ORIGINAL ARTICLE

New proconsuloid postcranials from the early Miocene of Kenya

Daniel L. Gebo · Nasser R. Malit · Isaiah Odhiambo Nengo

Abstract New early Miocene forelimb fossils have been recovered from the Songhor and Lower Kapurtay localities in southwestern Kenya. We describe four specimens that are similar in size and functional capabilities. Their specific allocation is problematic but these forelimb specimens must belong to either *Rangwapithecus gordoni* or *Proconsul africanus*. If these new postcranial specimens should belong to *R. gordoni*, on the basis of size and common dental specimens found at Songhor, they represent a new elbow complex. The morphology of these fossils is anatomically and functionally similar to that of *Proconsul*. The proconsuloid elbow complex allows extensive forelimb rotations and is capable of performing arboreal quadrupedalism and climbing activities. No suspensory adaptations are apparent. The proconsuloid elbow complex remains a good ancestral condition for hominoid primates.

Keywords Miocene · *Rangwapithecus* · *Proconsul* · Elbow anatomy

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Introduction

Renewed fieldwork in Kenya at the Songhor locality and at a new locality, Lower Kapurtay, a site close to Songhor (Fig. 1), has produced several unassociated postcranial specimens from the early Miocene of East Africa. These four new specimens involve the elbow complex and are most likely allocated on the basis of size and morphology to either *Rangwapithecus gordoni* or *Proconsul africanus* (see below). We follow Harrison (2002) in placing the genera *Afropithecus*, *Heliopithecus*, *Mabokopithecus*, *Nyanzapithecus*, *Proconsul*, *Rangwapithecus*, and *Turkanapithecus* within Proconsuloidea; *Dendropithecus*, *Micropithecus*, and *Simiolus* within Dendropithecoidea; and *Limnopithecus*, *Kalepithecus*, and *Kamoyapithecus* within superfamily *incertae sedis*. In contrast, the living apes and their close relatives (e.g., *Dryopithecus*, *Griphopithecus*, *Morotopithecus*, *Oreopithecus*, *Pierolapithecus*, and *Sivapithecus*) are taxonomically within Hominoidea. However, we view Proconsuloidea as a post-cercopithcoid clade, in contrast to Harrison (2002). Here we describe four specimens of proconsuloids and comment on elbow function in proconsuloid and hominoid primates.

Sites and geology

Songhor (SO) is an early Miocene locality situated in western Kenya (Nyanza Province; MacInnes 1943; Pickford and Andrews 1981; Andrews 1981). Hominoid taxa from Songhor date to 19–20 mya (Bishop et al. 1969; Pickford 1983; Andrews et al. 1997). The geology of the Songhor locality is described in detail by Pickford and Andrews (1981). I.O. Nengo and N.R. Malit continued the paleontological work at Songhor in collecting area 5 (Red

