

An Oreopithecid Proximal Humerus from the Middle Miocene of Maboko Island, Kenya

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A proximal humerus, recently recovered from the middle Miocene of Maboko Island, Kenya, provides the earliest evidence of postcranial structure and adaptation of Oreopithecidae. Provisionally attributed to Nyanzapithecus pickfordi (Harrison, 1986), the specimen manifests a globose head, subequally large tuberosities, and a broad, shallow bicipital groove. Although readily distinguished from the fundamentally cercopithecoïd proximal humeral morphology of Victoriapithecus (Senut, 1986), the Maboko Island oreopithecid shows none of the derived features that are characteristic of the proximal humeri of extant hominoids. It is inferred from proximal humeral anatomy that the Maboko Island oreopithecid was an active arboreal scansor with moderate mobility at the shoulder but lacking adaptations for circumduction of the arm. In combination with craniodental evidence, proximal humeral morphology indicates that Oreopithecidae was a clade of hominoids which originated before the last common ancestor of extant apes and went extinct, without issue, in the later Miocene.

KEY WORDS: Oreopithecidae; humerus; anatomy; Miocene; Africa.

INTRODUCTION

An oreopithecid proximal humerus was recently recovered from middle Miocene deposits of Maboko Island, Kenya. The fossil augments a growing sample of early catarrhine proximal humeri from the Oligocene and Miocene of Africa, Asia, and Europe (Zapfe, 1960; Ginsburg and Mein, 1980; Fleagle and Simons, 1982; Senut, 1986; Gebo *et al.*, 1988; Rose,

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1989). Functional capabilities of the oreopithecoid shoulder joint are inferred from correlates of proximal humeral morphology to patterns of posture and movement among living monkeys and apes. Features of the proximal humerus are used to critically assess the phylogenetic relationships of the Oreopithecidae.

The family-tree relationships of the Oreopithecidae, originally and still best known from *Oreopithecus bambolii* of the later Miocene of Italy (Gervais, 1872; Hurzeler, 1949, 1958), have long been debated. Various workers, emphasizing dental characteristics, have supported an affinity to cercopithecoids (Schlosser, 1887; Szalay and Delson, 1979). Others, emphasizing aspects of postcranial morphology, have suggested an affinity to hominoids (Straus, 1963; Sarmiento, 1987). A third view, hypothesizing special relationships to *Apidium* (Gregory, 1922; Simons, 1960), is essentially refuted by profound differences in dental formula, tympanic construction, and postcranial anatomy (Fleagle and Kay, 1987). A hominoid affinity for *Oreopithecus* seems most likely, especially because of shared derived abbreviation of the ulnar olecranon process, reduction in the number of lumbar vertebrae, and increased number of sacral segments, apparently in combination with loss of the tail (Hurzeler, 1958; Straus, 1963; Sarmiento, 1987; Harrison, 1987a). On the other hand, dental characteristics of *Oreopithecus* are not especially similar to those of cercopithecoids (fossil or modern) and may be viewed as a very uniquely derived transformation of the hominid dentition involved with a folivorous dietary specialization (Hurzeler, 1949, 1958; Butler and Mills, 1959; Harrison, 1987a). Above and beyond general trends toward cingular reduction and elongation and narrowing of the maxillary and mandibular check teeth, the most distinctive dental features of *Oreopithecus* are the presence of a protoconule, a discrete crest linking the hypocone to the *crista obliqua*, and the development of a distinct accessory cuspule, the centroconid, mesiolingual to the hypoconid (Butler and Mills, 1959).

The presence of Oreopithecidae in the middle Miocene of eastern Africa was first suggested by Leakey (1967a, b, 1968, 1969) and Von Koenigswald (1969). Leakey (1967a, b, 1968, 1969) referred isolated teeth from Forth Ternan to *Oreopithecus* sp. Von Koenigswald (1969) established a new genus and species of oreopithecoid, *Mabokopithecus clarki*, to accommodate an unworn lower third molar (KNM-MB 76) from Maboko Island manifesting a very elongated crown, reduced buccal cingulum, and the presence of a centroconid in the talonid basin. However, subsequent workers questioned the primate affinity of these remains, suggesting in some instances that the teeth belong to a suid (Andrews and Walker, 1976; Szalay and Delson, 1979; Andrews, 1981; Shipman *et al.*, 1981).

Matters rested here until 1982–1984, when screening operations of tailings from early excavations at Maboko Island resulted in recovery of a large

sample of teeth and a premaxilla with I¹⁻² attributable to Oreopithecidae (Harrison, 1986). One of these, KNM-MB 9742, is a lower third molar with a morphology very similar to that of the type-specimen of *Mabokopithecus clarki* (Harrison, 1986). Harrison (1986) proposed a new genus, *Nyanzapithecus*, for the remainder of the Maboko Island oreopithecid sample, transferring specimens formerly assigned to *Rangwapithecus vancouveringi* to it as the type-species and referring the Maboko Island material to the species *Nyanzapithecus pickfordi*. Although somewhat less derived than conditions seen in the type-genus (Leakey and Leakey, 1988), upper molars of the Maboko Island oreopithecid sample possess a protoconule and hypocone-trigon crest, as well as manifesting a degree of mesiodistal elongation not otherwise seen in Miocene catarrhines (Harrison, 1986). Unfortunately, Harrison's (1986) diagnosis of *Nyanzapithecus* is inadequately differential with respect to *Mabokopithecus*. Hence, doubts persist concerning the validity of *Nyanzapithecus* (Harrison, 1986) as anything more than a junior synonym of *Mabokopithecus* (Von Koenigswald, 1969).

