—	—	—	32 = 45	3245	35·8	50·8	13·4	—	—	—
Pan . .	H	30	85	115	230	274	265	769	3245	3245	37·0	50·0	13·0	30·0	35·6	34·4
Ateles .	B	15	40	65	120	166	163	449	3425	4325	33·3	54·1	12·6	26·7	37·0	36·3
Ateles .	C	16	42·5	67	125·8	182	179	586·8	3425	4 = 235	33·8	53·4	12·8	25·8	37·4	36·8
Presbytis .	A	14	35	53	102	130	134	366	32 = 45	3425	34·3	52·0	13·7	27·9	35·5	36·6
Presbytis .	B	15	36·5	55	106·5	134	136	376·5	3245	3 = 425	34·3	51·6	14·1	28·3	35·6	36·1
Papio .	A	24	52	60	136	198	223	657	3425	3425	38·2	44·1	17·7	24·4	35·6	40·0
Papio .	C	18	44	48·5	110·5	162	178	450·5	3425	3425	39·8	43·9	16·3	24·5	36·0	39·5
Papio .	G	22	49	55	126	195	216	537	2345	34 = 25	38·8	43·9	17·5	23·5	36·3	40·2
Papio .	H	20	46	64	130	—	—	—	23 = 45	3425	35·4	49·2	15·4	—	—	—
Papio .	J	22	39	46	107	183	187	477	2345	3425	36·4	43·0	20·6	22·4	38·4	39·2
Cerco .	A	13	29	46	88	123	122	333	3245	3425	33·0	52·4	14·6	26·4	37·0	36·6
Cerco .	B	10·5	24	38	72·5	103	102	277·5	3245	3425	33·1	52·5	14·4	26·1	37·1	36·8
Cerco .	C	10·5	22	32	64·5	86·5	84	240	3245	3425	34·1	49·6	16·3	27·4	36·8	35·8
Cerco .	D	13·5	31	49·5	94	134	130	358	3245	3425	33·0	52·6	14·4	26·3	37·4	36·3
Cerco .	E	13·5	31	49·5	94	129	132	355	3245	3425	33·0	52·6	14·4	26·5	36·3	37·2
N.W.M. genera .	A	12·5	22	41	75·5	103	83	261·5	3425	3245	29·1	54·3	16·6	28·9	39·4	31·7
N.W.M. genera .	C	8·5	22	43·5	74	97	90	261	3245	3254	30·0	58·8	11·2	28·4	37·2	34·4
N.W.M. genera .	D	7	16	26·2	49	63	56	168	3245	3 = 425	32·5	53·3	14·2	29·2	37·5	33·3
N.W.M. genera .	E	9	20	36	65	92	85	242	3245	3 = 245	30·8	55·4	13·8	26·9	38·0	35·1
Proconsul africanus		21	38	57	116	182	156	454	3245	3245	32·7	49·1	18·1	25·5	40·1	34·4

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EXPLANATION OF PLATES

PLATE I

EXPLANATION OF PLATE 1

Proconsul africanus Hopwood

(Specimen Rs 51/1499)

FIG. 1. Occlusal view of mandible.
FIG. 2. Inferior view of mandible.
FIG. 3. Lateral view of right maxilla.
FIG. 4. Occlusal view of right maxilla.
FIG. 5. Medial view of right maxilla.
FIG. 6. Postero-medial view of right temporal bone.
FIG. 7. Lateral view of right temporal bone.
FIG. 8. Superior view of occipital fragment.
FIG. 9. Left lateral view of occipital fragment.

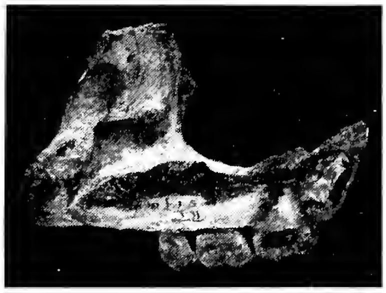
All the above natural size.