Fig. 1 Map of Songhor and the Lower Kapurtay locality
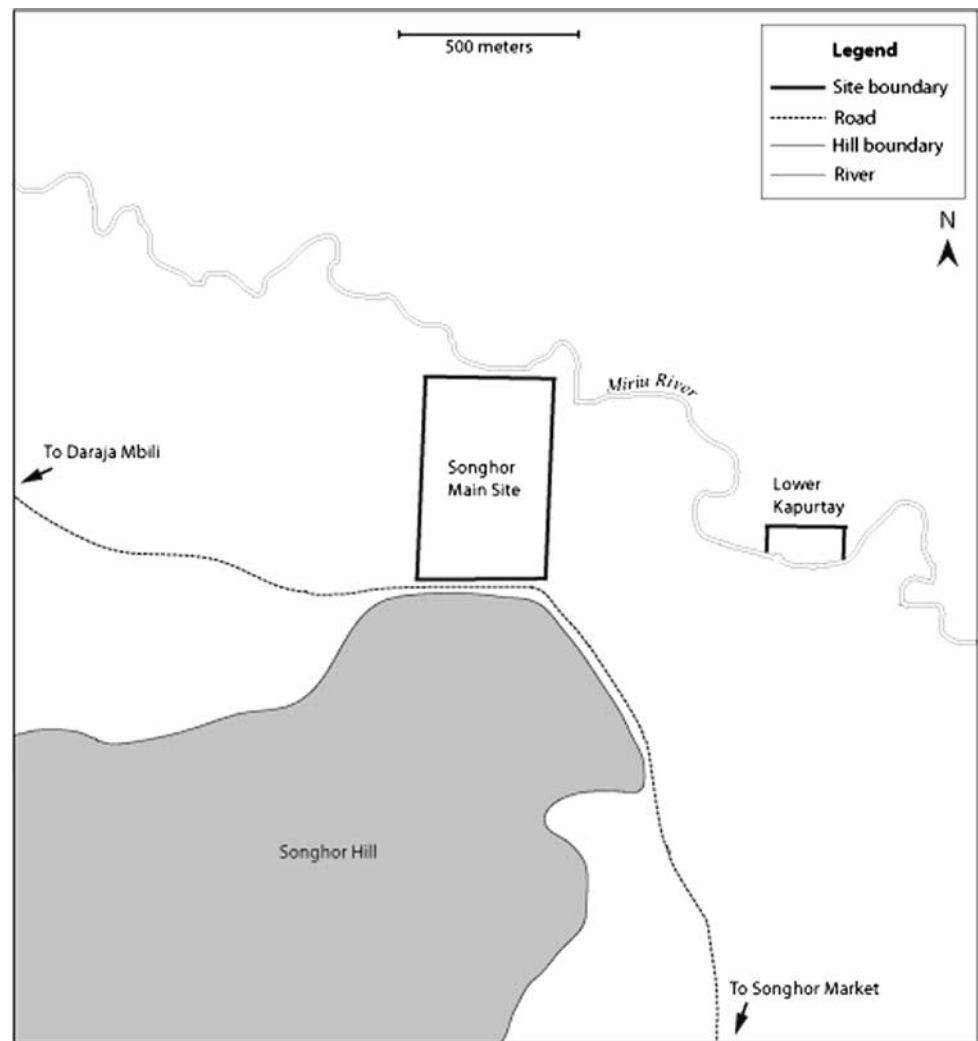
Beds Member Bed 6 of Pickford and Andrews 1981) in 1989, 1990, 1996, and 1998. Initially, dental and postcranial specimens of fossil primates were recovered in 1989 and 1990, including *Limnopithecus evansi*, *Proconsul major*, *R. gordoni*, and *Kalepithecus songhorensis* (Odhiambo Nengo and Rae 1992). The postcranial specimens include a partial ulna attributed to *P. major* and two entocuneiforms attributed to *R. gordoni* (Odhiambo Nengo and Rae 1992). The later excavations in 1996 and 1998 yielded additional postcranial material. The KNM-SO 31232 humerus described here was recovered in bed 6 in the 1996 excavation in collecting area 5 (Pickford and Andrews 1981). The KNM-KT 38000 forelimb elements described in this manuscript are associated elements and were recovered at a new locality, Lower Kapurtay (KT), in 1998. Lower Kapurtay is situated close to Songhor (Fig. 1) and was discovered in 1996. This site produced additional primate material in the 1996 and 1998 field seasons. There are no radiometric dates for this site but all of the mammalian fauna found at Lower Kapurtay are recorded at

Songhor (Table 1; see Pickford and Andrews 1981; Odhiambo Nengo and Rae 1992). The maximum age of the Lower Kapurtay fossil assemblage can be correlated in time with Songhor (approximately 19–20 mya; Pickford 1983; Andrews et al. 1997).

Body size and allocation

The KNM-SO 31232 distal humerus from Songhor is a mid-sized specimen. It is similar in size to the distal humerus attributed to *Kenyapithecus wickeri* (KNM-FT 2751), which has a body weight estimated to be 27 kg (Fleagle 1999). In terms of absolute bicondylar width, the KNM-SO 31232 humerus (Fig. 2) is similar to a variety of baboon taxa, especially adult males of *Theropithecus gelada* (11.2–19 kg), *Papio anubis* (13.3–25.1 kg), *Papio ursinus* (14.8–29.8 kg), and *Mandrillus sphinx* (12.9–31.6 kg), as well as *Nasalis larvatus* (9.8–20.4 kg; Smith and Jungers 1997). Using the regression equation from