Recently, Harrison (1987b) suggested that *Proconsul* and the "small-bodied apes" of the early Miocene of eastern Africa are catarrhines belonging to a clade (or clades) which originated before the last common ancestor of the Cercopithecoidea and the Hominoidea. In contrast, Harrison (1986, p. 282) treats material attributed to *Nyanzapithecus* as "the earliest representative" of the Hominoidea. However, it is readily apparent that a hominoid affinity for *Oreopithecus* is based exclusively on postcranial (instead of craniodental) anatomy. Thus, hominoid affinity for *Nyanzapithecus* rests on Harrison's (1986, p. 281) expectation that the structure of the postcranial skeleton would resemble living apes (Leakey and Leakey, 1988). Unfortunately, the proximal humerus of the *Oreopithecus bambolii* skeleton IGF 11778 (Hurzeler, 1958) is so badly crushed that meaningful assessment (including comparison to the specimen described here) is impossible. Nevertheless, the proximal humerus from Maboko Island not only constitutes the first test of Harrison's (1986, 1987b) hypothesis, but also provides an unprecedented perspective on the relationships and adaptive history of the Oreopithecidae.

The proximal humerus was recovered in January 1989 during excavation of an indurated white clay of Bed 5 of the Maboko Formation at Maboko Main (Benefit and McCrossin, 1989), the principal fossil-bearing locality on Maboko Island (Pickford, 1986). Geological and biostratigraphic evidence indicate that fossiliferous deposits on Maboko Island are approximately 14–16 million years old, being younger than the ca. 16–18 ma occurrences on Rusinga Island and older than the 14 ma site of Fort Ternan (Bishop *et al.*, 1969; Van Couvering and Van Couvering, 1976; Andrews *et al.*, 1981; Pickford, 1981; Feibel and Brown, 1991).

MATERIALS AND METHODS

The fossil specimen, KNM-MB 21206, is housed in the collections of the Paleontology Department of the National Museums of Kenya, Nairobi. KNM-MB 21206 was compared to the humeri of 25 genera of extant anthropoids and with original specimens or casts of the following humeri of other early catarrhines: DPC 1275—*Aegyptopithecus zeuxis* (Fleagle and Simons, 1982); OE 304—*Pliopithecus vindobonensis* (Zapfe, 1960); KNM-RU 17376—*Dendropithecus macinnesi* or *Proconsul africanus* (Gebo *et al.*, 1988); and KNB-MB 12044—*Victoriapithecus macinnesi* (Senut, 1986).

Extant anthropoid proximal humeri measured include the following genera (and numbers of specimens): *Alouatta* (8), *Ateles* (2), *Cacajao* (1), *Chiropotes* (1), *Cebuella* (1), *Saguinus* (1), *Cebus* (2), *Saimiri* (2), *Cercocebus* (2), *Cercopithecus* (20), *Erythrocebus* (2), *Lophocebus* (3), *Macaca* (12), *Mandrillus* (5), *Miopithecus* (1), *Papio* (10), *Theropithecus* (1), *Colobus* (16), *Nasalis* (10), *Presbytis* (12), *Pygathrix* (2), *Hylobates* (25), *Pongo* (5), *Gorilla* (11), and *Pan* (15). In addition, humeri of the following extant strepsirhine genera were examined for comparative purposes: *Lemur*, *Varecia*, *Indri*, *Galago*, *Galagoides*, *Otolemur*, *Loris*, *Nycticebus*, and *Perodicticus*.

Nine dimensions of KNM-MB 21206 were measured (Table I): (1) mediolateral breadth of the head (BH), (2) anteroposterior thickness of the head (TH), (3) proximodistal height of the head (HH), (4) bituberosity diameter (BD), (5) lesser tuberosity diameter (LD), (6) greater tuberosity diameter (GD), (7) projection of the greater tuberosity above the head (GP), (8) breadth of the bicipital groove (BB), and (9) depth of the bicipital groove (DB) (Rose, 1989, Figs. 7a–e, h, k–m). A head module (sum of humeral head breadth, thickness, and height/3) was employed to facilitate size comparisons. Four indices were calculated for the fossil and extant anthropoids (Table II): (1) head breadth (mediolateral breadth of head \times 100/anteroposterior thickness of the head), (2) greater tuberosity projection (projection of the greater tuberosity above the head \times 100/bituberosity diameter), (3) lesser tuberosity size (lesser tuberosity diameter \times 100/head module), and (4) bicipital groove breadth (breadth of the bicipital groove \times 100/head module).