1


2


3


4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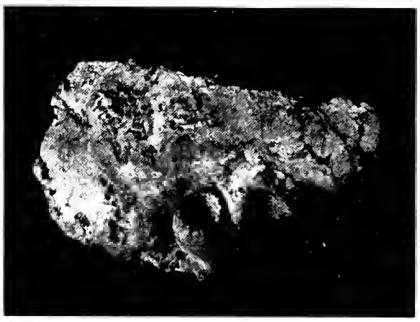
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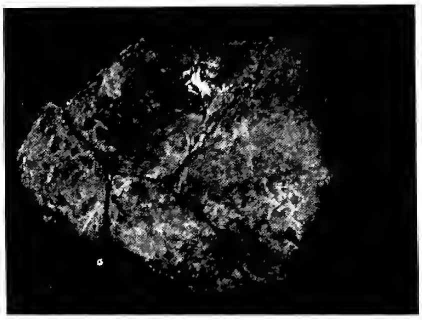
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PROCONSUL

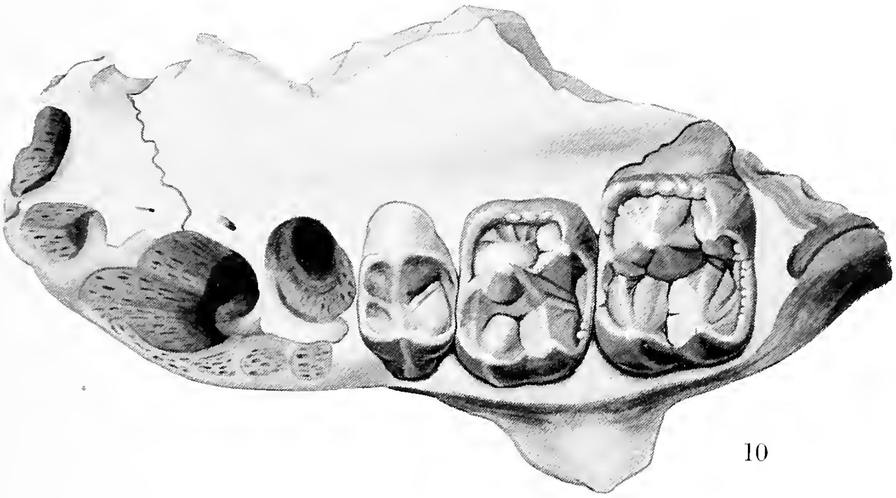
PLATE 2

EXPLANATION OF PLATE 2

Proconsul africanus Hopwood

FIG. 10. Occlusal aspect of the right maxilla. × 2·5.

FIG. 11. Occlusal aspect of the mandible. × 1·5.



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PROCONSUL

PLATE 3

EXPLANATION OF PLATE 3

Proconsul africanus Hopwood

FIG. 12. Anterior aspect of left humerus.

FIG. 13. Posterior aspect of left humerus.

FIG. 14. Lateral aspect of left humerus.

FIG. 15. Palmar view of the wrist and hand fragments after identification and sorting. The pisiform is seen from the lateral aspect.

All natural size.


