

William J. Sanders &
Brian E. Bodenbender
*Museum of Paleontology, The University
of Michigan, Ann Arbor, Michigan
48109, U.S.A.*

Morphometric analysis of lumbar vertebra UMP 67-28: Implications for spinal function and phylogeny of the Miocene Moroto hominoid

Received 14 December 1992
Revision received 27 August
1993 and accepted 1 October
1993

Keywords: Moroto, lumbar vertebra, Miocene, Afropithecini, *Afropithecus*, *Proconsul*, functional morphology, phylogeny

Fossil hominoid remains from the Miocene site of Moroto II include a well preserved lumbar vertebra (UMP 67-28). This vertebra is associated with a palate that has been included in the hominoid tribe Afropithecini and referred by some to *Afropithecus*. UMP 67-28 originally was described as having close morphological affinities with lumbar vertebrae from African apes and humans (Walker & Rose, 1968). The present analysis, however, indicates that UMP 67-28 shares no exclusive proportional or structural similarities with lumbar vertebrae from any particular extant catarrhine. The Moroto vertebra is the size of lumbar elements from female chimpanzees and orang-utans or large male cercopithecoids. Regression analysis of vertebral body surface area suggests that the individual represented by UMP 67-28 had a body weight of approximately 38 kg. UMP 67-28 is similar to large-bodied hominoids in general, in position and orientation of its transverse process, absence of anapophyses, inclination of its neural spine, and pedicular shape, marking the earliest appearance in the catarrhine fossil record of lumbar morphology resembling that of modern hominoids. Conversely, vertebral body proportions in UMP 67-28 most closely resemble those in male baboons, and in other traits the specimen cannot be differentiated between hominoids and cercopithecoids. The overall morphology of UMP 67-28 indicates that lumbar vertebrae of the Moroto hominoid were more derived toward the great ape condition than those of *Proconsul heseloni* and *P. nyanzae*. In contrast to *Proconsul*, UMP 67-28 shares features with other dorso-stable-backed mammals, suggesting that the Moroto hominoid and *Proconsul* possessed very different locomotor capabilities. Dental traits linking the Moroto hominoid with other afropithecins are thought to correspond functionally to a fundamental shift in diet, relative to the primitive catarrhine condition. It is possible that evolution of the lumbar region of early hominoids toward the morphotype of extant large-bodied hominoids, evidenced in UMP 67-28, was adaptively driven by modifications in substrate use coincident with changes in resource acquisition.

Journal of Human Evolution (1994) **26**, 203–237

Introduction

The middle Miocene site of Moroto II in Karamoja, eastern Uganda has yielded hominoid fossils dated radiometrically to ca. 14 m.y. (Bishop *et al.*, 1969; Pickford, 1986). Among these fossils is a nearly complete palate, initially identified as that of a large form of *Proconsul* (Bishop & Whyte, 1962) and subsequently placed in *Proconsul major* (Allbrook & Bishop, 1963; Bishop, 1964). Moroto II also has produced a primate lumbar vertebra in good condition, labeled UMP 67-28 (Figure 1). This specimen and fragments of four other vertebrae are thought to belong with the palatal remains (Walker & Rose, 1968). As no other primate taxa were identified among the meager faunal remains from the site, and as UMP 67-28 is a good match for the Moroto palate in size, it is most parsimoniously attributed to the same individual as the palate.

Recently, the Moroto palate was tentatively reassigned to the genus *Afropithecus* based on comparison with new fossil hominoid material, including the type specimen of *Afropithecus turkanensis*, from Kalodirr in northern Kenya (Leakey *et al.*, 1988). Since then, others have also recognized the Moroto hominoid as congeneric or conspecific with *Afropithecus turkanensis*, or as

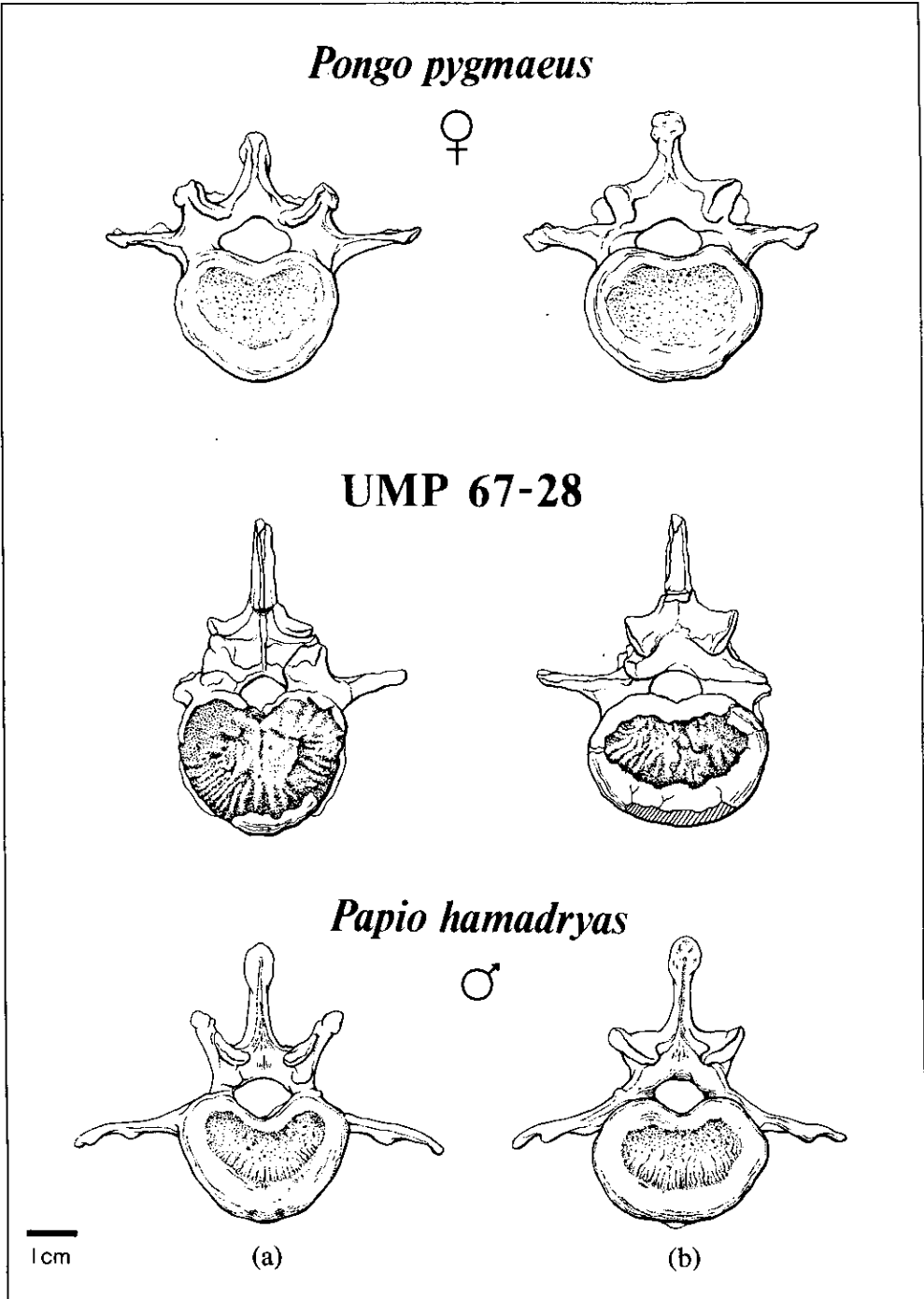


Figure 1a.

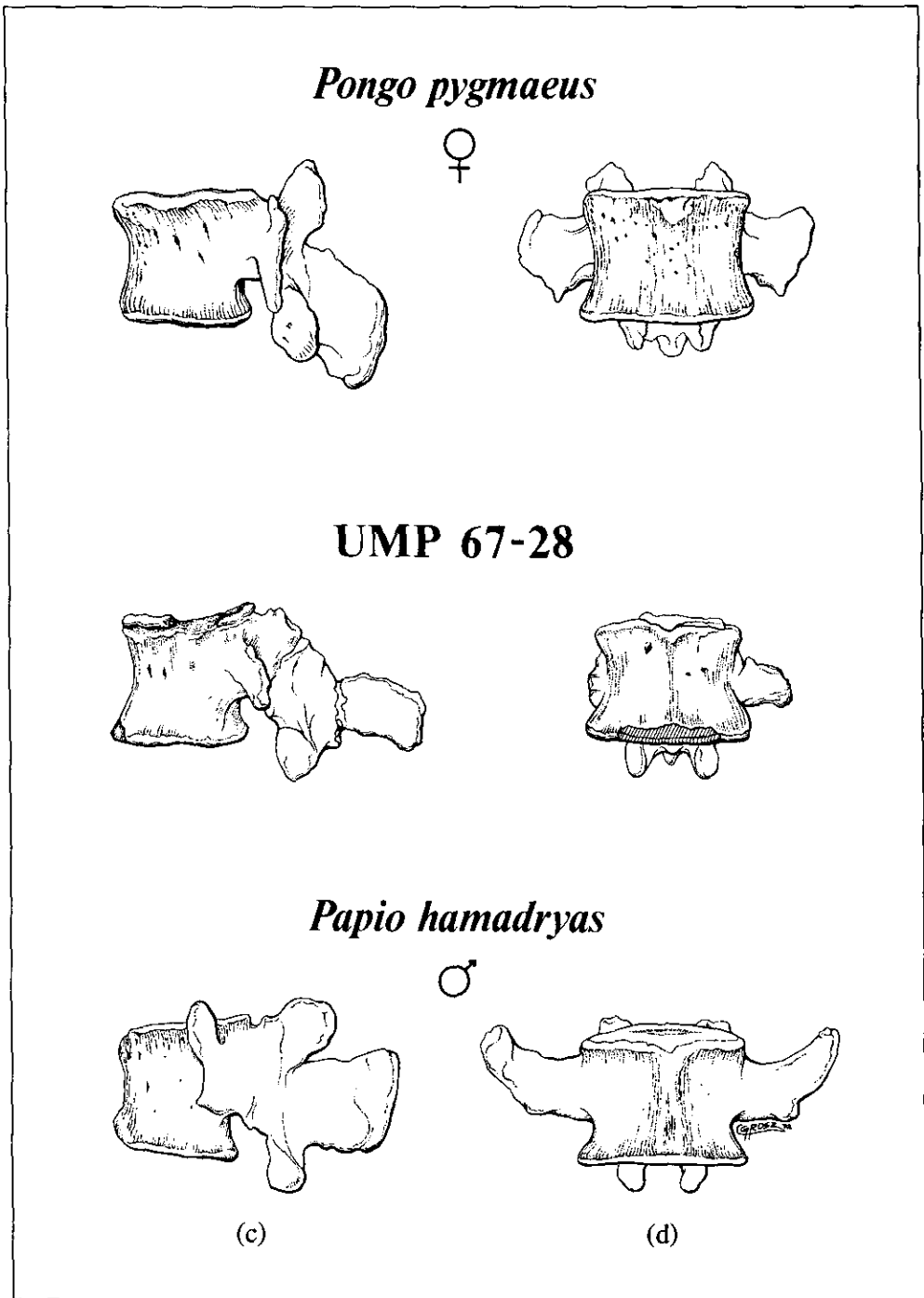


Figure 1b.