ATTRIBUTION

Six fossil anthropoid species are known from Maboko Island: cf. *Limnopithecus legetet*, "*Micropithecus*" *leakeyorum*, *Victoriapithecus macinnesi*, *Nyanzapithecus pickfordi*, *Mabokopithecus clarki*, and *Kenyapithecus africanus* (MacInnes, 1943; Le Gros Clark and Leakey, 1950, 1951; Leakey, 1967b; Von Koenigswald, 1969; Benefit and Pickford, 1986; Harrison, 1986,

Table I. Dimensions (mm) of the Proximal Humerus of *Nyanzapithecus* and Some Other Early Catarrhines^a

	BH	TH	HH	BD	LD	GD	GP	BB	DB
<i>Nyanzapithecus</i>	14.7	16.0	11.9	19.2	10.5	11.6	-2.0	4.7	1.5
<i>Aegyptopithecus</i>	15.5	17.9	16.0	24.0	12.5	15.7	0.0	5.5	1.5
<i>Pliopithecus</i>	17.1	17.1	16.5	21.1	11.4	14.3	-1.0	3.8	1.8
KNM-RU 17376	17.5	19.0	16.5	21.3	12.1	14.5	-3.0	4.4	1.8
<i>Victoriapithecus</i>	11.5	13.3	9.6	15.1	6.7	10.3	-0.7	3.5	1.2

^aSee Materials and Methods for explanation of abbreviations. *Nyanzapithecus* (all dimensions) and *Victoriapithecus* (HH, BD, and GP) were measured by the author. Other dimensions are from the following sources: (1) Fleagle and Simons (1982, Table 1)—BD, BB, and DB of *Aegyptopithecus*; (2) Gebo *et al.* (1988, Table 1)—LD, GD, and GP of *Aegyptopithecus*; BD, LD, GD, GP, and BB of *Pliopithecus* and KNM-RU 17376; (3) Harrison (1989a, Table 2)—BH, TH, LD, GD, BB, and DB of *Victoriapithecus*; (4) Rose (1989, Tables 2, 3A)—TH and HH of *Aegyptopithecus*; TH, HH, and DB of *Pliopithecus* and KNM-RU 17376. BH of *Aegyptopithecus* is the mean of values published by Fleagle and Simons (1982, Table 1) and Rose (1989, Table 2). BH dimensions of *Pliopithecus* and KNM-RU 17376 are means of values published by Gebo *et al.* (1988, Table 1) and Rose (1989, Table 2).

1989a). Additional and more complete fossils recovered from Maboko Island in 1987–1989 reveal that the hypodigm (including type-specimen) of “*Micropithecus*” *leakeyorum* (Harrison, 1989a) is actually referable to *Simiolus* (Leakey and Leakey, 1988), a genus of “small-bodied ape” known originally from Kalodirr in northern Kenya (Benefit, 1991).

Due to lack of definite association with craniodental remains of any particular species, taxonomic attribution of KNM-MB 21206 is primarily based on estimation of body size. Absolute dimensions of KNM-MB 21206 (bituberosity diameter, head module) are matched by individuals of *Presbytis cristatus*, monkeys weighing 8.1–8.6 kg (Gingerich *et al.*, 1982). KNM-MB 21206 is clearly too large to represent cf. *Limnopithecus legetet* or “*Micropithecus*” *leakeyorum*. The anatomy of KNM-MB 21206 diverges markedly from the known proximal humeral morphology of *Victoriapithecus macinnesi* (Senut, 1986; Harrison, 1989b). Moreover, the fossil is certainly much smaller than B.M.(N.H.)M. 16634, a hominoid humeral shaft from Maboko Island (Le Gros Clark and Leakey, 1951), which is attributable to *Kenyapithecus africanus* (Leakey, 1967b: 163). Lower third molars of *Mabokopithecus clarki* and *Nyanzapithecus pickfordi* (Von Koenigswald, 1969; Harrison, 1986) fall within the size range (7.5–8.2 kg) of the rhesus macaque (Swindler, 1976; Gingerich *et al.*, 1982). Accordingly, the size of KNM-MB 21206 is congruent with attribution to either *Mabokopithecus clarki* or *Nyanzapithecus pickfordi*. While only two specimens have been attributed to *Mabokopithecus clarki* (Von Koenigswald, 1969), *Nyanzapithecus pickfordi* is known from a sample of more than 80 specimens (Harrison, 1986). In light of these considerations, it is most probable that KNM-MB

21206 pertains to *Nyanzapithecus pickfordi*. Nevertheless, identification of KNM-MB 21206 as an oreopithecoid suffices for all present analytical purposes, regardless whether the specimen, in fact, pertains to *Nyanzapithecus pickfordi* or should ultimately prove to represent *Mabokopithecus clarki*.

DESCRIPTION

KNM-MB 21206 is a right proximal humerus, broken at the surgical neck (Fig. 1, Table I). The specimen is free of erosion, but the anterior aspect of the shaft is slightly damaged on either side of the distal portion of the intertubercular sulcus where segments of bone have been removed (medially) and compressed inward (laterally), possibly as a result of carnivore action.