12


13


14


15

PROCONSUL

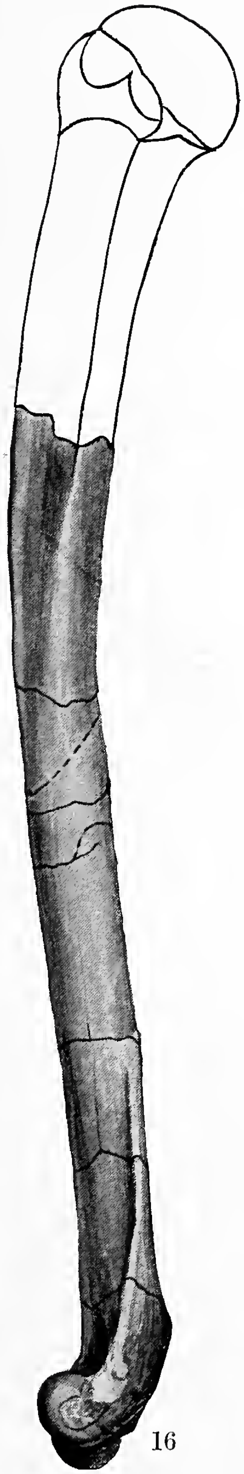
PLATE 4

EXPLANATION OF PLATE 4

Proconsul africanus Hopwood

FIG. 16. Graphic reconstruction of the left humerus as seen from the lateral aspect. Natural size. Post-mortem angulation of the fragment at the dotted lines has been corrected. The unshaded region is hypothetical.

FIG. 17. Graphic reconstruction of the anterior aspect of the left humerus. Natural size. Post-mortem angulation of the fragment at the dotted lines has been corrected. The unshaded regions are hypothetical.



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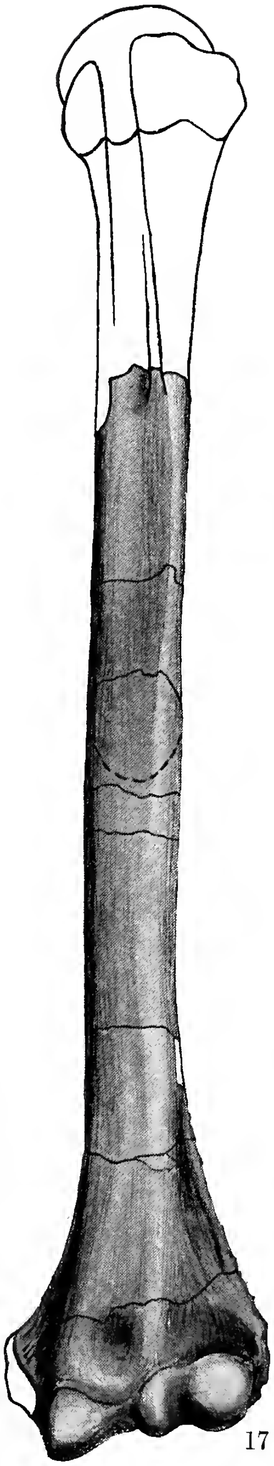

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PROCONSUL

PLATE 5

EXPLANATION OF PLATE 5

FIG. 18. Left humeri of different genera, seen from the anterior aspect. (*a*) *Papio* E, (*b*) *Cercopithecus* D, (*c*) *Pithecia* B, (*d*) *Pan* A, (*e*) *Ateles* C, (*f*) *Presbytis* A, (*g*) Graphic reconstruction of *Proconsul africanus*. Not to scale.

FIG. 19. Left humeri of different genera, seen from the lateral aspect. (*a*) *Papio* E, (*b*) *Cercopithecus* D, (*c*) *Pithecia* B, (*d*) *Pan* A, (*e*) *Ateles* C, (*f*) *Presbytis* A, (*g*) Graphic reconstruction of *Proconsul africanus*. Not to scale.

[For details of the specimens see Table I.]