Figure 1. Specimen UMP 67-28, compared to vertebrae L VI from a female individual of *Pongo pygmaeus* and a male *Papio hamadryas*. The modern vertebrae are from individuals of body size similar to that inferred for the individual from which UMP 67-28 is derived. Reconstruction of the ventral margin of the vertebral body of UMP 67-28 at its caudal end is indicated by hatched lines. (a) cranial view; (b) caudal view; (c) left lateral view; (d) ventral view.

a close sister taxon (Fleagle, 1988; Harrison, pers. comm.). Also, Andrews (1992) has included the Moroto palate in his newly-erected hominoid tribe Afropithecini. There is little question that the dentition of the Moroto palate is distinct from that of *Proconsul* and more closely resembles the dental remains of *Afropithecus turkanensis* (Andrews & Martin, 1987*a,b*; Fleagle, 1988; Cameron, 1991; Andrews, 1992). Nonetheless, while it is morphologically reasonable to include the Moroto palate in the Afropithecini, as more becomes known about craniodental variation among early-middle Miocene hominoids it is possible that the Moroto hominoid will be recognized as generically distinct from *Afropithecus* (Harrison, pers. comm.). Moreover, Ward (1991, 1993*a*) maintains that the Moroto vertebra *cannot* belong to *Afropithecus*, on the premise that the close appendicular similarities observed for *Proconsul* and *Afropithecus* (from Kalodirr) should be matched by equally similar axial morphologies whereas the Moroto vertebra differs structurally from lumbar vertebrae of *Proconsul*. Although there is no *a priori* reason to assume that all postcranial regions should be identical in *Proconsul* and *Afropithecus*, given that evolutionary change may be mosaic, no direct evidence is available to test Ward's assertion. Refinement of the taxonomic status of the Moroto individual and resolution of its relationship to *Afropithecus turkanensis* will require further comparative study of the Moroto palate and recovery of associated vertebral and appendicular fossils. We therefore prefer to avoid generic designation for the palate and vertebra. In the present study the Moroto fossils together are referred to as the "Moroto hominoid."

UMP 67-28 is the only well preserved specimen of the axial postcranial skeleton known for the Afropithecini. This specimen is especially valuable because fossil vertebrae are poorly represented in collections of Miocene catarrhine primates from East Africa. Since the discovery of the Moroto vertebra, a small number of vertebral elements have been reported for *Proconsul heseloni* and *P. nyanzae* (Walker & Pickford, 1983; Kelley, 1986; Walker & Teaford, 1989; Ward, 1990, 1991, 1993*a*; Ward *et al.*, 1991; Ward *et al.*, 1993). A vertebral body of an indeterminate catarrhine from the early Miocene site of Buluk also has been recovered (Leakey & Walker, 1985; Rose *et al.*, 1992). Walker & Rose (1968) observed that the Moroto vertebra appears to share "eclectic resemblances" with the lumbar vertebrae of modern hominoids, particularly African apes and humans. This opinion, which achieved popular acceptance (Pilbeam, 1972; Simons, 1972), suggests a special phylogenetic relationship between the Moroto hominoid and the African ape and human clade. In their 1968 paper, however, Walker & Rose made clear the need for further investigation of the morphological resemblances of UMP 67-28.

The present study is a more comprehensive comparison between the Moroto vertebra and lumbar vertebrae of extant and fossil catarrhine primates. The structural affinities of UMP 67-28 have implications for the systematics of the species which it represents, especially in regard to other Miocene catarrhines and to extant hominoids. Such systematic information from postcranial morphology is especially critical (Harrison, 1988) for understanding the still largely unresolved phyletic positions and classification of early and middle Miocene catarrhine primates (Andrews & Martin, 1987*a*; Harrison, 1987, 1988, 1993). The special utility of lumbar vertebrae for phylogenetic analysis is indicated by contrasts in musculoskeletal and proportional features of the lower spine between modern representatives of the major catarrhine subtaxa (Schultz, 1930, 1938, 1961; Benton, 1967, 1974; Ankel, 1967*a,b*, 1972; Clauser, 1980). Significantly, UMP 67-28 marks the earliest appearance in the catarrhine fossil record of vertebral morphology resembling that of modern hominoids. Nonetheless, the results of our study do not indicate any special morphological similarity between the Moroto vertebra and the lumbar vertebrae of either African apes or humans. Instead, UMP 67-28 is

unique in its overall morphology and in a number of features resembles all great apes and humans.

The morphology of UMP 67-28 also conveys useful information about lower back function and positional behavior in the hominoid species from which it derives. Among mammals, diversity in the structure of the lumbar region corresponds closely with locomotor and postural differences (Hatt, 1932; Slijper, 1946, 1947; Smith & Savage, 1955; Hildebrand, 1959; Howell, 1965; Gambaryan, 1974). The construction of UMP 67-28 resembles that of lumbar elements from dorsostable- rather than dorsomobile-backed modern catarrhines. Our analysis of the lumbar vertebrae of *Proconsul* suggests that these catarrhines had more flexible lower spines than the Moroto individual and probably employed a different positional repertoire (see also Ward, 1991, 1993a). If the Moroto hominoid is *Afropithecus*, this observation would call into question the idea that *Proconsul* and *Afropithecus* were similar in positional behavior (Leakey *et al.*, 1988).

Materials and methods

Lumbar vertebrae from 186 individuals of 27 extant catarrhine species were selected for comparative study (Table 1). All were wild-caught, and adult on the basis of dental and epiphyseal criteria. The humans sampled are from the Hamann-Todd Collection in Cleveland and were 25–30 years of age at the time of death. The fossil sample is comprised of lumbar vertebrae from the Moroto hominoid (UMP 67-28), *Proconsul nyanzae* (KNM-MW 13142 J, K) (Ward, 1991, 1993a; Ward *et al.*, 1993), and *Proconsul heseloni* (KNM-RU 2036 cz, cd, cy) (Walker & Pickford, 1983; Kelley, 1986; Walker *et al.*, 1993).

To establish comparable vertebral levels among individuals possessing different numbers of lumbar vertebrae, we have grouped together (and labeled with Roman numerals) vertebrae with similar roles in columnar force transmission (Sanders, 1990) and similar positions relative to the branching patterns of their lumbar spinal nerves (Sanders, 1991). For example, lumbar spinal nerves L4 in humans, L3 in great apes, L4 in gibbons, and L5 or L6 in cercopithecoids contribute branches to both the femoral and sciatic nerves (Sonntag, 1924a,b; Danforth & Wilson, 1925; Hartman & Straus, 1933; Raven & Hill, 1950; O’Rahilly, 1986; Sanders, 1991), suggesting equivalency of the fourth lumbar vertebra (L4) of humans and gibbons to the L3 of great apes and the L5 or L6 of cercopithecoids for the purpose of making interspecific comparisons of vertebral dimensions such as neural canal size. In the numbering system summarized in Figure 2, these vertebrae are labeled “L VI.”

UMP 67-28 originally was described as a middle lumbar vertebra (Walker & Rose, 1968). The transition from circular to ovate reniform surfaces between the cranial and caudal ends of the vertebral body in UMP 67-28 (Figure 1) most closely matches the condition found in lower middle lumbar vertebrae of catarrhine primates, such as the L3 vertebra in pongids (in series of L1–4), the L4 element in humans and gibbons (in series of L1–5), and the L5 or L6 level in cercopithecoids (in series of L1–6 or 7). Therefore the Moroto specimen is compared with the penultimate lumbar vertebra of each catarrhine individual in the sample. With the exception of the last lumbar vertebra, dimensional differences between adjacent lumbar vertebrae in a series are usually slight (Sanders, in preparation). Our overall results do not differ materially if UMP 67-28 is compared to modern catarrhine vertebrae more cranial in the lumbar series, e.g., great ape L1 or L2, human and gibbon L2 or L3, and cercopithecoid L4 or L5. In addition to data from the penultimate lumbar level (L VI), results for comparisons between UMP 67-28 and vertebrae from other catarrhines at higher levels (L IV, L V) are given in

Table 1 Modern catarrhine sample used in the study

Species	Abbreviations	n (Male/Female)	Mean body weight ¹ (kg)	
			Male	Female
<i>Homo sapiens</i>	HS	20 (10/10)	70.7	56.5
<i>Pan troglodytes</i>	PT	18 (9/9)	60.0	47.4
<i>Gorilla gorilla</i>	GG	20 (10/10)	169.5	71.5
<i>Pongo pygmaeus</i>	PP	13 (8/5)	86.3	38.7
<i>Hylobates concolor</i>	HC	10 (6/4)	5.6	5.8
<i>Hylobates muelleri</i>	HM	3 (2/1)	5.8	5.7
<i>Mandrillus sphinx</i>	MS	8 (4/4)	26.9	11.5
<i>Mandrillus leucophaeus</i>	ML	1 (1/0)	20.0	—
<i>Papio hamadryas</i> ²	PH	9 (6/3)	28.2	13.6
<i>Theropithecus gelada</i>	TG	1 (1/0)	19.0	—
<i>Cercocebus atbigena</i>	CA	8 (6/2)	9.0	6.4
<i>Cercocebus galeritus</i>	CG	3 (3/0)	10.2	—
<i>Cercocebus torquatus</i>	CT	4 (3/1)	8.0	5.5
<i>Macaca fascicularis</i>	MF	5 (3/2)	4.9	3.1
<i>Macaca nemestrina</i>	MN	3 (1/2)	10.2	6.4
<i>Erythrocebus patas</i>	EP	2 (2/0)	11.1	—
<i>Cercopithecus aethiops</i>	CAc	8 (4/4)	5.4	3.4
<i>Cercopithecus mitis</i>	CM	8 (4/4)	7.6	4.4
<i>Cercopithecus neglectus</i>	CN	2 (2/0)	7.0	—
<i>Colobus angolensis</i>	CoA	3 (2/1)	9.8	9.1
<i>Colobus guereza</i>	CoG	12 (6/6)	9.6	8.0
<i>Colobus polykomos</i>	CoP	8 (4/4)	10.0	7.7
<i>Ptilocolobus badius</i>	PB	3 (3/0)	8.3	—
<i>Presbytis cristata</i>	PC	5 (2/3)	6.9	6.0
<i>Presbytis entellus</i>	PE	2 (1/1)	18.4	11.4
<i>Nasalis larvatus</i>	NL	6 (4/2)	20.4	9.8
<i>Pygathrix nemaeus</i>	PN	1 (1/0)	10.9	—

Sample specimens are from collections at the American Museum of Natural History (New York City), the Field Museum (Chicago), the National Museum of Natural History (Washington, D.C.), and the Cleveland Museum of Natural History (Cleveland).