Table 1 Lower Kapurtay mammal faunal list. All of these species are present at Songhor

Rodentia	*Bathyergoides neotetarius*, *Diamantomys luederitzi*, *Paranomalurus bishopi*, *Paraphiomys pigotti*
Primates	*Kalepithecus songhorensis*, *Proconsul major*, *Rangwapithecus gordoni*
Artiodactyla	*Dorcatherium songhorensis*, *Nguruwe kijivium*
Carnivora	*Cynelos euryodon*

Rafferty et al. (1995) for the KNM-SO 31232 humeral shaft produces a weight estimate of 25.3 kg. The measured anteroposterior (AP) and mediolateral (ML) width values of the KNM-SO 31232 shaft (at the 35% level) are slightly below the position used by Rafferty et al. (1995) at the 40% level. Using the articular regression equations for African apes in Jungers and Susman (1984) provides lower body size estimates of 17.9 kg (using articular width of the distal humerus) and 20.6 kg (using trochlear width) for the KNM-SO 31232 humerus. On the basis of these body size estimates and our overall comparative size assessment, KNM-SO 31232 is best viewed as a baboon-sized fossil primate between 20 and 25 kg.

Three associated postcranial elements have been found at Lower Kapurtay: KNM-KT 38000A, a humeral shaft; KNM-KT 38000B, a proximal ulna; and KNM-KT 38000C, a proximal radius (Figs. 3, 4, 5). All three specimens are mid-sized and similar in size to adult male baboons as noted above for KNM-SO 31232. All of the Lower Kapurtay specimens are similar in size to the KNM-

Fig. 3 KNM-KT 38000A, distal humerus (anterior: left view; posterior: right view); *bar* 1 cm. KNM-KT 38000 is the correct museum accession number for all of the Kapurtay specimens. All other *numbers* labeled on these specimens are simply field notations

SO 31232 humerus. Using the diameter of the radial head to estimate body size from Jungers and Susman (1984) provides a size estimate for KNM-KT 38000C of 18.8 kg. These three postcranial elements also fit best with a 20–25 kg fossil primate.

Fig. 2 KNM-SO 31232, distal humerus (*left* to *right*: anterior, distal, and posterior views) *Scale* is in centimeters

KNM-KT 38000B

Fig. 4 KNM-KT 38000B, proximal ulna (*top* lateral view; *bottom* medial view); *bar* 1 cm

KNM-KT 38000C

Fig. 5 KNM-KT 38000C, proximal radius (left to right: posterior, anterior, medial and superior views); *bar* 1 cm

On the basis of size and morphology (see below), the distal humerus from Songhor and the three Lower Kapurtay specimens are best attributed to a mid-sized proconsuloid. Fossil primates from Songhor include the following taxa: *P. major* (or *Ugandapithecus major*; see Senut et al. 2000), *P. africanus*, *R. gordoni*, *Nyanzapithecus vancouveringorum*, *L. evansi*, *K. songhorensis*, and *Dendropithecus macinnesi* (Table 2; Pickford and Andrews 1981; Pickford 1986; Harrison 1989; Andrews et al. 1997). Tibial and talar body size estimates by Rafferty et al. (1995) and Walker (1997) for *Proconsul* show *P. africanus* and *P. heseloni* to be the smallest,

similar in size, and approximately 11 kg (a species mean size estimate; see also Walker and Pickford 1983). Harrison (2002, p. 315) also notes that *P. africanus* "is comparable in size to *Proconsul heseloni*" and suggests that large dental remains for *Proconsul heseloni* (and conceivably for *P. africanus* as well) indicate body weights up to 20 kg. In contrast, the mean weight of *P. major* (or *U. major*), estimated at 75.1 kg (range 63.4–86.7 kg; Rafferty et al. 1995), is well beyond the size range of the new postcranial elements described here. Harrison's (2002) estimated body weights for *N. vancouveringorum* (8–11 kg), *D. macinnesi* (5–9 kg), *L. evansi* (around 5 kg), and *K. songhorensis* (around 5 kg) are all too small for the postcranial specimens described here. In contrast, *R. gordoni*, is a medium-sized primate "similar in dental size to *P. africanus* and *P. heseloni*" (Harrison 2002, p. 323). Thus on the basis of size, these new postcranial specimens from Songhor and Kapurtay could either belong to a male specimen of *P. africanus* or *R. gordoni*. There are forelimb elements associated with the juvenile skeleton of *Proconsul heseloni* (KNM-RU 2036) and a few other incomplete forelimb elements attributed to other species of *Proconsul*, but only a questionable humeral shaft is attributed to *R. gordoni* (Harrison 1982). The few isolated postcranial elements that have been assigned to *Rangwapithecus* all show a similar morphology to *Proconsul* according to Harrison (2002), suggesting that morphology alone may not help us sort out the correct taxonomic attribution.