The humeral head faces posteroproximally and is slightly narrower (mediolaterally) than it is thick (anteroposteriorly). The articular surface is globose, elevated moderately above the greater tuberosity, and extends anteriorly to the intertubercular sulcus. Well-defined grooves demarcate the articular surface from the tuberosities. Both tuberosities are moderately large, the greater tuberosity being only slightly more massive than the lesser one. The tuberosities are symmetrically disposed on either side of a fairly broad and shallow intertubercular sulcus. The greater tuberosity is positioned anterolaterally and extends only slightly farther proximally than its lesser counterpart. A large, but shallow, crescentic scar (narrow posteriorly but broadening somewhat anteriorly) for the insertion of *m. supraspinatus* is evident on the anteroproximal aspect of the greater tuberosity. The in-

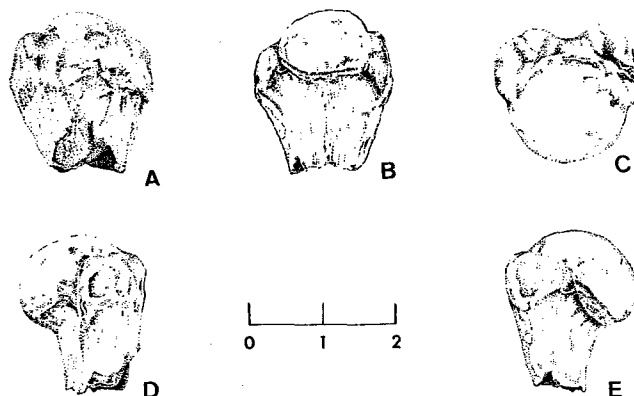


Fig. 1. The right proximal humerus provisionally attributed to *Nyanzapithecus pickfordi* (KNM-MB 21206) in anterior (A), posterior (B), proximal (C), lateral (D), and medial (E) views. (Scale bar is in centimeters. Drawing by J. Massey.)

sersion area of *m. infraspinatus* is marked by a deep and proximodistally elongated oval fossa on the lateral aspect of the greater tuberosity. Slightly distal and somewhat posterior to this, the surface of the greater tuberosity bears a vertically disposed series of raised lines which represent the insertion of *m. teres minor*. The lesser tuberosity is positioned anteromedially. An ill-defined, shallow depression on its lateral face marks the insertion area of *m. subscapularis*. Farther distally, an irregularly roughened patch of bone on the medial side of the buttress running distally from the lesser tuberosity probably signals the insertion of *m. coracobrachialis profundus*. In posterior view, this buttress forms a continuous curve from the lesser tuberosity to the shaft proper. In its distal portion, the medial buttress attenuates to form a sharp crest for the proximalmost extent of the insertion of *m. teres major*. The medial boundary of the bicipital groove is very poorly defined, being essentially flush with the level of ambient surfaces. However, the lateral edge of the bicipital groove is quite salient and angles medially as it courses distally. This edge marks conjunction of the insertions of *mm. deltoideus* and *pectoralis major*, forming an anteromedially directed deltopectoral crest. A flattish, slightly convex, and well-defined deltoid plane continues distally from the greater tuberosity on the anterolateral aspect of the shaft. The posterior aspect of the shaft is marked by a columnar buttress at midline and is excavated medially and laterally just below the area where the tuberosities border the head. This surface represents an extensive area of origin for the lateral head of *m. triceps brachii*. Laterally, a blunt but perceptible deltotriceps crest is developed where this origin abuts against the deltoid plane. The shaft is mediolaterally broad, anteroposteriorly compressed, and moderately gracile with respect to the proximal end.

COMPARISONS

Living Anthropoids

KNM-MB 21206 has rather eclectic resemblances to the proximal humeri of extant monkeys and apes. The overall shape and orientation of the head are most similar to the ball-like and posteroproximally facing humeral heads of cebines and pitheciines. In terms of head breadth (Table II), the value of 92 for KNM-MB 21206 is matched by the means for *Cacajao* and *Lophocebus* and approached closely by the means for *Cebus* (93), *Saimiri* (93), *Mandrillus* (93), and *Macaca* (91). The head is relatively broader and faces more medially and proximally in living hominoids and in *Ateles* (Fleagle and Simons, 1982) (Table II). The anteroproximal portion of the head tends to the flattened in Old World monkeys, especially the

terrestrial and semiterrestrial cercopithecines (Gebo *et al.*, 1988, p. 397, Fig. 3).

As in most anthropoids, the articular surface of the head projects moderately above the head of the greater tuberosity. The value of -10 for the index of greater tuberosity projection of KNM-MB 21206 falls within the ranges of all five extant anthropoid families considered here (Table II) and is most closely approached by the means for *Cacajao* (-11), *Ateles* (-9), and *Gorilla* (-9). The head is further elevated above the greater tuberosity in *Alouatta* (mean = -14, range = -20 to -11), *Pongo* (mean = -17, range = -20 to -15), and the majority of hylobatids (Table II). Cercopithecids differ from other anthropoids in exhibiting tendencies toward projection of the greater tuberosity above the head (Jolly, 1967) (Table II).

KNM-MB 21206 resembles cercopithecids, cebids, indriids, and some atelids in possessing a relatively large and anteromedially positioned lesser tuberosity (Fleagle and Simons, 1982, Figs. 4a-c; Rose, 1989) (Table II). The lesser tuberosity size index value of 74 for KNM-MB 21206 (Table II) is matched by the mean for *Cercocebus* and is closely approached by the means for *Papio* (76), *Cacajao* (70), *Nasalis* (69), and *Erythrocebus* (69). The lesser tuberosities of living hominoids are much smaller and are positioned farther anteriorly (Fleagle and Simons, 1982, p. 181, Figs. 4h-i; Larson, 1988) (Table II). Tendencies toward reduction and anterior migration of the lesser tuberosity are also seen in *Ateles* (Fleagle and Simons, 1982, Fig. 4g) (Table II).