¹Body weight estimates are taken from the literature (Gingerich *et al.*, 1982; Jungers & Susman, 1984; Harvey & Clutton-Brock, 1985; Uehara & Nishida, 1987; Fleagle, 1988; Markham & Groves, 1990) except for *Homo sapiens* (weights calculated from autopsy reports) and *Cercocebus galeritus* and *Cercocebus torquatus* (weights derived from field records).

²Because their skeletons are indistinguishable, various species of *Papio* are treated as one "superspecies", *Papio hamadryas* (see Szalay & Delson, 1979).

accompanying tables. Vertebral specimens KNM-MW 13142 J and K from *Proconsul nyanzae* were identified as antepenultimate (L V) and penultimate (L VI) lumbar (Ward, 1991, 1993a), respectively, and are included in tabular presentations of vertebral dimensions and indices. As it is difficult to assign vertebral specimens KNM-RU 2036 cz, cd, and cy to their true columnar positions with any certainty, and because none of these vertebrae appear to represent a penultimate lumbar (Ward, pers. comm.), the proportions of these elements are not included in the tables.

Vertebrae were measured using Brown and Sharpe digital calipers accurate to ± 0.02 mm. Some additional measurements were taken from scaled photographs of vertebral specimens using an Optimas video digitizing system (BioScan, Inc., 1988). Each measurement is depicted in Figure 3. Observations on the Moroto vertebra were made on a good quality cast produced by the Wenner-Gren Foundation. The accuracy of the cast was confirmed using published

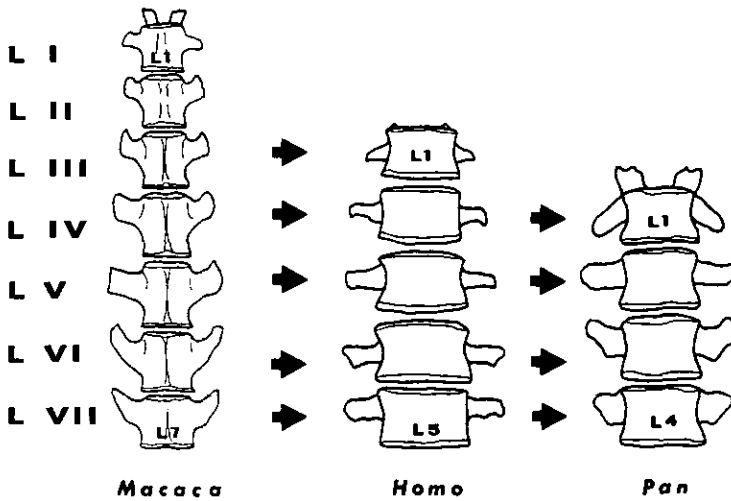


Figure 2. Labelling system for comparing equivalent vertebrae among individuals having lumbar series with different numbers of vertebrae. Equivalent lumbar spinal levels are designated with the same Roman numerals. In this system, for example, vertebrae L6 of *Macaca*, L4 of *Homo*, and L3 of *Pan* are considered equivalent for purposes of morphological comparison and are labeled "L VI".

measurements taken on the original specimen (Walker & Rose, 1968). A small damaged portion of the caudal outline of the centrum of UMP 67-28 was reconstructed (see Figure 1) so that the surface area at that end of the vertebral body could be estimated. The restored area is only 5% of the unrestored caudal surface and did not affect the outcome of proportional analyses. Observations on lumbar vertebrae from *Proconsul nyanzae* and *Proconsul heseloni* were made on good quality casts and were checked against notes and measurements made on original specimens (Ward, 1991). Despite erosional and carnivore damage to cranial and caudal surfaces of the vertebral bodies of KNM-MW 13142 J and K (Ward, 1991, 1993a), they remain largely intact and it is possible to obtain some complete measurements and to estimate most dimensions with confidence.

The caudal outline of the vertebral body served as the basis for a comparison of body shape between UMP 67-28 (represented by the originally reconstructed outline in Figure 1 and two extreme alternative reconstructions, one flattened and one expanded) and 104 penultimate lumbar vertebrae from 11 species of extant catarrhines. Vertebral body shape was described by an elliptic Fourier analysis of 128 points spaced at equal intervals around camera-lucida tracings of each centrum outline. Various Fourier methods can be used to describe shapes of biological specimens (Kaesler & Waters, 1972; Younker & Ehrlich, 1977; Rohlf & Archie, 1984; Ferson *et al.*, 1985), but elliptic Fourier analysis offers practical advantages over other Fourier methods in that the results can be made invariant to size, starting point, orientation, and location of the outlines being analysed. A complete derivation of the elliptic Fourier method can be found in Kuhl & Giardina (1982), while Bookstein *et al.* (1982) discuss some limitations of Fourier methods in general, particularly regarding reification of harmonic coefficients and applications to systematics. Our analysis employed a slight modification of the Fortran program EFA (by J. S. Rohlf & S. Ferson) accompanying Rohlf (1990) to completely standardize all outlines and to compute harmonic coefficients, each of which quantifies an independent aspect of outline shape. For each

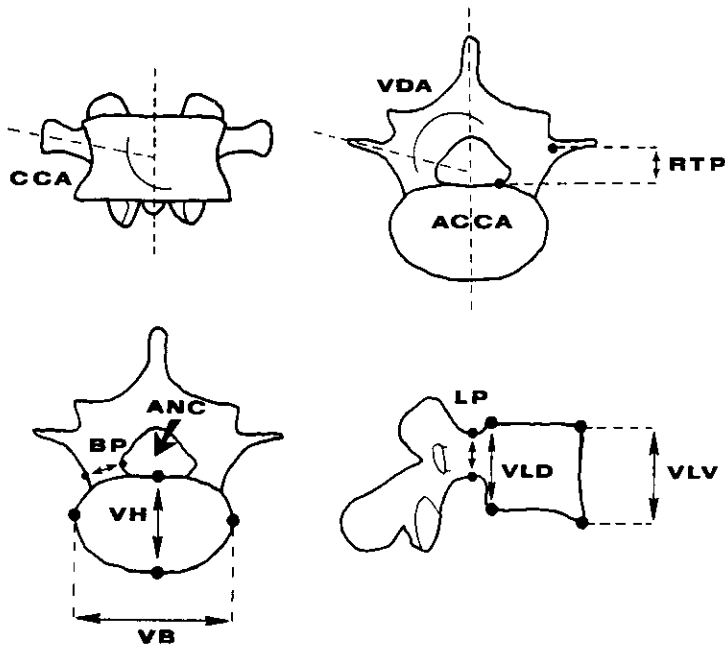


Figure 3. Vertebral measurements used in the study. Abbreviations: VB=vertebral body width, cranial end; VH=vertebral body height, cranial end; VLV=vertebral body length, ventral margin; VLD=vertebral body length, dorsal margin; BP=minimum pedicular width; LP=minimum pedicular length; ACCA=caudal surface area of the vertebral body; ANC=minimum cross-sectional area of the vertebral foramen; RTP=distance of mid-point of the transverse process root from the dorsal margin of the vertebral body; VDA=dorsoventral angle of the transverse process from a sagittal line bisecting the vertebra; CCA=craniocaudal angle of the transverse process formed by the intersection of a line through the middle of the base and center of the tip of the transverse process and a sagittal line bisecting the vertebra.

outline 28 harmonic coefficients, which on average accounted for more than 99% of the information inherent in the outline, were retained as potentially informative shape descriptors. A principal components analysis then summarized the variation in these coefficients among all vertebral outlines.

Some dimensions of lumbar vertebrae in catarrhine primates are intimately linked with body size, and therefore differences in lumbar vertebral morphology between taxa in part are due to size-shape scaling factors (Rose, 1975; Sanders, 1990, in preparation). Conversely, similar-sized organisms that maintain equivalent function are expected to be dimensionally convergent. In the present study, both model I least-squares linear regression and model II reduced major axis regression are used to quantify the relationship between individual vertebral dimensions and body size (Sokal & Rohlf, 1987; Aiello, 1992). Both methods fit straight lines, expressed by the equation $\log Y = \log a + b \log M$, to log-transformed variables (Calder, 1984; Sokal & Rohlf, 1987). The ratio of change between a dimension of interest and body size is given by b , the slope of the line. The goodness-of-fit of data points to the line is indicated by a coefficient of correlation, r^2 , which describes the amount of variation in the dimension that is accounted for by variation in body size (Sokal & Rohlf, 1987). If r^2 is high, the slopes generated using least-squares linear regression (LSR) are quite similar to those generated by reduced major axis regression (RMA) (Jungers, 1985; Aiello, 1992). Because

CENTRUM SURFACE AREA ALLOMETRY IN CATARRHINES VERTEBRAL LEVEL L VI

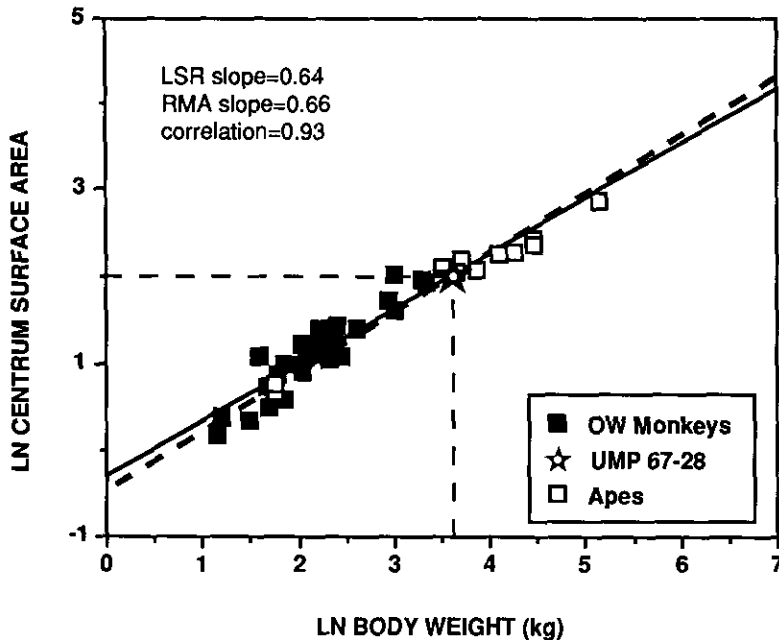


Figure 4. Regression of vertebral body surface area at vertebral level L VI against body weight in extant non-human catarrhines. Data points represent sex-specific means for all non-human taxa listed in Table 1. The solid regression line is the LSR slope; the dashed regression line is the RMA slope. If vertebral body surface area in UMP 67-28 scaled to body weight in the same manner as it does in modern catarrhines, the individual from which UMP 67-28 derives would have weighed approximately 37.6 kg.

there is a close correlation between most vertebral dimensions and body size in catarrhine-primates (Sanders, 1990, 1991), we found few significant differences between LSR and RMA results in our analyses.