On the basis of number of dental specimens, *R. gordoni* is far more common at Songhor than is *P. africanus* (Harrison, personal communication), suggesting that *Rangwapithecus* is the best taxon to attribute these postcranial elements to. A few postcranial specimens have already been attributed to *Rangwapithecus*, although largely on the basis of size (Odhiambo Nengo and Rae 1992). Although we are unable to be more definitive at this time, given the morphological and size similarities between *R. gordoni* and *P. africanus*, *R. gordoni* is our best guess attribution for these specimens at present.

Table 2 Songhor taxa

Pickford and Andrews, 1981	Pickford, 1986	Harrison, 1989
Proconsul major	*Proconsul major*	*Proconsul major*
Proconsul africanus	*Proconsul africanus*	*Proconsul africanus*
	?Proconsul nyanzae	
Rangwapithecus gordoni	*Rangwapithecus gordoni*	*Rangwapithecus gordoni*
Nyanzapithecus vancouveringi	*Nyanzapithecus vancouveringi*	*Nyanzapithecus vancouveringorum*
Limnopithecus legetet	*Limnopithecus evansi*	*Limnopithecus evansi*
Kalepithecus songhorensis	*Kalepithecus songhorensis*	*Kalepithecus songhorensis*
Dendropithecus macinnesi	*Dendropithecus macinnesi*	*Dendropithecus macinnesi*

Table 3 Humeral measurements

	KNM-SO 31232	KNM-KT 38000A
AP shaft diameter (∼35% level)	14.8 mm	–
ML shaft diameter (∼35% level)	17.2	16.9
Length of brachioradialis flange	84.8	>77.4
Brachioradialis flange width	8.1	6.2
Bicondylar breadth	44.3	–
Articular width	31.8	–
Trochlear width (anterior)	16.1	–
Capitular + zona width	15.7	–
Zona conoidea width	5.0	–
Zona conoidea height	10.9	–
Capitular width	10.7	–
Capitular height	12.7	–
Lateral capitular depth	22.3	–
Medial trochlear rim height	15.6	–
Lateral trochlear rim height	12.5	–
Trochlear notch height	10.7	–
Medial trochlear depth	15.4	–
Posterior breadth of distal articulation	12.8	–
Posteromedial height of distal articulation	15.2	–
Maximum breadth of olecranon fossa	19.6	–
Maximum height of olecranon fossa	16.0	–

Results

KNM-SO 31232

KNM-SO 31232 is an adult right distal humerus (Fig. 2). KNM-SO 31232 is 95.8 mm in length and represents the distal third of an intact humerus. Several cracks permeate this specimen but the elbow region is largely intact with broken edges along the anteromedial trochlear rim and the

lateral trochlear rim posteriorly. All humeral measurements and ratios are listed in Tables 3 and 4.

KNM-SO 31232 has a well-developed brachioradialis flange extending 84.8 mm in length. This flange is broader than that of *P. heseloni* (KNM-RU 2036AH) and bows outward. The lateral crest of the brachial flange extends anteriorly as it moves distally to meet the lateral epicondyle. There is a tubercle at this intersection. The flattened surface of the brachioradialis flange provides a wide area of attachment for several muscles (*brachioradialis*, *extensor carpi radialis longus*, and *carpi radialis brevis*). The radial fossa is much larger and deeper than the coronoid fossa. The lateral epicondyle is small while the medial epicondyle is pronounced and retroflexed posteriorly (angle of 30°). This retroflexion is similar to *P. heseloni* and to other Miocene taxa such as *Dendropithecus* and *Simiolus* (Rose et al. 1992). The radial collateral ligament pit faces laterally on the medial epicondyle.