The greater tuberosity resembles those of cebids, atelids, and hominoids in being anterolaterally positioned (Fleagle and Simons, 1982, Figs. 4d, g-i). In cercopithecids, the greater tuberosity is positioned farther anteriorly (Fleagle and Simons, 1982, Figs. 4a-c, f). The pit for insertion of *m. infraspinatus* differs from those of cercopithecids, in which it tends to be anteroposteriorly elongated (Rose, 1989), and of living hominoids, in which it faces proximally (Gebo *et al.*, 1988); it is most similar to the proximodistally elongated and laterally facing arrangement seen in *Alouatta*.

The broad, shallow bicipital groove of KNM-MB 21206 is like those of most anthropoids. The bicipital groove breadth index value of 33 for KNM-MB 21206 (Table II) is matched by the mean of *Colobus* and is approached closely by the means of *Cercopithecus* (34), *Saimiri* (35), *Nasalis* (35), *Theropithecus* (35), *Cacajao* (31), and *Miopithecus* (31). Living hominoids and some atelids, especially spider monkeys, have much narrower and deeper bicipital grooves (Fleagle and Simons, 1982, Fig. 4) (Table II).

Extinct Catarrhines

Aegyptopithecus zeuxis (DPC 1275)

KNM-MB 21206 differs from the proximal humerus of *Aegyptopithecus* as follows: (1) the head is slightly broader, (2) the articular surface is elevated much farther above the greater tuberosity, (3) the lesser tuberosity is slightly smaller, (4) the deltoid plane is more distinct and flatter, and (5) a distinct deltotriceps crest is present laterally (Table II).

Pliopithecus vindobonensis (OE 304)

Compared to *Pliopithecus*, KNM-MB 21206 differs as follows: (1) the head is slightly narrower, (2) the articular surface is elevated slightly farther above the greater tuberosity, (3) the lesser tuberosity is slightly larger, (4) the bicipital groove is slightly broader and shallower, (5) the deltoid plane is more distinct and flatter, and (6) a distinct deltotriceps crest is present laterally (Table II).

Dendropithecus macinnesi or *Proconsul africanus* (KNM-RU 17376)

KNM-MB 21206 differs from KNM-RU 17376 as follows: (1) the articular surface is slightly less elevated above the greater tuberosity, (2) the lesser tuberosity is slightly larger, and (3) the bicipital groove is slightly broader and shallower (Table II).

Victoriapithecus macinnesi (KNM-MB 12044)

Compared to *Victoriapithecus*, KNM-MB 21206 differs as follows: (1) the head is slightly broader, (2) the articular surface is convex anteroproximally and elevated slightly farther above the greater tuberosity, (3) the lesser tuberosity is slightly larger, (4) the bicipital groove is slightly broader and shallower, (5) the greater tuberosity is positioned farther laterally, (6) the deltoid plane is flatter and better defined, and (7) the deltotriceps crest is more strongly developed.

In general, proportional differences between the extinct catarrhine proximal humeri are minor. Values of head breadth for *Aegyptopithecus*, *Pliopithecus*, KNM-RU 17376, *Victoriapithecus*, and KNM-MB 21206 (Table II) fall within the range of *Macaca* (82–104). Similarly, values of lesser tuberosity size for the extinct catarrhines (Table II) fall within the range

of *Nasalis* (55–76). Likewise, values of bicipital groove breadth for the extinct catarrhines (Table II) fall within the range of *Cercopithecus* (22–58). Among proportions examined here, only the values exhibited by the extinct catarrhines for greater tuberosity projection may not be subsumed within the range of a single extant genus. Nevertheless, values of greater tuberosity projection of the Miocene catarrhines (excluding *Aegyptopithecus*, an Oligocene form) fall within the ranges of both Atelidae and Hylobatidae (Table II).

INFERRED FUNCTION

Certain functional attributes of the shoulder joint of the Maboko Island oreopithecoid may be inferred from the morphology of KNM-MB 21206. The moderately broad and proximally projecting head of KNM-MB 21206 indicates a mobile shoulder, permitting a wide range of movements, like those of active climbers such as *Cebus* and *Cacajao*. However, KNM-MB 21206 does not exhibit the extreme breadth and proximal projection of the head seen among extant hominoids and related to circumduction of the arm during suspension (Fleagle and Simons, 1982). But KNM-MB 21206 lacks the anterior flattening of the articular surface, which is typical of cercopithecids and which reduces mobility (especially rotation) during full protraction (Ziemer, 1978; Harrison, 1989a; Rose, 1989). Moreover,

Table II. Proportions of the Proximal Humerus of *Nyanzapithecus* and Some Other Early Catarrhines Compared to Extant Cebidae, Atelidae, Cercopithecidae, Hylobatidae, and Pongidae

	Head breadth	Greater tuberosity projection	Lesser tuberosity size	Bicipital groove breadth
<i>Nyanzapithecus</i>	92	-10	74	33
<i>Aegyptopithecus</i>	87	0	76	33
<i>Pliopithecus</i>	100	-5	67	22
KNM-RU 17376	92	-14	68	25
<i>Victoriapithecus</i>	87	-5	58	30
Cebidae	91	-8	57	36
	(84–100)	(-12–6)	(50–72)	(27–41)
Atelidae	96	-12	57	33
	(79–122)	(-20–5)	(33–63)	(19–42)
Cercopithecidae	95	1	68	37
	(82–117)	(-10–13)	(55–85)	(22–59)
Hylobatidae	120	-12	35	17
	(105–143)	(-21–4)	(26–47)	(12–24)
Pongidae	112	-8	41	16
	(100–129)	(-20–0)	(30–55)	(10–26)

KNM-MB 21206 does not exhibit the anterior migration and elevation of the greater tuberosity that is characteristic of cercopithecids. These latter features are advantageous for effecting rapid protraction of the arm during quadrupedal walking and running (Jolly, 1967).