As linear dimensions are expected to change in a predictable manner relative to body weight (Jungers, 1985), body weight was chosen to represent size in the regression analyses. Sex-specific mean body weights have been assembled for all sample taxa and are presented in Table 1. Among extant non-human catarrhines, articular surface areas of the lumbar vertebral bodies vary quite closely with body weight and therefore are useful indicators of body size (Figure 4). Because we do not have an independently-calculated body weight for the individual from which UMP 67-28 derives, vertebral body surface area is substituted for body weight in the bivariate plots and proportional analyses that include this fossil specimen.

Results

To illustrate our overall interpretation of UMP 67-28, we have used a principal components analysis to graphically summarize most of the measurements discussed in this section (Figure 5). Our evaluation of all quantitative and qualitative data suggests that UMP 67-28 is morphologically more closely allied with hominoids than with cercopithecoids, whereas the converse is true for the *Proconsul nyanzae* specimen, KNM-MW 13142K. It should be

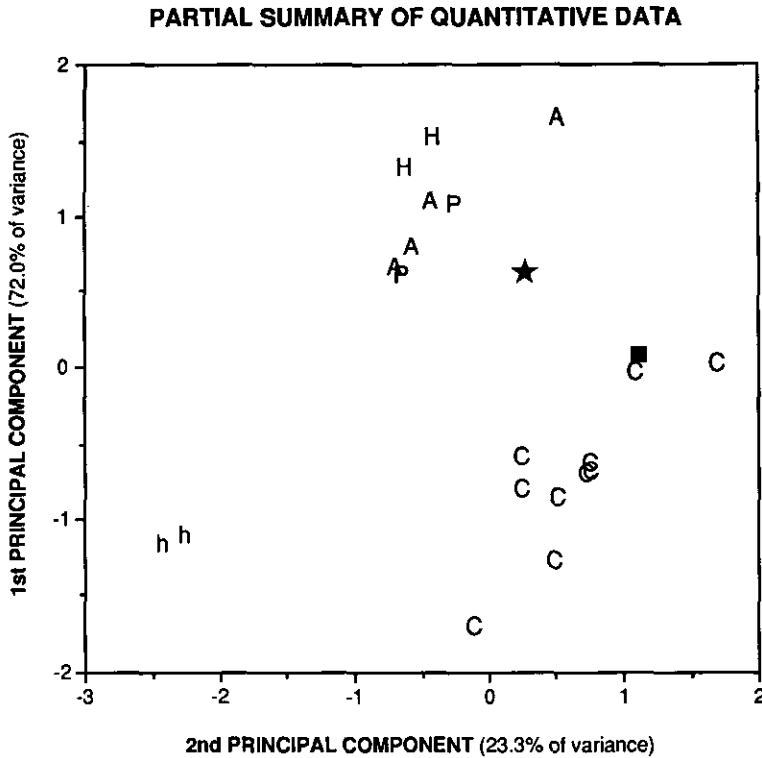


Figure 5. First two principal components summarizing sex-specific averages of nine variables for 10 extant catarrhine species and two fossil individuals. Although PCA does not address polarity, similarities among taxa implied by these variables are compatible with the overall results from the full analysis of individual quantitative and qualitative characters. Symbols: C=cercopithecoids; A=African apes; H=humans; h=hylobatids; P=orang-utans; star=UMP 67-28; square=KNM-MW 13142K. Extant taxa used are HS, PT, GG, PP, HC, HM, MS, PH, CoP, CoG, and CAe (abbreviations in Table 1). Variables analysed are VDA, VB, VH, VLV, BP, LP, RTP, and square roots of ACCA and ANC (abbreviations in Figure 3). All values except RTP and VDA were logged, and all variances were standardized.

emphasized that our conclusions are *not* based on interpretation of the multivariate analysis in Figure 5, which is only a summary of a majority of our quantitative data. Rather, as is detailed in the following paragraphs, we reach our conclusions by considering each variable individually or in conjunction with an estimator of body size.

Vertebral body surface area and body size

Body size differences have a profound effect on vertebral proportions (Sanders, 1990, 1991). Therefore, taxonomic inferences based on the proportions of fossil vertebrae can be misleading (see Rose, 1975) unless made by comparing vertebrae from similar-sized taxa. In the present study, care is taken to compare the dimensions of UMP 67-28 with those of extant catarrhine primates having body weights close to the inferred body weight of the individual from which UMP 67-28 is derived. Walker & Rose (1968) felt that specimen UMP 67-28 is the same general size as lumbar vertebrae from adult male chimpanzees. However, the vertebral body surface area of the Moroto specimen most closely matches mean values for middle lumbar vertebrae of adult female chimpanzees and orang-utans, and is also equaled by areas for some large male baboons (Table 2). If vertebral body surface area in the Moroto hominoid scaled to

Table 2 UMP 67-28 measurements compared with vertebral dimensions of selected catarrhine species at spinal levels L VI, L V, and L IV

Species	Sex	n	ACCA ¹ (cm ²)	VLV ² (mm)	VR ³ (mm)	Spinal level L VI		ANC ⁵ (cm ²)	BP ⁶ (mm)	LP ⁷ (mm)
						VH ⁴ (mm)	BP ⁶ (mm)			
<i>Homo sapiens</i>	F	10	mean	27.8	45.7	30.9	1.94	10.1	13.1	
			range	9.3-12.2	24.7-31.2	40.3-52.8	28.7-33.8	1.42-2.28	6.0-14.1	11.0-14.6
<i>Homo sapiens</i>	M	10	s.d.	0.9	1.7	3.4	0.25	2.1	1.1	
			mean	14.5	28.6	50.6	33.4	2.03	11.5	13.8
<i>Pan troglodytes</i>	F	9	range	11.8-18.2	25.4-31.2	44.6-56.9	1.69-2.72	8.9-14.0	11.1-15.1	
			s.d.	1.9	1.7	3.6	2.5	0.33	1.5	0.9
<i>Pan troglodytes</i>	M	9	mean	8.0	22.5	34.5	0.94	7.5	14.0	
			range	5.6-11.0	18.5-26.7	31.6-41.7	21.0-29.1	0.61-1.29	6.0-9.4	11.4-18.2
<i>Pan troglodytes</i>	M	9	s.d.	1.3	1.5	1.6	0.14	0.9	2.0	
			mean	9.4	23.4	37.5	28.3	1.02	8.0	13.9
<i>Pongo pygmaeus</i>	F	5	range	6.9-13.5	21.0-25.9	31.6-44.2	0.68-1.37	6.2-9.0	11.7-17.4	
			s.d.	1.7	1.5	3.4	3.2	0.16	0.9	1.5
<i>Papio hamatryas</i>	M	6	mean	7.7	23.3	33.5	0.91	7.7	13.5	
			range	6.7-9.3	22.2-25.3	32.0-35.2	24.3-27.1	0.72-1.05	6.8-8.3	11.1-16.3
<i>Papio hamatryas</i>	M	6	s.d.	1.0	1.2	1.2	0.15	0.6	2.5	
			mean	7.0	26.0	33.3	24.0	0.56	5.4	18.3
<i>Amandillus sylvanus</i>	M	4	range	5.8-8.9	24.2-27.7	30.1-36.6	0.41-0.74	4.4-5.9	15.1-21.7	
			s.d.	1.0	1.3	1.9	2.5	0.13	0.7	2.5
UMP 67-28	?	1	mean	7.0	30.9	33.7	0.49	5.6	20.7	
			range	5.5-8.5	29.1-33.5	30.6-37.7	20.0-27.4	0.42-0.58	4.4-6.7	19.7-21.6
KINM-MW 13142K (<i>Proconsul nyanzae</i>)	?	1	s.d.	1.1	1.7	2.6	0.06	0.9	0.8	
			mean	7.6	27.4	33.7	24.4	0.70	8.0	18.1
				29.0	30.0	21.0	0.80	5.5	20.2	

Table 2 UMP 67-28 measurements compared with vertebral dimensions of selected catarrhine species at spinal levels L VI, L V, and L IV

Species	Sex	n	mean range s.d.	ACCA ¹ (cm ²)	VLV ² (mm)	VB ³ (mm)	Spinal level L V		ANC ⁵ (cm ²)	BP ⁶ (mm)	LP ⁷ (mm)
							VH ¹ (mm)	VH ¹ (mm)			
<i>Homo sapiens</i>	F	10	mean range s.d.	10.8 9.4-12.0 0.8	27.3 24.3-30.4 1.5	43.4 38.3-51.4 3.3	30.2 26.7-34.5 2.2	1.86 1.57-2.17 0.21	8.7 4.3-12.1 2.1	13.9 12.1-16.5 1.1	
<i>Homo sapiens</i>	M	10	mean range s.d.	14.4 11.3-18.1 1.8	28.0 25.6-30.4 1.4	48.7 43.0-55.1 3.3	32.0 29.3-39.1 2.5	1.92 1.51-2.51 0.29	9.8 7.2-12.1 1.3	14.4 12.9-16.5 1.2	
<i>Pan troglodytes</i>	F	9	mean range s.d.	7.5 5.9-9.2 1.2	22.1 18.7-25.6 2.0	33.5 30.0-37.7 2.3	25.1 22.6-28.1 1.8	1.05 0.83-1.38 0.16	7.3 5.6-11.1 1.5	14.3 11.9-17.4 1.9	
<i>Pan troglodytes</i>	M	9	mean range s.d.	9.0 6.6-12.4 1.5	22.0 19.8-24.1 1.2	36.3 30.9-41.0 2.9	27.5 23.1-32.3 2.7	1.11 0.82-1.38 0.15	8.4 6.1-10.2 1.1	14.9 13.0-16.4 1.1	
<i>Pongo pygmaeus</i>	F	5	mean range s.d.	7.5 7.0-8.7 0.6	22.9 20.9-25.5 1.6	32.4 30.2-34.2 1.5	24.5 23.4-25.4 0.7	1.00 0.77-1.35 0.19	8.6 6.4-10.2 1.3	14.4 11.2-16.8 2.3	
<i>Papio hamadryas</i>	M	6	mean range s.d.	6.7 5.3-8.5 1.0	26.5 24.7-27.8 1.4	33.0 30.7-36.5 2.0	23.5 20.6-26.5 2.1	0.76 0.46-1.07 0.22	4.3 3.1-5.2 0.9	18.0 15.6-19.1 1.3	
<i>Mandrillus sphinx</i>	M	4	mean range s.d.	6.8 5.4-8.5 1.2	30.5 28.0-32.9 2.0	32.7 29.9-36.7 2.9	23.7 20.1-25.8 2.5	0.65 0.49-0.77 0.13	3.6 3.1-4.0 0.4	21.4 19.8-22.6 1.3	
UMP 67-28	?	1		7.6	27.4	33.7	24.4	0.70	8.0	18.1	
K.N.M-MW 13142] (<i>Proconsul nyanzai</i>)	?	1		—	27.3	30.0	22.1	—	4.5	22.5	

Table 2 UMP 67-28 measurements compared with vertebral dimensions of selected catarrhine species at spinal levels L VI, L V, and L IV