At the joint surface, the anterior articular surface is about three-quarters the length of the bicondylar breadth (Tables 3 and 4; 31.8 mm/44.3 mm = 0.72). The anterior trochlear surface has a shallow indentation (minimum spooling) similar to that of *P. heseloni*. The medial trochlear rim is longer and more pronounced distally compared with that of the lateral trochlear rim (medial/lateral trochlear height = 15.6 mm/12.5 mm = 1.25). The medial edge of the medial trochlear rim curves laterally as this surface moves posteriorly. The zona conoidea is shallow in KNM-SO 31232 with a width about half that of the capitulum (5 mm/10.7 mm = 0.47; see Rose 1988 and Szalay and Dagosto 1980, for measurement points). The capitulum is taller than it is wide (height/width = 12.7 mm/10.7 mm = 1.19). Capitular and zona width (15.7 mm) to total articular width (31.8 mm) is 49% of the anterior articular surface. Capitular (22.3 mm) depth to trochlear depth (15.4 mm; anteroposteriorly) is 1.45. Posteriorly, the lateral trochlear rim is situated well above the

Table 4 Humeral ratio comparisons

	?R. gordoni KNM-SO 31232	P. heseloni KNM-RU 2036AH	K. wickeri KNM-FT 2751
Bicondylar width	44.3 mm	31.5	43.23
Articular width/bicondylar width	0.72	0.81	0.79
Brachioradialis flange width/bicondylar width	0.18	0.11	0.09
Mediolateral shaft width/anteroposterior width (at ∼35% level)	1.17	1.11	1.27
Capitulum + zona width/trochlear width	0.98	0.91	0.97
Zona width/capitular width	0.47	0.44	0.44
Capitular height/capitular width	1.19	1.11	1.17
Medial trochlear rim height/lateral trochlear rim height	1.25	1.23	1.25
Anterior trochlear width/posterior trochlear width	1.28	1.35	1.30
Lateral epicondylar width/bicondylar width	0.40	0.41	0.51

surface of the shaft, representing a prominent buttress for the ulna. The coronoid fossa is moderately deep and mediolaterally oval in shape. A dorsoepitrochlear fossa or pit is present. Anterior (16.1 mm) to posterior articular width (12.8 mm) is 1.26. In overall morphology, the distal humerus of KNM-SO 31232 is similar in several aspects to that of *P. heseloni* (KNM-RU 2036AH; see Table 4) and to other proconsuloids. KNM-SO 31232 differs from *P. heseloni* in one particular aspect, the brachioradialis flange is wider (flange width/bicondylar width = 0.18 versus 0.11), extends vertically upward to a much greater degree, and bows outward, being convex relative to the concave curvature for *P. heseloni*. Although the brachioradialis flange is clearly prominent in KNM-SO 31232, this anatomical comparison is between a juvenile specimen (KNM-RU 2036AH) relative to that of an adult male (KNM-SO 31232). Table 4 lists all of the humeral ratios between *P. heseloni* and KNM-SO 31232, with most showing only slight differences between the two taxa. Articular width, anterior trochlear width, the capitular and zona width, and capitular height ratios show the greatest differences between these two specimens.

KNM-RU 7696 is a badly broken distal humerus described by Senut (1986, 1989) and later attributed to *Proconsul nyanzae*. KNM-RU 7696 differs from KNM-SO 31232 in having a more prominent and robust lateral epicondylar region. In the other anatomical parts that can be compared with KMN-RU 7696, the KNM-SO 31232 distal humerus appears similar.

The KNM-SO 1007 broken distal humerus does possess a large brachioradialis flange and this specimen has been allocated to *P. major* (Harrison 1982; Senut 1989). Although the KNM-SO 1007 humerus is badly damaged with no elbow articular morphology preserved to compare between the two specimens, it could be similar to the KNM-SO 31232 humerus on the basis of the brachioradialis flange. On the basis of overall size, KNM-SO 1007 is a much larger specimen. The only intact comparative region to measure and evaluate size for both Songhor humeri is the proximal shaft. Here the m-l shaft width for KNM-SO 1007 is 58% larger than the same measure for KNM-SO 31232. On this basis, the KNM-SO 1007 humerus is a much larger specimen and better allocated to the large taxon at Songhor, *Proconsul* (or *Ugandapithecus*) *major*.