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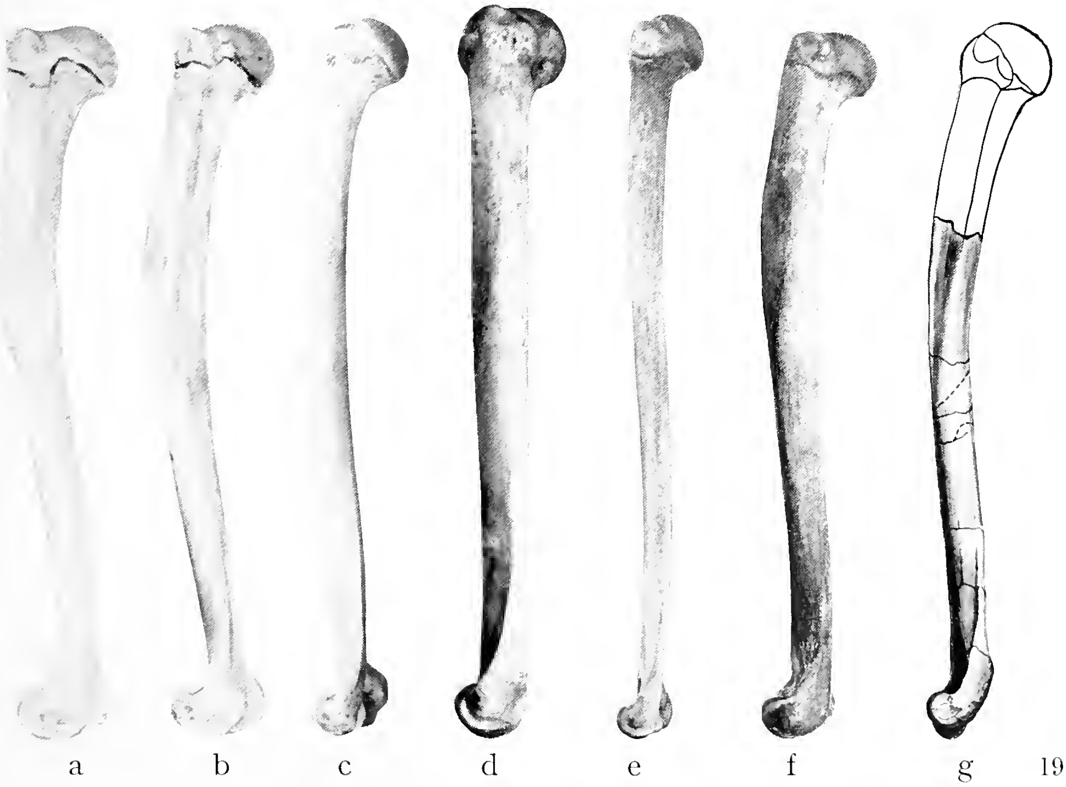

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PRIMATE HUMERI

PLATE 6

EXPLANATION OF PLATE 6

FIG. 20. Anterior views of the radius in (*a*) *Papio* E, (*b*) *Cercopithecus* D, (*c*) *Pithecia* B, (*d*) *Presbytis* A, (*e*) *Ateles* A, (*f*) *Pan* A, (*g*) Graphic reconstruction of *Proconsul africanus*. Not to scale.

[For details of the specimens see Table I.]

PRIMATE RADII

PLATE 7

EXPLANATION OF PLATE 7

Proconsul africanus Hopwood

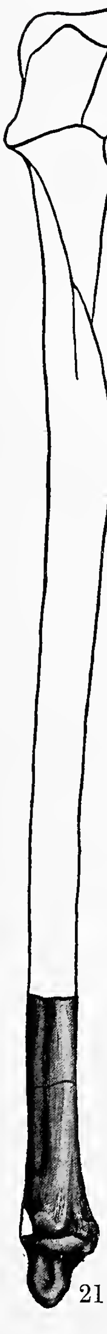
FIG. 21. Graphic reconstruction of the anterior aspect of the left ulna. The unshaded areas are hypothetical.

FIG. 22. Graphic reconstruction of the radius from the anterior aspect. Post-mortem angulation of the fossil bone has been corrected at the dotted lines. The unshaded areas are hypothetical.

FIG. 23. Graphic reconstruction of the lower end of the radius as seen from the dorsal aspect. The unshaded area is hypothetical.

FIG. 24. Graphic reconstruction of the lower end of the radius as seen from the medial aspect. The unshaded area is hypothetical.