Species	Sex	n	ACCA ¹ (cm ²)	Spinal level L IV				BP ⁶ (mm)	ANC ⁵ (cm ²)	LP ⁷ (mm)
				VLV ² (mm)	VB ³ (mm)	VH ⁴ (mm)	BP ⁶ (mm)			
<i>Homo sapiens</i>	F	10	mean	26.8	41.5	28.4	7.1	2.08	14.3	
			range	23.5-29.3	38.0-49.1	25.4-32.4	4.2-10.0	1.68-2.56	11.7-16.0	
<i>Homo sapiens</i>	M	10	s.d.	1.6	2.9	2.0	1.8	0.30	1.2	
			mean	26.9	46.7	31.7	8.5	2.20	14.9	
<i>Pan troglodytes</i>	F	9	range	24.5-29.0	41.5-52.7	27.4-38.0	6.6-10.7	1.90-2.77	13.3-18.4	
			s.d.	1.5	2.9	2.7	1.2	0.28	1.2	
<i>Pan troglodytes</i>	M	9	mean	21.1	32.1	23.6	6.4	1.11	14.7	
			range	18.5-23.4	29.3-34.6	20.9-26.4	4.9-9.2	0.98-1.23	11.8-16.9	
<i>Pongo pygmaeus</i>	M	9	s.d.	1.5	1.8	1.8	1.3	0.10	1.5	
			mean	20.9	34.5	25.5	8.2	1.21	14.0	
<i>Pongo pygmaeus</i>	F	5	range	18.5-23.2	30.2-38.5	21.8-29.8	6.7-9.3	0.98-1.42	12.8-15.8	
			s.d.	1.4	2.7	2.6	0.8	0.12	0.9	
<i>Papio hamadryas</i>	M	6	mean	22.4	31.6	23.6	7.7	1.14	14.2	
			range	21.3-24.3	28.7-33.2	22.3-24.6	7.0-8.6	0.89-1.45	11.0-15.9	
<i>Mandrillus sphinx</i>	M	4	s.d.	1.4	1.7	0.9	0.6	0.19	1.9	
			mean	25.4	32.4	22.6	3.5	0.87	17.9	
<i>Mandrillus sphinx</i>	M	4	range	22.1-27.2	30.0-35.7	20.4-27.6	2.6-4.5	0.67-1.16	16.4-20.0	
			s.d.	2.1	1.9	2.6	0.8	0.21	1.3	
UMP 67-28	?	1	mean	29.5	32.0	23.3	3.1	0.74	20.8	
			range	5.1-8.0	29.7-36.5	19.2-25.3	2.5-4.0	0.65-0.83	19.2-22.0	
UMP 67-28	?	1	s.d.	1.9	3.0	2.8	0.7	0.08	1.3	
			mean	27.4	33.7	24.4	8.0	0.70	18.1	

The extant non-human species listed were chosen on the basis of similarity in body size to the individual from which UMP 67-28 is derived. Bold means indicate samples from which UMP 67-28 differs with 95% confidence (test in Sokal & Rohlf, 1981: 229-231).

¹ACCA = caudal surface area, vertebral body; ²VLV = length of vertebral body, ventral margin; ³VB = width of vertebral body; ⁴VH = height of vertebral body; ⁵ANC = cross-sectional area, vertebral foramen; ⁶BP = pedicular width; ⁷LP = pedicular length.

body weight in the same manner as it does in modern catarrhines, the individual from which UMP 67-28 derives would have weighed 37.6 kg (Figure 4) with 95% confidence limits ranging from 33.8–43.4 kg, similar in bulk to females of *Pan troglodytes* and *Pongo pygmaeus* and to big males of *Papio hamadryas* and *Mandrillus sphinx*. In comparison with other Miocene catarrhine primates, the Moroto individual is most similar in estimated size to *Proconsul major* (Gingerich *et al.*, 1982) and *Afropithecus turkanensis* (Harrison, 1993).

In overall size, the lumbar vertebrae from *Proconsul nyanzae* (KNM-MW 13142) are smaller than UMP 67-28 and are similar to lumbar vertebrae from male proboscis monkeys (*Nasalis larvatus*) (Sanders, in preparation), which weigh an average of about 20 kg (Fleagle, 1988). Based on scaling patterns observed for modern catarrhines, surface area of the penultimate lumbar vertebral body from KNM-MW 13142 suggests a body weight of 17.8 kg with 95% confidence limits ranging from 16.0–19.4 kg. Augmenting caudal body surface area by a very generous twenty percent to account for damage to the penultimate lumbar vertebral body in KNM-MW 13142 increases estimated body weight to 23.4 kg, with 95% confidence intervals between 22.6 and 29.4 kg. These results differ from earlier estimations of 31–36 kg for this individual, but body weight estimations from augmented surface areas overlap with species estimates for *P. nyanzae* of 26–38 kg, calculated from femoral proportions (Ruff *et al.*, 1989). Regression analyses of dimensions from different parts of the skeleton commonly result in disparate body weight predictions for fossil animals (Gingerich, 1990; Jungers, 1990). As they both transmit body weight and share close relationships with body mass (Ruff, 1990; Ruff *et al.*, 1989; Sanders, in preparation), cross-sectional and articular dimensions of vertebrae and femora should each be reliable predictors of body weight in fossils. It is possible, however, that either vertebral or femoral dimensions, or both, do not scale with body weight in *P. nyanzae* in the same fashion as in extant catarrhines. Differences between past and present results indicate a need for additional study of the relationship between skeletal dimensions and body weight in *P. nyanzae*.

Walker & Pickford (1983) approximated a body weight of approximately 11 kg for *Proconsul heseloni* by matching the skeleton of KNM-RU 2036 with skeletons of extant catarrhines. Lumbar vertebrae from KNM-RU 2036 are comparable in overall size with lumbar elements from modern catarrhines of slightly smaller mean body weights, such as gibbons and males of the species *Cercopithecus neglectus*, ranging in size from about 5 to 8 kg (Sanders, in preparation). This observation is slightly closer to body weight estimates from regressions of femoral dimensions of 8–10 kg for this species (Ruff *et al.*, 1989; Ruff, 1990).

Vertebral body shape

Caudal outline. While the harmonic coefficients from elliptic Fourier analysis describe aspects of shape within a single outline, a principal components analysis summarizes the variation among these coefficients over the entire sample of L VI caudal body outlines (Figure 6). Principal components analysis of harmonic coefficients reveals large amounts of intraspecific variation in outline shape. Despite this, UMP 67-28 shows a pattern of variation in coefficients, as summarized on the first principal component, that is distinct from that of all taxa except *Pan* and *Papio*. A single outline from an individual having six lumbar vertebrae extends the range of *Papio* to overlap UMP 67-28, but it is not justifiable to dismiss this specimen as an outlier because the specimen shows no apparent morphological anomalies and six lumbar vertebrae is a commonly observed condition in *Papio*. Specimens plotting farthest from the origin on each component make the greatest contribution to the aspects of shape variation summarized by that component over the entire sample. In contrast, specimens plotting at the origin are

SUMMARY OF ELLIPTIC FOURIER SHAPE DESCRIPTORS

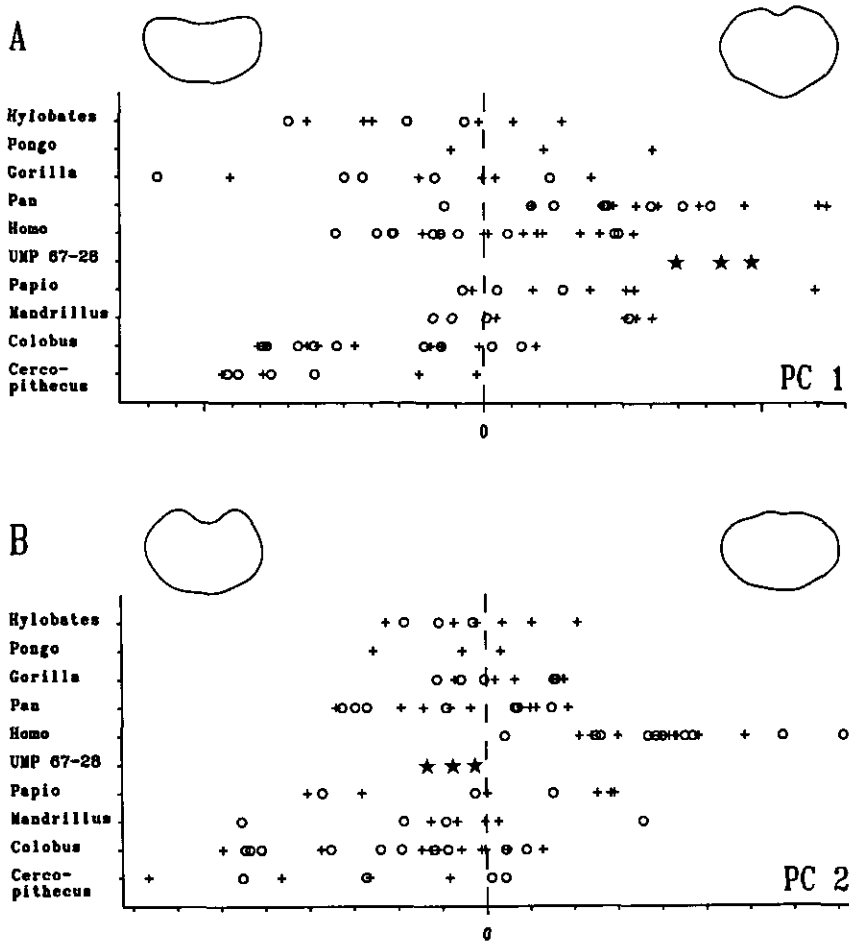


Figure 6. Specimen scores on first 2 principal components from analysis of 28 Fourier harmonic coefficients characterizing the outlines of caudal vertebral body surfaces. The original and 2 extreme reconstructions of the UMP 67-28 vertebral body outline are included in the analysis. Component axes are marked at 0.01 intervals. Crosses (+) are male individuals, open circles (O) are females. Outlines depict representative specimens with low and high scores on the associated axis, but the shapes shown also reflect some influence of other axes and therefore are not exact representations of the shapes contrasted by variation along the axis. (A) 1st principal component, accounting for 62.0% of variance in harmonic coefficients. UMP 67-28 overlaps only ranges of values observed for *Pan* and *Papio*, indicating that all other sampled taxa differ from UMP 67-28 in vertebral body outline shape. (B) 2nd principal component, accounting for 18.3% of variance.

uncorrelated with the particular aspects of shape summarized by a component. Since UMP 67-28 scores strongly on the first principal component and is overlapped only by some *Pan* and *Papio* specimens, all of the other taxa are shown to differ from UMP 67-28 in the aspects of shape summarized by the first principal component. UMP 67-28 continues to fall within the ranges of both *Pan* and *Papio* on the second through fifth components, which together with the first summarize 92% of the variation in harmonic coefficients among all outlines. Thus,

although the first principal component clearly shows that UMP 67-28 differs from all taxa except *Pan* and *Papio*, the second through fifth components fail to further distinguish UMP 67-28 from either *Pan* or *Papio* in the pattern of variation of its harmonic coefficients.