The KNM-SO 31232 distal humerus is similar in size to the distal humerus attributed to *K. wickeri* (KNM-FT 2751; bicondylar breath = 44.3–43.2 mm, respectively) but both are quite different in morphology. KNM-SO 31232 differs from that of *Kenyapithecus* in (1) its wider brachioradialis flange that bows outward, (2) a more projecting medial epicondyle with greater bony buttressing toward the trochlea, (3) the medial trochlear rim extends farther distally and is more steeply angled, (4) a more flared medial

aspect of the trochlea (distal view), and (5) the posterolateral epicondylar region is narrow and less buttressed than in *Kenyapithecus* (lateral epicondylar width/bicondylar width = 0.40–0.51; Table 4).

The KNM-WK 17009A/B humerus attributed to *Simiolus* (Rose et al. 1992) is quite distinctive distally from that of KNM-SO 31232 with a less pronounced brachioradialis flange, a less pronounced and more rounded medial epicondylar edge, and a symmetrical olecranon fossa.

The KNM-MO 17022A distal humerus attributed to *?Dendropithecus* (Rose et al. 1992) is particularly distinct from KNM-SO 31232 in capitular and trochlear morphology. The capitulum of KNM-MO 17022A lacks circularity and a clear definition of the lateral capitular edge next to a less indented zona conoidea and a straight trochlear joint surface relative to KNM-SO 31232.

In terms of elbow function, Rose (1988) and Rose et al. (1992) have discussed the functional capabilities of the *Proconsul heseloni* elbow in detail. *Proconsul* is best viewed as an arboreal quadrupedal primate with extensive rotational positions for the forearm, suggesting frequent quadrupedalism and climbing activities. The elbow morphology of KNM-SO 31232 fits well with Rose's assessment (Rose 1988; Rose et al. 1992). The elbow morphology of KNM-SO 31232 is quite distinct from that of the more terrestrially oriented *Kenyapithecus* (McCrossin and Benefit 1997). Taxa such as *Equatorius* (Ward et al. 1999; Sherwood et al. 2002) and *Nachalopithecus* (Nakatsukasa et al. 1998; Ishida et al. 2004; Nakatsukasa 2004), although arboreal, all share with *Kenyapithecus* a posteriorly oriented medial epicondyle, a feature quite distinct from proconsuloid elbows. KNM-SO 31232 differs from *Simiolus* or *Dendropithecus* relative to *Proconsul* as noted by Rose et al. (1992). The elbow morphology of extant hominoids is distinct from proconsuloids in capitular morphology, particularly in the depth of the zona conoidea, a greater spool-shaped trochlea, and in the depth of the olecranon fossa.

KNM-KT 38000

Humerus. The KNM-KT 38000A left distal humeral fragment (Table 3; Fig. 3) is a large humerus (110.3 mm in known length) that represents several pieces of the humeral shaft that have been glued together. No articular morphology remains and most of the posterior aspect of the shaft is broken away. It is clear that a brachioradialis flange was present and extensive. This flange was at least 77.8 mm in length and 6.2 mm in overall width. The posterolateral aspect of the brachial flange is preserved and extends to the proximal aspect of the olecranon fossa.

Ulna. KNM-KT 38000B is a left proximal ulnar fragment that measures 93.3 mm in its known length (Table 5;

Table 5 Ulna measurements (after Richmond et al. 1998)

	KNM-KT 38000B
Sigmoid notch depth (SND)	14.1 mm
AP lateral articular thickness (LAH)	10.1
AP thickness at distal beak of trochlear notch	23.0 estimated
AP thickness of radial notch (RAP)	10.2
Proximodistal length of radial notch (RPD)	10.8
Proximal shaft AP thickness at distal margin of radial notch (PAP)	17.6
Mediolateral width of sigmoid notch (SML)	11.7
Proximal articular mediolateral breadth of radial notch and trochlea (PAB)	15.8 estimated
AP breadth of shaft at midpoint	17.0
ML breadth of shaft at midpoint	10.2
AP breadth at the distal shaft	14.9
ML breadth at the distal shaft	8.3