All natural size.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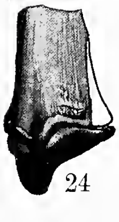
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PROCONSUL

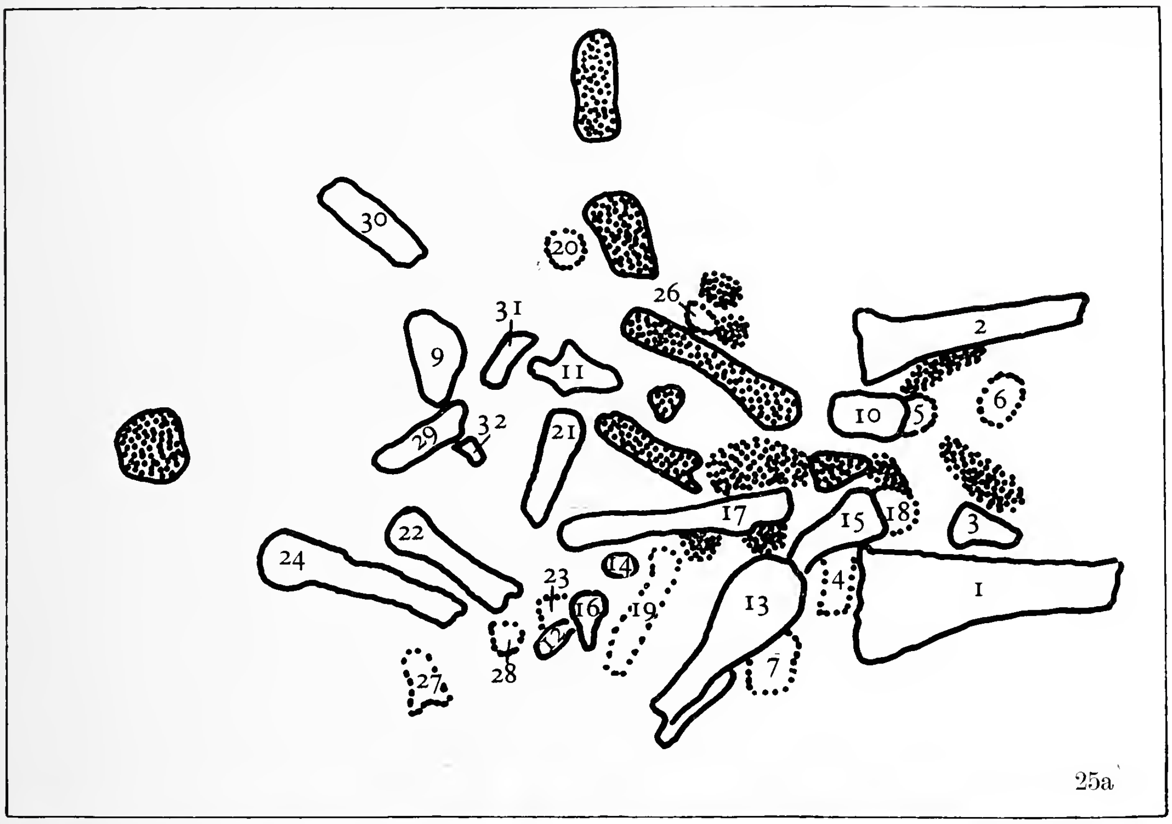
PLATE 8

EXPLANATION OF PLATE 8

Proconsul africanus Hopwood

FIG. 25. A photograph of the block of matrix containing the hand bones before development, together with a key giving the position and identification of each fragment. In the key, those bones on the surface of the original block are given a continuous outline, and those which were beneath the surface have a dotted outline. Bones pertaining to the foot are shaded.