The Moroto specimen also falls within the range of values for *Pan* and *Papio* in all harmonic coefficients having the strongest loadings on the first five axes, suggesting that individuals within the three taxa share similar shape descriptors rather than just showing similar patterns of variation among descriptors. Rohlf (1990) demonstrated that the choice of method for measuring outline shape is essentially arbitrary and that different methods may produce different discriminations and distances between shapes. It is therefore difficult to make general statements about the degree to which UMP 67-28 differs in vertebral body outline from the lumbar vertebrae of other catarrhines. Nonetheless, it can be concluded that in the elliptic Fourier characterization of vertebral body outline shape, the Moroto specimen does not exclusively resemble either hominoids or cercopithecoids, but rather resembles some species having similar body weights, regardless of phylogenetic affinity.

Vertebral body surfaces. One other aspect of vertebral body surface morphology also fails to distinguish UMP 67-28 as cercopithecoid- or hominoid-like. Hominoids typically display ring apophyses of the cranial and caudal body surfaces, formed of thickened compacta. Walker & Rose (1968) draw attention to apparent ring apophyses at both ends of the body of UMP 67-28 (Figure 1). These, however, could be artifacts of preservation. The thin middle portion of cercopithecoid body endplates frequently is detached when vertebrae become disarticulated; the remaining endplate margins resemble the ring apophyses of hominoids (Figure 1).

Width, height, and length. Vertebral body shape, as expressed by the ratio of width to length, varies in modern catarrhines as a function of positional adaptations and body size. In association with the greater importance of dorsoventral flexion of the spine during running and leaping (Fleagle, 1977; Wells *et al.*, 1977; Hurov, 1982, 1985, 1987), cercopithecoids possess relatively more elongate lumbar regions and vertebral bodies than do hominoids (Figure 7; also Mivart, 1865; Schultz, 1938, 1961; Benton, 1967, 1974).

Because non-human catarrhines share a similar, close scaling of lumbar vertebral body width and height with body weight (Table 3), these dimensions are very similar in Old World monkeys and apes of equivalent body weights (Table 2). Differences in overall vertebral body shape between cercopithecoids and hominoids, exclusive of body-size effects, are due primarily to variation in length (Table 2). Although in non-human catarrhines as a whole the relative lengths of lumbar vertebrae and the lumbar region are reduced with increasing body size (Jungers, 1984; Sanders, 1990, in preparation), *y*-intercept differences between separate regressions for cercopithecoids and hominoids indicate that at equivalent body sizes, cercopithecoids are predicted to have longer lumbar bodies than hominoids (Table 3). The r^2 for regression of cercopithecoid lumbar vertebral body length against body weight is low, and consequently the results of LSR and RMA analyses differ substantially for this dimension. In least-squares regression, cercopithecoids exhibit strong negative scaling for lumbar vertebral body length relative to body weight (observed $b=0.19$; expected $b=0.33$). In reduced major axis regression, cercopithecoids scale isometrically for lumbar vertebral body length (observed $b=0.32$; expected $b=0.33$), but data points for large baboons fall below the line of regression (Sanders, in preparation). Both analyses, then, indicate that the largest modern cercopithecoids have relatively shorter lumbar vertebral bodies than more diminutive monkeys, possibly in response to the dangers of greater

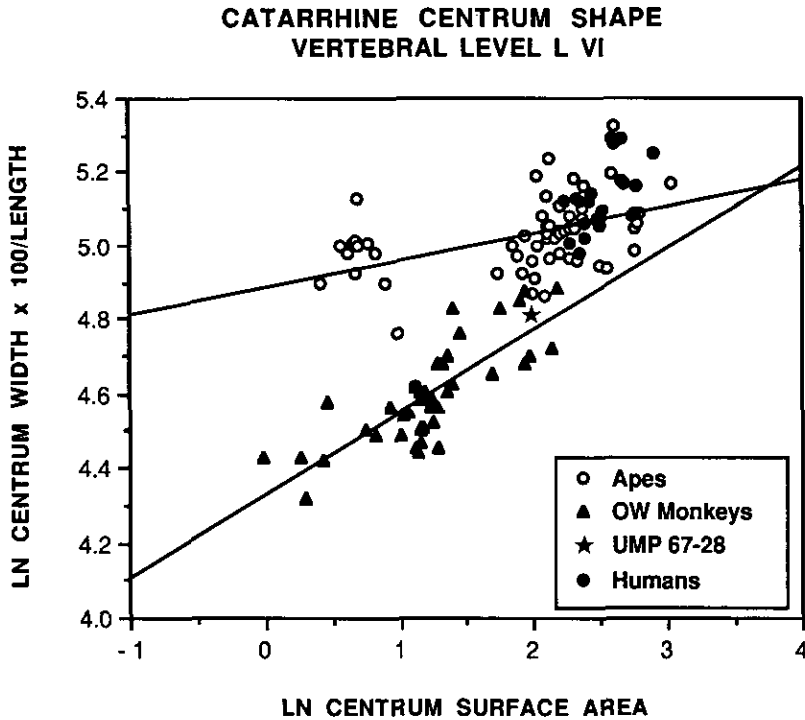


Figure 7. Bivariate plot of vertebral body shape and vertebral body surface area at vertebral level L VI for catarrhine primates. Vertebral body shape is expressed by the ratio of vertebral body width to length, $VB/VLV, \times 100$ (see Figure 3). Data points represent individual values for the following taxa: HS, PT, GG, PP, HC, HM, MS, PH, CoP, CoG, CAe (abbreviations in Table 1). The straight lines represent correlative trends between vertebral body shape and body size, as inferred from vertebral body surface area, for hominoids and cercopithecoids. In this plot, UMP 67-28 clusters with male baboons.

longitudinal bending stresses in vertebral bodies (and the lumbar column as a whole) with increasing body size (Rose, 1975).

Compressive force along the spine is primarily transmitted through the bodies of vertebrae (Rockwell *et al.*, 1938; Young, 1962). Ventroflexion of the lower back during running, bounding, and leaping displaces the application point of compression from the centers of lumbar bodies slightly toward their ventral margins. Moving the point of compression more than a short distance from the center of a vertebral body produces bending stress (Badoux, 1974). Resistance to bending moments is calculated as bh^2/l (b =width, h =height, l =length) (Slijper, 1946; Clauser, 1980), and can be increased by reducing vertebral body length, or by expanding the dimensions of width and height. Vertebral height is the most critical dimension for resistance to bending moments in the sagittal plane, and correspondingly in cercopithecoids (and other non-human catarrhines) vertebral height is positively allometric in relation to increasing body weight (Table 3; Sanders, in preparation). Heavy-bodied cercopithecoids such as baboons also reduced bending stresses along the back as a whole by limiting lower-spine mobility (see Rose, 1977).

The shape of the vertebral body in the Moroto lumbar vertebra is not particular to extant pongids (*contra* Walker & Rose, 1968). Although the width (and height) of the Moroto vertebra is close to mean values for female chimpanzees and orang-utans, and for male baboons, the

Table 3 Regression of \log_{10} body weight (kg) on lumbar vertebral dimensions at spinal level L VI

Dimension	Group	Analysis ⁶	r ²	y-intercept	Observed slope (b)	Expected slope (b) ⁷
ACCA ¹	Non-human catarrhines	LSR	0.93	-0.29	0.64	0.67
		RMA		-0.35	0.66	
VB ²	Non-human catarrhines	LSR	0.92	2.46	0.30	0.33
		RMA		2.43	0.31	
VH ³	Non-human catarrhines	LSR	0.90	1.80	0.37	0.33
		RMA		1.75	0.39	
VI.V ⁴	Non-human catarrhines	LSR	0.25	2.82	0.11	0.33
		RMA		2.49	0.24	
VLV	Non-human hominoids	LSR	0.95	2.08	0.27	0.33
		RMA		2.06	0.28	
VLV	Cercopithecoids	LSR	0.36	2.71	0.19	0.33
		RMA		2.44	0.32	
ANC ⁵	Non-human catarrhines	LSR	0.88	-2.13	0.52	0.67
		RMA		-2.22	0.56	

The species used in the regressions are listed in Table 1.

¹ACCA=caudal surface area of the vertebral body; ²VB=vertebral body width; ³VH=vertebral body height; ⁴VLV=vertebral body length, ventral margin; ⁵ANC=cross-sectional area, vertebral foramen; ⁶LSR=Least Squares (Model I) Regression; RMA=Reduced Major Axis (Model II) Regression; ⁷the expected slope is the regression coefficient predicted by geometric similarity (McMahon, 1973).

ventral length of the Moroto vertebra is significantly greater than mean lengths and exceeds ranges of values recorded for similar-sized pongids, and is most similar to vertebral body lengths of male baboons (Table 2). Thus, the width/length index of the vertebral body of UMP 67-28 is somewhat low compared to hominoids of similar body size (Table 4; also Rose, 1975: Table 3) and indicates a shape more like a lumbar vertebra of a large-bodied cercopithecoid (Figure 7). Both absolutely and relative to vertebral body surface area and inferred body weight, the lumbar vertebral bodies of KNM-MW 13142 (*Proconsul nyanzae*) are longer than those of extant hominoids and are similar to those of extant cercopithecoids (Table 2 and Table 4; also Ward, 1991, 1993a). The lumbar vertebral bodies of KNM-RU 2036 (*P. heseloni*) also are proportioned like those of cercopithecoids (Velte, 1987; Ward, 1991).