Table 6 Radial measurements (after Rose et al. 1992)

	KNM-KT 38000C
Radial head width (b)	18.4 mm
Neck height (c)	11.8
Neck width (d)	11.0
Radial head articular surface (minimum anterior width; f)	4.4
Radial head articular surface (maximum anterior width; g)	5.8
Radial head articular surface (minimum proximodistal width; h)	2.8
Radial head articular surface (maximum proximodistal width; i)	4.8
Radial head to bicipital tuberosity length (k)	36.1
Height of radial depression (l)	12.6

Fig. 4). The olecranon process is broken away from this specimen as is the distal two-thirds. Some of the articular surface (sigmoid notch) is preserved as is the radial facet. In overall appearance, KNM-KT 38000B is very similar to the proximal ulna fragment of *P. heseloni* (KNM-RU 2036CF). The sigmoid notch is moderately broad as in other species of *Proconsul* (Richmond et al. 1998). It lacks the great width of living apes. There is a slightly raised mid-line articular region along the sigmoid articular facet indicating a slight trochlear notch in the distal humerus. The radial facet is flat and aligned along the shaft (lateral orientation) with a shallow angle to the vertical (28°). This angle is very similar to values attributed to *P. heseloni* (30°) and *P. nyanzae* (31°; Richmond et al. 1998). The radial facet is broader relative to that of *P. heseloni* (maximum breadth/height = 0.93–0.78). There is a well-delineated depression for the annular ligament anterodistal to the radial facet in KNM-KT 38000B. Below this depression is an elevated bony crest for supinator. On the medial side, there is a prominent notch for the insertion of the brachialis muscle, a feature commonly found among the living apes (Richmond et al. 1998). The distal end of the ulnar shaft is tall and oval in cross section (AP width = 14.9 mm; ML width = 8.3 mm; AP/ML width = 1.8). The AP and ML cortical thickness at the distal shaft is 4.5 and 3.0 mm, respectively (AP/ML cortical thickness = 1.5). In sum, the ulnar joint surfaces and the prominent brachialis insertion is consistent with an arboreal quadrupedal and climbing-adapted primate and contrasts with the ulnar morphology found among forelimb suspensory and brachiating hominoid primates.

Radius. The left proximal radial fragment, KNM-KT 38000C (Table 6; Fig. 5), is also associated with the Kapurtay ulna and humerus. It is 57.2 cm in its known length but broken just distal of the bicipital tuberosity. A little over half of the medial radial head is preserved. The radial head of KNM-KT 38000C is circular, like that of KNM-RU 2036CE, with a large surface area for articulation with the capitulum. The articular surface is well depressed centrally with about equal articular surface around the circle. A lateral lip exists for articulation with the zona conoidea and the articular surface is slightly beveled. This is true for *Proconsul heseloni* (KNM RU 2036CE) as well (Rose et al. 1992). A lateral lip is commonly found among quadrupedal nonhominoid anthropoids (Rose et al. 1992). These attributes suggest that pronation and supination at the elbow was extensive and that the humeroradial joint was secure throughout its range of motion (Rose et al. 1992). The radial head morphology of KNM-KT 38000C also suggests that a "stable position for full pronation" (Rose et al. 1992, p. 192) was still present, implying a quadrupedal movement pattern.

The radial neck is robust and similar in width to the radial shaft. A longer and narrower radial neck is observed in *Simiolus* (Rose et al. 1992) relative to KNM-KT 38000C. The KNM-KT 38000C neck is not elongated as in suspensory hominoids and thus is relatively close to the bicipital tuberosity. The bicipital tuberosity, the insertion site for *biceps brachii*, is well developed with two prominent ridges and a groove in between in KNM-KT 38000C. This bicipital groove runs up onto the radial neck. The distal end of the radial shaft is oval in cross-section (AP width = 10.0 mm; ML width = 11.5 mm; AP/ML width = 0.9; AP cortical thickness = 3.3 mm; ML cortical thickness = 2.8 mm). The radial morphology suggests an arboreal quadrupedal primate with good stable rotation abilities at the elbow for climbing activities.