1, Radius. 2, Ulna. 3, Lower ulna epiphysis. 4, Scaphoid. 5, Lunate. 6, Triquetral. 7, Pisiform. 9, Hamate. 10, Capitate. 11, Trapezium. 12, Epiphysis, 1st metacarpal. 13, 2nd metacarpal. 14, Epiphysis, 2nd metacarpal. 15, 3rd metacarpal. 16, Epiphysis, 3rd metacarpal. 17, 4th metacarpal. 18, Epiphysis, 4th metacarpal. 19, 5th metacarpal. 20, Epiphysis, 5th metacarpal. 21, 1st proximal phalanx. 22, 2nd proximal phalanx. 23, Epiphysis, 3rd proximal phalanx. 24, 4th proximal phalanx. 25, Epiphysis, 4th proximal phalanx. 26, Epiphysis, 5th proximal phalanx. 27, 2nd middle phalanx. 28, Epiphysis, 2nd middle phalanx. 29, 3rd middle phalanx. 30, 4th middle phalanx. 31, 5th middle phalanx. 32, 3rd distal phalanx.



25a

25b

PROCONSUL

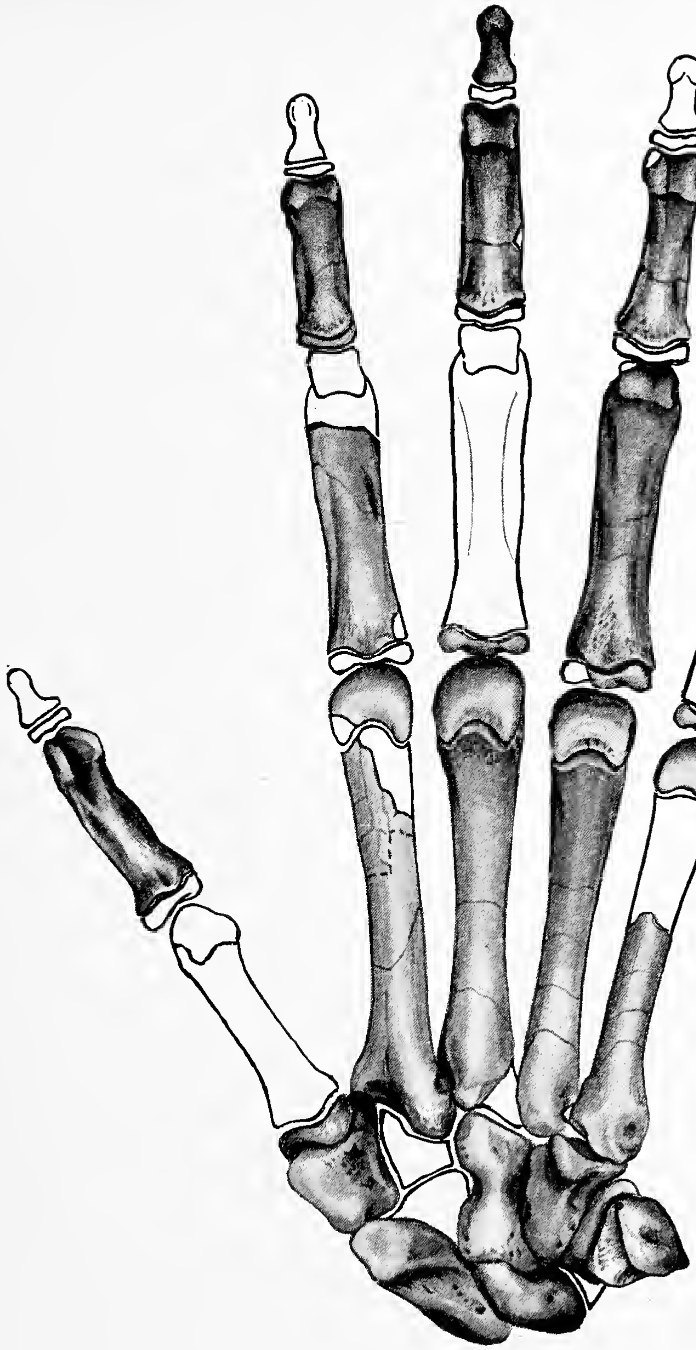
PLATE 9

EXPLANATION OF PLATE 9

Proconsul africanus Hopwood

FIG. 26. A graphic reconstruction of the left hand, viewed from the palmar aspect. Distortion of the second metacarpal has been corrected at the dotted line. The unshaded areas are hypothetical. × 1·5.