The relatively large and anteromedially positioned lesser tuberosity of KNM-MB 21206 suggests an important role of *m. subscapularis* in initiating abduction and medial rotation of the arm. In contrast, the anteriorly positioned lesser tuberosities of living hominoids, indicate that contraction of *m. subscapularis* results in medial rotation of the arm through a greater axis of rotation. The greatly reduced lesser tuberosity of living hominoids may indicate that *m. subscapularis* acts primarily to medially rotate (instead of forcefully abducting) the arm rapidly to attain pronated hand positions during bimanual suspension.

In summary, KNM-MB 21206 exhibits adaptations for active arboreal climbing with moderate mobility at the shoulder. However, KNM-MB 21206 lacks the extreme modifications of the proximal humerus that are shared by all living apes and which are related plausibly to a common ancestral mode of locomotion involving arm-hanging and vertical climbing (Hunt, 1991). KNM-MB 21206 also lacks the specializations of the proximal humerus that are shared by living cercopithecids and which are related to rapid rectilinear protraction and retraction of the arm for locomotion over large supports.

PHYLOGENETIC RELATIONSHIPS OF OREOPITHECIDAE

Lacking firm evidence to the contrary, KNM-MB 21206 is regarded here as retaining the primitive structural plan for the last common ancestor of living catarrhines. If we accept that the dental resemblances between *Oreopithecus bambolii* and the Maboko Island oreopithecids are derived features, inherited from a common ancestor (Von Koenigswald, 1969; Harrison, 1986), then this result can be interpreted in three ways.

First, on the basis of olecranon process abbreviation, a reduced number of lumbar vertebrae, and an increased number of sacral segments (documented for *Oreopithecus bambolii* but unknown and only assumed for *Nyanzapithecus pickfordi*), Oreopithecidae is a clade of hominoids that diverged after the node that joins *Proconsul* with all other hominoids. Contrary to Harrison (1987b), the trapezium/first metacarpal joint of *Proconsul africanus* (Napier and Davis, 1959; Beard *et al.*, 1986) exhibits similarities to catarrhines in general and hominoids in particular (Rafferty, 1991) and does not support divergence of *Proconsul* before the last common ancestor of living catarrhines. Furthermore, the derived loss of a tail

(Walker and Teaford, 1989; Ward *et al.*, 1989) and moderate development of a lateral keel on the trochlea of the distal humerus (Napier and Davis, 1959) support a hominoid affinity for *Proconsul* (*contra* Harrison, 1987b). However, retention of a direct bony contact between the ulnar styloid process and the pisiform/triquetral embrasure (Napier and Davis, 1959; Beard *et al.*, 1986) indicates that *Proconsul* diverged before the last common ancestor of living hominoids.

Homologues of *Proconsul nyanzae* manifest more primitive conditions than those of *Oreopithecus bambolii*, with a longer olecranon process and probably more lumbar vertebrae (Fleagle, 1983; Ward, 1990). However, on the basis of a proximal humeral morphology retained from the condition for the last common ancestor of living catarrhines (documented for *Nyanzapithecus pickfordi* but ill-known and only assumed for *Oreopithecus bambolii*), the oreopithecid clade diverged before the node that joins the extant hominoids together (Fig. 2A). This model holds true even if the proximal humerus of *Oreopithecus bambolii* proves to possess all of the derived features of extant hominoids. Because of the plesiomorphic condition of the proximal humerus of its sister taxon (*Nyanzapithecus*), hypothetical acquisition of extant hominoid-like features of the proximal humerus of *Oreopithecus bambolii* would, of necessity, merely be convergent upon those acquired by the last common ancestor of living apes.

Second, solely on the basis of a plesiomorphic configuration of the proximal humerus, the oreopithecid clade diverged from a node trichotomously joining *Proconsul* with Oreopithecidae and a clade leading to the last common ancestor of extant hominoids. Thus, the olecranon process abbreviation, reduced number of lumbar vertebrae, and increased number of sacral segments documented for *Oreopithecus* would merely be convergent upon these same conditions in the last common ancestor of extant hominoids (Fig. 2B).

Third, Oreopithecidae diverged subsequent to the last common ancestor of extant hominoids (Fig. 2C) as reflected by shared derived olecranon process abbreviation, reduced number of lumbar vertebrae, and increased number of sacral segments of *Oreopithecus bambolii* and extant hominoids. In this case, the derived proximal humeral morphology, reconstructed for the last common ancestor of extant hominoids, secondarily reverted to the plesiomorphic condition for living catarrhines, as seen in *Nyanzapithecus pickfordi*.