Discussion

Fieldwork at Songhor and at a new Kenyan locality, Lower Kaputray, has produced four additional postcranial specimens that are unassociated with dentitions from the early Miocene of Africa. These four specimens are similar in size and functional capabilities and are most likely allocated to either *R. gordoni* (our preference) or *P. africanus*. The elbow morphology of these new specimens is anatomically and functionally similar to that already described for *Proconsul*, implying a mobile forearm capable of extensive rotations during arboreal quadrupedal and climbing activities (Walker and Pickford 1983; Rose 1988, 1993; Senut 1989). No suspensory adaptations are recognized at the elbow for this material nor for the forelimb of *Proconsul* (Morbeck 1975; O'Connor 1976; Rose 1988, 1993; Senut 1989).

This new elbow material from Songhor and Lower Kaputay differs from other early Miocene Kenyan taxa (e.g., *Dendropithecus* or *Simiolus*) in several morphological aspects, as does that of *Proconsul*'s. For example, both the elbow of *Proconsul* and KNM-SO 31232 possess a moderately developed medial trochlear keel like that of extant hominoids, although less pronounced. In contrast, *Dendropithecus* lacks this distal humeral feature, being morphologically similar to cebids (Rose 1988). The zona conoidea is "a mediolaterally wide, proximodistally shallow, and mostly proximally facing surface" in *Dendropithecus* whereas in *Proconsul*, this feature forms "a narrow, deep, and proximolateral facing gutter" similar to living hominoids (Rose 1988, p. 201). The radial head, which articulates with the capitulum, is morphologically similar between *Dendropithecus* and nonhominoid anthropoids, but lacks the extensive pronation–supination movement capabilities; whereas the radial head morphology of *Proconsul* is viewed as more similar to extant hominoid morphology and in its range of joint motion (Rose 1988). Rose (1988, pp. 205–206) states "The expression of these features on the radial head of *Proconsul* is intermediate between that of extant hominoids and that of the other group. This, together with other features, suggests that the amplitude of forearm pronation-supination may have been similarly intermediate." The functional assessment for *Dendropithecus* is the same as *Simiolus* (Rose et al. 1992) and contrasts with proconsuloid elbows. Thus, overall elbow function in *Dendropithecus* and *Simiolus* is similar to quadrupedal anthropoids (Rose 1988; Rose et al. 1992), whereas elbow morphology in proconsuloids shows a few hominoid features at the humeroradial and radioulnar joints (Rose 1988, 1993, 1997), implying increased rotational movements at these joints for "enhanced" climbing activities. All of these morphological distinctions hold for the new

Songhor and Lower Kaputay specimens described here. Hominoid features related to trochlear spooling and the depth of the zona conoidea are also reported in mid-Miocene taxa such as *Kenyapithecus*, *Equatorius*, and *Nachalopithecus* (McCrossin and Benefit 1997; Ward et al. 1999; Nakatsukasa et al. 1998), with only *Nachalopithecus* being reported with forelimb-dominated positional behaviors (Ishida et al. 2004; Nakatsukasa 2004).

Although the elbow morphology of proconsuloids shares several features with hominoids, it also lacks many of the derived shoulder and thorax features associated with brachiating and suspensory apes found among the living apes, *Dryopithecus*, *Oreopithecus*, and *Pierolapithecus* (Sarmiento 1987; Harrison 1987; Moyà-Soyà and Köhler 1993; Rose 1997; contra Moyà-Soyà et al. 2004). This evidence suggests that elbow morphology changes prior to shoulder or back morphology in the morphological transition toward brachiating apes. Perhaps a reassessment of the arm morphology of dendropithecoids and pliopithecoids as low-frequency brachiators is in order given the relatively new quantitative data for *Lagothrix* as a low-frequency brachiator (Defler 1999; Cant et al. 2001, 2003), given this taxon's nonhominoid elbow and shoulder morphology. This assessment may help us better understand why elbow changes are occurring among proconsuloids. In the end, proconsuloid elbow morphology remains, as has been noted before, a plausible ancestral condition for hominoid elbow morphology.

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