Wedging. Vertebral wedging, described by the ratio of ventral to dorsal length of vertebral bodies, does not distinguish Old World monkeys from apes at vertebral levels L VI-IV (Table 4; Sanders, in preparation) and is unremarkable in the Moroto specimen compared with other catarrhine primates. The Moroto vertebra, with a wedging index of 96, is ventrally-wedged and differs only from human specimens, which usually have index values above 100 (dorsal wedging) for centra at the penultimate lumbar level (Table 4; Sanders, 1990). The estimated degree of centrum wedging at the penultimate lumbar level in *Proconsul nyanzae* is close to that of the Moroto specimen, but is much lower at the antepenultimate lumbar level (Table 4), though because of carnivore damage it is difficult to gauge the accuracy of these estimates. If correct, wedging indices for KNM-MW 13142 suggest that ventral/dorsal ratios of vertebral body length in *P. nyanzae* lumbar match the proportions of comparable vertebrae in cercopithecoids as well as in non-human hominoids (Table 4; Sanders, in preparation). Vertebral bodies cd, cy, and cz of individual KNM-RU 2036 (*Proconsul heseloni*) are also ventrally-wedged, with index values of 89-92. These specimens also resemble comparable

Table 4 Comparative vertebral indices of selected species at spinal levels L VI, L V, and L IV

Species	Sex	n	Spinal level L VI				
			Vertebral body shape index ¹	Pedicular robusticity index ²	Relative position, transverse process ³	Vertebral body wedging index ⁴	
<i>Homo sapiens</i>	F	10	mean	165	79	-26	106
			range	145-196	61-110	(-18)-(-34)	98-114
			s.d.	14	16	7	5
<i>Homo sapiens</i>	M	10	mean	177	85	-20	104
			range	159-199	65-100	(-13)-(-27)	96-113
			s.d.	15	10	5	4
<i>Pan troglodytes</i>	F	9	mean	154	52	-19	93
			range	129-188	42-70	(-10)-(-28)	83-99
			s.d.	16	8	7	6
<i>Pan troglodytes</i>	M	9	mean	161	57	-18	93
			range	138-174	39-73	(-14)-(-21)	80-99
			s.d.	17	11	4	7
<i>Gorilla gorilla</i>	F	10	mean	153	63	-19	99
			range	136-177	44-80	(-13)-(-23)	96-103
			s.d.	12	11	4	3
<i>Gorilla gorilla</i>	M	10	mean	166	76	-14	95
			range	146-179	54-88	(-7)-(-24)	88-99
			s.d.	11	16	6	4
<i>Pongo pygmaeus</i>	F	5	mean	143	53	-14	91
			range	130-154	48-61	(-9)-(-21)	87-97
			s.d.	10	5	5	4
<i>Pongo pygmaeus</i>	M	8	mean	162	62	-12	92
			range	139-181	55-77	(-6)-(-19)	86-97
			s.d.	16	12	4	4
<i>Hylobates</i> spp.	F	5	mean	142	37	+12	94
			range	117-169	28-47	(+10)-(+14)	93-97
			s.d.	16	7	2	2
<i>Hylobates</i> spp.	M	8	mean	143	37	+4	92
			range	134-149	26-45	(-9)-(+11)	85-98
			s.d.	7	8	6	7
<i>Papio hamadryas</i>	M	6	mean	128	30	+25	94
			range	124-132	25-35	(+19)-(+35)	89-100
			s.d.	4	5	5	5
<i>Mandrillus sphinx</i>	M	4	mean	109	27	+25	91
			range	105-112	22-32	(+19)-(+30)	88-93
			s.d.	3	4	4	3
UMP 67-28 (<i>Afropithecus</i> sp.)	?	1		123	44	-11	96
KNM-MW 13142K (<i>Proconsul nyanzae</i>)	?	1		103	27	+14	94

Species	Sex	n	Spinal level L V				
			Vertebral body shape index ¹	Pedicular robusticity index ²	Relative position, transverse process ³	Vertebral body wedging index ⁴	
<i>Homo sapiens</i>	F	10	mean	159	65	-36	103
			range	138-179	49-88	(-25)-(-45)	96-113
			s.d.	11	14	7	5
<i>Homo sapiens</i>	M	10	mean	175	67	-26	100
			range	153-206	44-82	(-16)-(-33)	90-105
			s.d.	14	11	6	4

continued overleaf

Table 4 Comparative vertebral indices of selected species at spinal levels L VI, L V, and L IV

Species	Sex	n	Vertebral body shape index ¹	Spinal level L V			Vertebral body wedging index ⁴
				Pedicular robusticity index ²	Relative position, transverse process ³		
<i>Pan troglodytes</i>	F	9 mean	152	52	- 22	92	
		range	138-178	39-67	(- 14)-(- 34)	84-101	
		s.d.	14	10	7	6	
<i>Pan troglodytes</i>	M	9 mean	165	54	- 20	88	
		range	149-185	37-70	(- 14)-(- 23)	83-93	
		s.d.	12	10	7	3	
<i>Gorilla gorilla</i>	F	10 mean	150	53	- 20	99	
		range	127-169	34-73	(- 15)-(- 25)	93-106	
		s.d.	14	12	4	3	
<i>Gorilla gorilla</i>	M	10 mean	163	65	- 16	96	
		range	146-190	50-78	(- 11)-(- 24)	86-104	
		s.d.	14	11	5	5	
<i>Pongo pygmaeus</i>	F	5 mean	140	56	- 14	90	
		range	126-154	50-62	(- 10)-(- 18)	84-94	
		s.d.	10	6	3	4	
<i>Pongo pygmaeus</i>	M	8 mean	159	62	- 13	92	
		range	140-180	44-73	(- 7)-(- 20)	83-100	
		s.d.	13	9	4	5	
<i>Hylobates</i> spp.	F	5 mean	134	33	+11	95	
		range	112-158	24-38	(+9)-(+13)	90-99	
		s.d.	17	6	2	4	
<i>Hylobates</i> spp.	M	8 mean	136	31	+7	91	
		range	123-152	21-39	(- 7)-(+13)	84-97	
		s.d.	10	5	5	4	
<i>Papio hamadryas</i>	M	6 mean	126	24	+28	92	
		range	121-133	17-31	(+22)-(+39)	85-98	
		s.d.	5	6	6	6	
<i>Mandrillus sphinx</i>	M	4 mean	107	17	+30	90	
		range	104-112	16-19	(+28)-(+32)	87-95	
		s.d.	4	1	2	4	
UMP 67-28	?	1	123	44	- 11	96	
KNM-MW 13142J (<i>Proconsul nyanzae</i>)			110	20	+16	85	

Species	Sex	n	Vertebral body shape index ¹	Spinal level L IV			Vertebral body wedging index ⁴
				Pedicular robusticity index ²	Relative position, transverse process ³		
<i>Homo sapiens</i>	F	10 mean	155	51	- 39	100	
		range	130-176	33-68	(- 28)-(- 48)	92-105	
		s.d.	11	11	7	3	
<i>Homo sapiens</i>	M	10 mean	174	56	- 31	95	
		range	156-213	33-71	(- 21)-(- 39)	87-102	
		s.d.	14	10	5	4	
<i>Pan troglodytes</i>	F	9 mean	153	44	- 28	93	
		range	140-182	32-65	(- 15)-(- 36)	86-99	
		s.d.	13	10	7	4	
<i>Pan troglodytes</i>	M	9 mean	166	59	- 21	90	
		range	147-198	45-70	(- 11)-(- 31)	87-95	
		s.d.	15	8	7	6	
<i>Gorilla gorilla</i>	F	10 mean	154	58	- 19	95	
		range	141-166	53-62	(- 16)-(- 24)	92-100	
		s.d.	10	4	3	3	

Table 4 Comparative vertebral indices of selected species at spinal levels L VI, L V, and L IV

Species	Sex	n	Vertebral body shape index ¹	Spinal level L IV			Vertebral body wedging index ⁴
				Pedicular robusticity index ²	Relative position, transverse process ³		
<i>Gorilla gorilla</i>	M	10	mean	155	62	-17	97
			range	138-177	51-75	(-13)-(-20)	91-106
			s.d.	13	9	4	5
<i>Pongo pygmaeus</i>	F	5	mean	145	50	-23	92
			range	130-153	46-54	(-18)-(-32)	87-95
			s.d.	9	3	6	3
<i>Pongo pygmaeus</i>	M	8	mean	158	62	-22	93
			range	138-178	44-77	(-10)-(-29)	83-100
			s.d.	16	10	6	6
<i>Hylobates</i> spp.	F	5	mean	136	32	+10	92
			range	118-151	26-37	(+9)-(+12)	88-95
			s.d.	14	5	2	3
<i>Hylobates</i> spp.	M	8	mean	144	29	+7	89
			range	129-160	23-37	(-11)-(+16)	81-96
			s.d.	10	5	6	5
<i>Papio hamadryas</i>	M	6	mean	128	20	+35	91
			range	116-138	14-26	(+30)-(+43)	84-95
			s.d.	9	5	4	4
<i>Mandrillus sphinx</i>	M	4	mean	109	15	+41	91
			range	103-117	12-18	(+32)-(+48)	87-93
			s.d.	7	3	7	2
UMP 67-28	?	1		123	44	-11	96

¹The vertebral body shape index is the ratio of vertebral body width to length, $VB \times 100/VLV$.

²The pedicular robusticity index is the ratio of pedicle width to length, $BP \times 100/LP$.

³The relative position of the transverse process, on the left side of the vertebra, is expressed by the formula $RTP \times 100/VH$ (distance of the root of the transverse process from the dorsalmost margin of the vertebral body, divided by vertebral height); values preceded by a + sign indicate processes arising from the lateral surface of the vertebral body, while negative values denote processes arising from the pedicles.

⁴Wedging indices are calculated as the ratio of ventral to dorsal vertebral body length, $VLV \times 100/VLD$.

vertebrae from both cercopithecoid and non-human hominoid individuals in this aspect of vertebral body shape (Sanders, in preparation).

Pedicular construction

Pedicular shape can be expressed by the ratio of pedicular width to length. Large-bodied hominoids typically possess lumbar pedicles that are relatively broader and shorter than those of cercopithecoids (Table 2 and Table 4). There is some overlap in pedicular robusticity indices between gibbons and cercopithecoids, although at all comparable vertebral levels gibbons have higher mean values for this index (Table 4). Unlike the situation for centrum shape, the pedicles of the Moroto vertebra are more robustly built than those of any extant cercopithecoid and are proportioned more like pedicles of extant hominoids (Figure 8). Walker & Rose (1968) felt that the Moroto specimen particularly resembles gorillas in the "stoutness" of its pedicles. However, the pedicles of UMP 67-28 are not especially stout and the pedicular robusticity index for this fossil falls in the low end of the range of index values for great apes at all vertebral levels considered and at the high end of the range of indices for gibbons at vertebral level L VI (Table 4). UMP 67-28 groups

**CATARRHINE PEDICULAR ROBUSTICITY
VERTEBRAL LEVEL L VI**

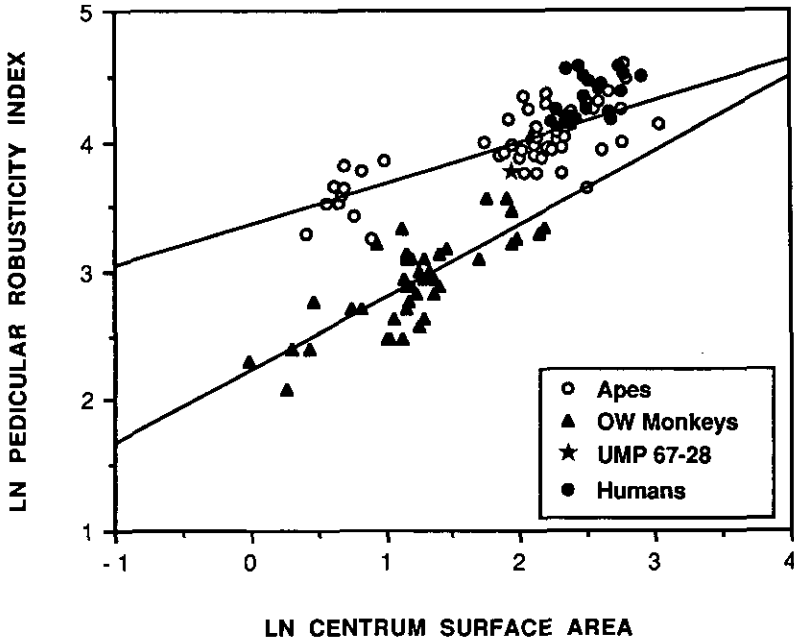


Figure 8. Bivariate plot of pedicular robusticity and vertebral body surface area at vertebral level L VI for catarrhine primates. Pedicular robusticity is expressed by the ratio of pedicle width to height, BP/LP, $\times 100$ (see Figure 3). Data points represent individual values for the following taxa: HS, PT, GG, PP, HC, HM, MS, PH, CoP, CoG, CAe (abbreviations in Table 1). The straight lines represent correlative trends between pedicle shape and body size, as inferred from centrum surface area, for hominoids and cercopithecoids. In this plot, UMP 67-28 clusters with female chimpanzees and orang-utans.

with hominoids, to the exclusion of cercopithecoids, in pedicular robusticity because its pedicular widths closely match mean widths for comparable-sized apes while greatly exceeding widths of even the largest extant cercopithecoids (Table 2). In contrast, pedicular length in UMP 67-28 overlaps the ranges of both large-bodied hominoids and cercopithecoids for this dimension (Table 2). In *Proconsul nyanzae* (Table 2 and Table 4), the proportions of the lumbar pedicles are like those of cercopithecoids. Lumbar vertebrae from KNM-RU 2036 (*P. heseloni*) have pedicular robusticity indices ranging from 23–28, which are typical index values for cercopithecoids but unlike those of hominoids.