FIG. 27. A photograph of the medial cuneiform, and the metatarsal and phalanges of the first digit of the right foot, viewed from the plantar aspect. Natural size.



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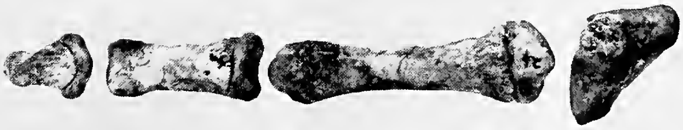

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PROCONSUL

PLATE 10

EXPLANATION OF PLATE 10

FIG. 28. Photographs of the proximal phalanx of the left thumb in (*a*) *Pan*, (*b*) *Papio*, (*c*) *Cercopithecus*, (*d*) *Cacajao*, (*e*) *Proconsul africanus*. × 1·5.

FIG. 29. Photographs of the proximal phalanx of the fourth left digit of the hand in (*a*) *Pan*, (*b*) *Papio*, (*c*) *Cercopithecus*, (*d*) *Ateles*, (*e*) *Pithecia*, (*f*) *Proconsul africanus*. Not to scale.

FIG. 30. Photographs of the middle phalanx of the fourth left digit of the hand in (*a*) *Pan*, (*b*) *Papio*, (*c*) *Cercopithecus*, (*d*) *Proconsul africanus*. Not to scale.

[See Table I]

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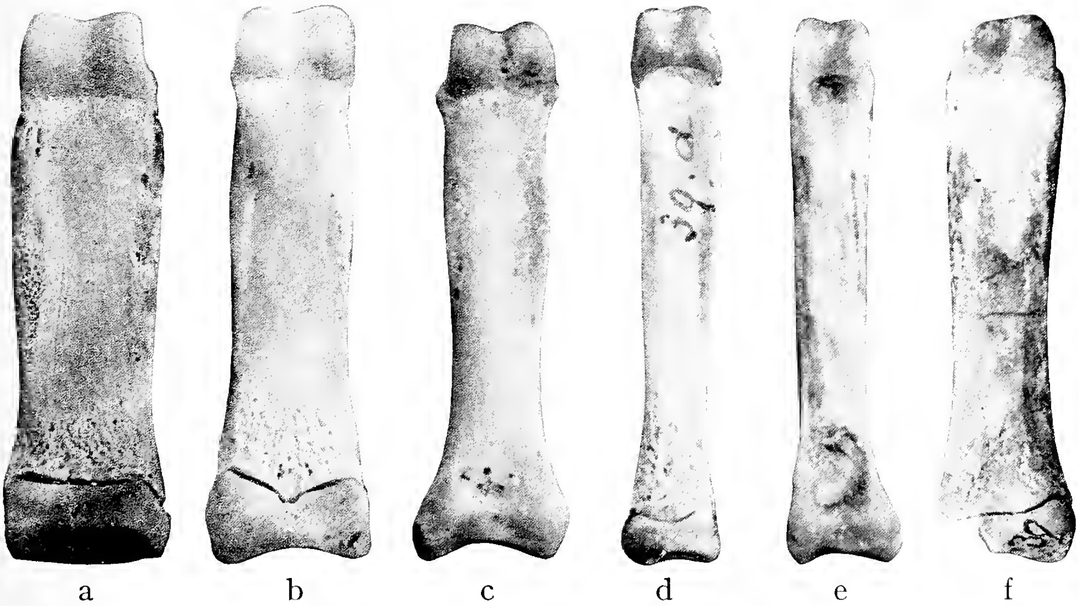

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PRIMATE PHALANGES