A fourth hypothesis is admissible if we allow for the possibility that *Nyanzapithecus pickfordi* and *Oreopithecus bambolii* convergently acquired their detailed dental resemblances. In this case, *Nyanzapithecus pickfordi* would be a dentally distinctive lineage that diverged from a node joining *Proconsul* with all other hominoids. Freed from the constraints imposed by

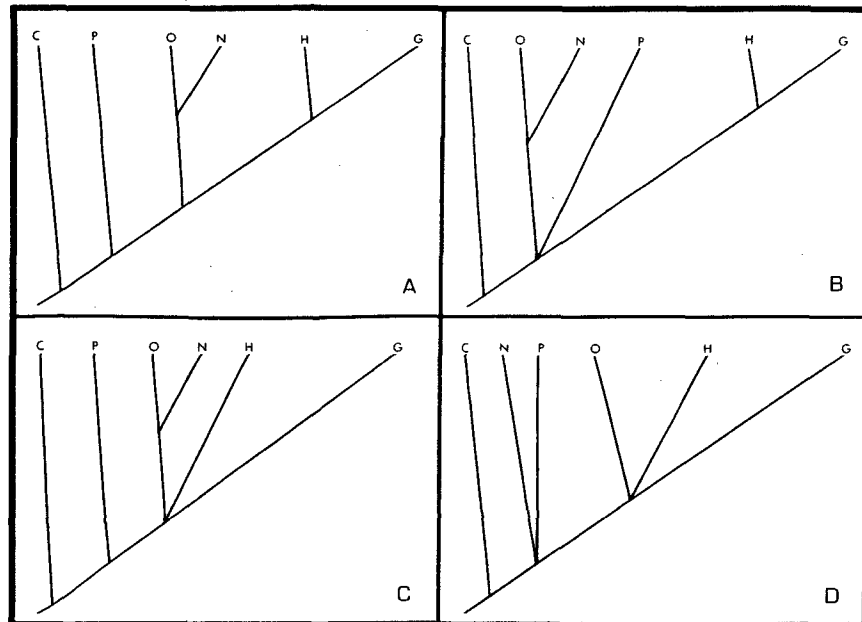


Fig. 2. Candidate branching diagrams of the relationships of *Nyanzapithecus* and *Oreopithecus* within the catarrhines. Symbols are as follows: C, *Cercopithecus*; P, *Proconsul*; O, *Oreopithecus*; N, *Nyanzapithecus*; H, *Hylobates*; G, *Gorilla*.

linkage to the plesiomorphic proximal humerus of *Nyanzapithecus pickfordi*, *Oreopithecus bambolii* would be a lineage within the monophyletic grouping of extant hominoids, albeit with a very specialized dentition excluding it from direct ancestry of Hylobatidae, Pongidae, or Hominidae (Fig. 2D).

Only one hypothesis requires no convergence or reversal on the basis of current knowledge: Oreopithecidae (including *Nyanzapithecus pickfordi*) is a clade of hominoids that is closer to living representatives than *Proconsul* is but which diverged before the last common ancestor of living apes. Although it is the most satisfactory of currently possible options, this hypothesis implicitly assumes that *Nyanzapithecus pickfordi* shared apomorphies of the elbow and lower back with *Oreopithecus bambolii* and extant hominoids. Only additional fossil discoveries can test this assumption. If *Nyanzapithecus pickfordi* should prove to retain plesiomorphic conditions for the elbow and lower back, then either the second or the fourth hypothesis would become more likely. That is, either (1) Oreopithecidae would no longer be linked with extant hominoids to any greater extent than *Proconsul* is or (2) *Nyanzapithecus pickfordi* is not, in fact, an oreopithecid.

DISCUSSION

Among extant and fossil catarrhines, KNM-MB 21206 is most similar to KNM-RU 17376, the proximal humerus from Rusinga Island attributed by Gebo *et al.* (1988) to either *Dendropithecus macinnesi* or *Proconsul africanus*. In KNM-RU 17376, Gebo *et al.* (1988) saw the beginning of a trend toward extant Hominoidea (with respect to *Aegyptopithecus*), especially vis-à-vis the slight expansion of its head, partial anterior migration of its lesser tuberosity, and general reduction in the size of both tuberosities. However, Rose (1989) indicated that the degree to which KNM-RU 17376 manifests these features does not exceed those of ceboids and cercopithecoids. The results presented here support Rose's (1989) findings. Like KNM-RU 17376, the morphology of KNM-MB 21206 does not even nascently approach a condition like that unique to living hominoids.

In contrast, *Victoriapithecus* displays derived features of the Cercopithecoidea. The anteroproximal portion of the articular surface is flattened and the greater tuberosity is positioned more anteriorly. By inference, *Victoriapithecus* was capable of rapid, rectilinear protraction of the arm, although to a lesser degree than in terrestrial Cercopithecoidea (Senut, 1986; Harrison, 1989b).

Thus, although derived attributes of the shoulder had been acquired by middle Miocene cercopithecoids, penecontemporaneous noncercopithecoid Catarrhini, including Oreopithecidae, maintained shoulder adaptations related to active arboreal climbing that are little removed from those of the common ancestor of living Catarrhini. Functional complexes other than the shoulder provide additional evidence for understanding the differentiation of locomotor adaptations of formative Old World monkeys and apes. *Proconsul* exhibits hominoid-like features in possessing a slightly broadened trochlea and moderately developed lateral trochlear keel of the distal humerus, together with very slight reduction in the length of the olecranon process relative to the height of the sigmoid notch (Napier and Davis, 1959; Fleagle, 1983; Rose, 1988; Harrison, 1989b). The elbow of *Oreopithecus bambolii* is fully derived in the direction of living hominoids, the lateral trochlear keel being more strongly developed, the olecranon process being very abbreviated, and the sigmoid notch being proximally oriented (Hurzeler, 1958; Straus, 1963; Sarmiento, 1987; Harrison, 1987a; Rose, 1988). Meanwhile, *Victoriapithecus* shows patently derived cercopithecoid features in possessing a strongly developed medial trochlear keel, narrow trochlea, a strong crest forming a well-defined lateral margin to the olecranon fossa, and slight posterior tilt of the olecranon process (Von Koenigswald, 1969; Simons, 1972; Delson, 1975; Senut, 1986; Harrison, 1989b).

Although early hominoids (including oreopithecids) retain a conservative structure of the shoulder, their elbows exhibit trends toward that of extant hominoids. Initially (in *Proconsul*), these changes were quite modest and may indicate no more than that the ulna was assuming a greater role (than the radius) in weight transference, possibly due to a shift toward more agile climbing and increasingly tensile (instead of compressive) forces at the elbow when the forearm was in maximum extension. Subsequently (in *Oreopithecus*), these changes were more profound and seem to indicate that the elbow was designed for full extension in suspensory postures.

In summary, the perspective afforded by postcranial remains of *Victoriapithecus* (Von Koenigswald, 1969; Delson, 1975; Senut, 1986; Harrison, 1989b) suggests that the evolutionary history of the Cercopithecoidea may have been characterized by relatively early, perhaps coeval and commensurate changes in the shoulder, elbow, and manus toward more efficient walking and running over large supports. It is not currently known whether conservative adaptations of the shoulder for active climbing and progressive adaptations of the elbow for suspension actually existed together in *Nyanzapithecus pickfordi* or *Oreopithecus bambolii*. Nevertheless, unlike cercopithecoids, the acquisition of forelimb characteristics which typify living hominoids seems to have followed a mosaic sequence, with changes in the elbow preceding those of the shoulder. It is tempting to suggest that changes enabling straightening out the forelimb were selected for initially because of the advantages they conferred in reaching out to pull oneself forward or to grasp fruits and leaves while feeding (Gebo *et al.*, 1988). In its first stages, this pattern of movement would only require a shoulder mobile enough for "diverse arm positions for climbing" (Gebo *et al.*, 1988, p. 399), a condition suspected here to have been retained from the common ancestor of Old World monkeys and apes. Among formative hominoids, increased use of extended elbow postures did not accompany greater glenohumeral stability and regularization of pronograde striding, as it evidently did among formative cercopithecoids, but instead may have involved further reliance on arm-swinging as a means of progression. Thus, the derived proximal humerus and wrist structure of extant hominoids probably evolved in response to more frequent bouts of arm-swinging, enabled initially by changes at the elbow, which in turn allowed full-blown bimanual hanging and brachiation by the last common ancestor of living apes.

CONCLUSION

Discovery of a proximal humerus attributable to *Nyanzapithecus pickfordi* provides insight into the adaptive history and phylogenetic

relationships of the Oreopithecidae. The functional anatomy of the proximal humerus of *Nyanzapithecus pickfordi* is reconstructed as displaying adaptations for active arboreal climbing and possibly arm-swinging but not for suspension or brachiation. It now seems possible that forelimb characteristics which typify living apes evolved in a mosaic fashion. Trends toward the elbow configuration of extant hominoids may have been initiated and even completed before changes in the shoulder. These results lend support to the notion that an actively scansorial stage, with bouts of arm-swinging, may have played an important role in the emergence of extant hominoid locomotor specializations (Fleagle, 1976; Fleagle *et al.*, 1981).

The proximal humeral morphology of *Nyanzapithecus pickfordi* conforms to that expected for the last common ancestor of living catarrhines. Assuming that the shared dental characteristics of *Oreopithecus bambolii* and the Maboko Island oreopithecids are derived features reflective of common inheritance (Von Koenigswald, 1969; Harrison, 1986), the proximal humeral morphology of *Nyanzapithecus pickfordi* allows consideration of two hypotheses concerning the phylogenetic relationships of the Oreopithecidae. One hypothesis, which is favored here, is that Oreopithecidae is a clade of hominoids which diverged after *Proconsul* but before the last common ancestor of extant hominoids. An alternative hypothesis is that the Oreopithecidae stem from a node that trichotomously joins *Proconsul*, the Oreopithecidae, and the lineage that gave rise to the common ancestor of extant hominoids. In either case, the plesiomorphic proximal humeral morphology of *Nyanzapithecus* substantively refutes Harrison's (1986) claim that the genus is the earliest-known representative of the Hominoidea. Although we cannot resolve which of these hypotheses is correct on the basis of current evidence, they are eminently (and, it is hoped, imminently) testable by discovery of additional fossil remains from Maboko Island.

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