Transverse process position and orientation

The greater robusticity of the lumbar pedicles in hominoids as compared with cercopithecoids is correlated with differences between these catarrhine subgroups in transverse process placement (see Table 4; also Benton, 1967; Ankel, 1972). Although the relationship between variations in placement and orientation of transverse processes, pedicular shape, and spinal function among mammals has gone largely unexplained in the literature, it seems likely that muscular force acting on transverse processes also affects portions of vertebrae providing attachment for these processes. In Old World monkeys, transverse processes arise from the sides of vertebral bodies and pedicles are thin. In apes and humans, muscular force must be

transmitted directly to the pedicles as the lumbar transverse processes are rooted on the pedicles, and it is reasonable to suppose that pedicular structure in these catarrhines is more robust as a consequence.

The position of the transverse processes relative to the vertebral body (RTP) is quantified in the present study as an index expressing the distance ventral to (+) or dorsal to (-) the dorsalmost margin of the body in relation to vertebral body height (see Figure 3 and Table 4). Mivart (1865:559) noted that the transverse processes appear to "spring from a higher point [more dorsally], with regard to the centrum, in Man than in any other Primate." At the vertebral levels surveyed, humans exhibit lumbar vertebrae with very dorsally-placed transverse processes and more negative mean index values than apes, although their index ranges overlap with indices from other large-bodied hominoids (Table 4). In comparison, the most ventrally-rooted processes among hominoids belong to individuals of *Hylobates*. In common with ateline primates, the lumbar transverse processes of gibbons normally originate from the vertebral bodies nearly at the centro-pedicular intersection (personal observation, WJS; Ankel, 1967a, 1972; Filler, 1986; Kelley, 1986; Kelley & Pilbeam, 1986). In UMP 67-28, the surviving left transverse process arises from the *pedicle* near the centro-pedicular junction (Figure 1; Walker & Rose, 1968; Filler, 1981), more ventrally-placed than is typical for modern great apes and humans. The RTP index for UMP 67-28 is at the high end of the range of indices recorded for large-bodied apes, and is outside the ranges seen for extant cercopithecoids and humans (Table 4; Sanders, in preparation). In *Proconsul nyanzae* (Ward, 1990, 1991, 1993a), transverse processes on the lumbar vertebrae arise from sites near the dorsal margins of the *vertebral bodies*. In this regard, *P. nyanzae* differs from great apes and humans. Index values for the antepenultimate and penultimate lumbar vertebrae of *P. nyanzae* individual KNM-MW 13142 indicate that the relative position of transverse processes on its lower lumbar vertebrae are intermediate between the average condition observed for cercopithecoids and hylobatids (Table 4; see also Ward, in press). While it has been stated that the position of transverse processes in the lumbar vertebrae of *Pronconsul heseloni* individual KNM-RU 2036 resembles the placement of these processes in gibbon lumbar vertebrae (Kelley, 1986; Kelley & Pilbeam, 1986), our observations favor the view that *P. heseloni* is more similar to *P. nyanzae* in this aspect of its vertebral morphology (Ward, 1993a).

Orientation as well as position of lumbar transverse processes is related to the capacity for lower back mobility (see Slijper, 1946). In cercopithecoids, the ventral and cephalad angulation of the transverse processes provides additional mechanical advantage for the long epaxial muscles to dorsiflex the spine. Cephalad elongation and orientation of these processes move the attachments of iliocostalis away from the point of rotation, or fulcrum, of each lumbar vertebra at the center of its caudal end, thereby increasing the effectiveness of this muscle by lengthening its lever arm (see Hildebrand, 1988). The same reasoning has been used to explain size and orientation of neural spines (Slijper, 1946; Walker, 1987). Species with a greater number of lumbar elements have longer axes of columnar movement (Benton, 1974; Ward, 1991). In such species, ventral orientation of the transverse processes places the line of action of iliocostalis closer to the sagittal plane, and provides potentially longer distances of contraction for fascicles of iliocostalis. The advantage of this structural arrangement is obvious for animals that increase stride length during running by ventral and dorsal movements of their lower backs. In addition, the ventral position of the transverse processes in cercopithecoids provides an enlarged lateral trough to accommodate thick sacrospinalis muscles (Benton, 1967, 1974). Hominoid lumbar vertebrae lack this mechanical arrangement, being distinguished from cercopithecoids by dorsal and occasional

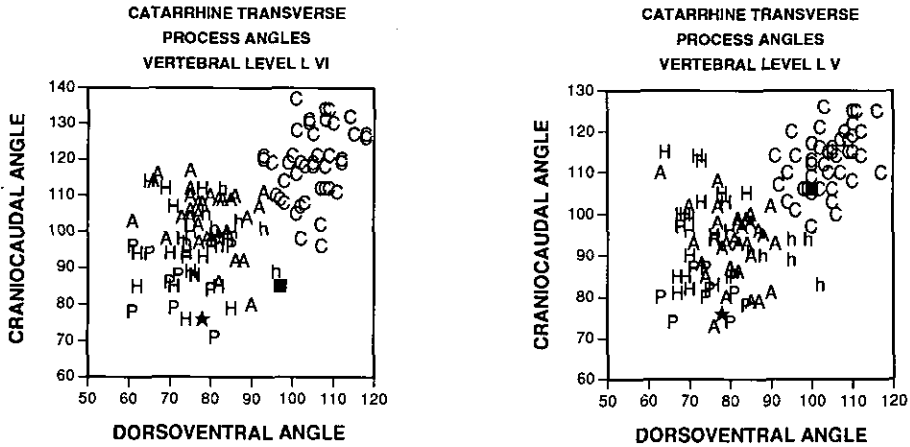


Figure 9. Bivariate plot of the dorsoventral and craniocaudal angulation of transverse processes at vertebral levels L VI, L V, and L IV for catarrhine primates. Symbols: C=cercopithecoids; A=African apes; H=humans; h=hylobatids; P=orang-utans; star=UMP 67-28; square=KNM-MW 13142. Taxa used in the plot include HS, PT, GG, PP, HC, HM, MS, PH, CoP, NL, PE, PC, CA, CG, and CT (abbreviations in Table 1). The axis labels indicate degrees. (A) Vertebral level L VI. UMP 67-28 clusters with humans and orang-utans and KNM-MW 13142 K is close to an outlying hylobatid data point. (B) Vertebral level L V. UMP 67-28 clusters with orang-utans and African apes, while KNM-MW 13142 J groups with data points for cercopithecoids.

caudal angulation of the transverse processes. The more dorsal position of the lumbar transverse processes in hominoids suggests a rheostatic, stiffening function for the sacrospinalis muscles. Placement and angulation of lumbar transverse processes in hominoids shift the attachments of iliocostalis and longissimus dorsad from the centers of rotation, increasing the moment of these muscles and enhancing their ability to resist flexion of the lower back (see Ward, 1993a). This configuration is advantageous for maintenance of orthograde postures, which helps explain why humans tend to have the most dorsally-placed transverse processes. The intact transverse process of UMP 67-28 is dorsally and caudally orientated (Figure 9a,b), resembling the condition found in hominoid but not cercopithecoid vertebrae. The disposition of transverse processes in the lumbar vertebrae of *Proconsul heseloni* individual KNM-RU 2036 is very similar to the condition in the Moroto vertebra. In *Proconsul nyanzae* individual KNM-MW 13142, the transverse processes of the lower lumbar vertebrae are slightly deflected ventrally and angle cranially at the antepenultimate level and caudally at the penultimate level. In this regard, vertebra KNM-MW 13142 K is similar to hylobatids, and vertebra KNM-MW 13142 J clusters with cercopithecoids (Figure 9a,b).

Anapophyses

Properly defined, vertebral accessory processes include cranially-projecting metapophyses and caudally-projecting anapophyses (Flower, 1885; Gadow, 1933). Anapophyses are strongly developed as styliform projections in the lower thoracic and lumbar regions of extant cercopithecoids, and are also ubiquitous in other dorsomobile mammals, such as felids and canids (pers. obs., WJS). These processes are usually diminished or absent at the level of the last two lumbar vertebrae. Cercopithecoid anapophyses arise from the caudal margin of the

pedicles, and provide attachment for separate tendons of the longissimus and extensor caudae lateralis muscles (pers. obs., WJS; Hartman & Straus, 1933; Benton, 1967, 1974; George, 1968; Clauser, 1972; Hill, 1974; Kimura *et al.*, 1986). They probably serve to increase the leverage of longissimus, which acts in concert with iliocostalis to extend the spine. Correspondingly, absence of styliform anapophyses likely relates to reduced importance of longissimus for lower back movement. In hominoids the absence of these processes is also correlated with the lack of a tail (Shapiro, pers. comm.). Martin (1986) considers the presence of anapophyses to be a primitive character state of the Catarrhini and the loss of these structures to be a shared derived condition for the Hominoidea. In general, in hominoids longissimus inserts onto the dorsum of the medial portion of the lumbar transverse processes, and is often evidenced skeletally by ridges and tubercles homologous to anapophyses on these structures (pers. obs., WJS; Benton, 1967). Some hylobatid individuals exhibit variably-sized anapophyses arising from the pedicles (pers. obs., WJS; Ankel, 1967*a*; Kelley & Pilbeam, 1986). Thus the lack of styliform anapophyses is synapomorphic only for the great ape and human clade. The absence of anapophyses in these hominoids parallels the condition observed for other dorsostable mammals, such as ungulates (pers. obs., WJS; Flower, 1885). UMP 67-28 has no anapophyses, and Ward (1991) reports that anapophyses are missing in the other Moroto lumbar elements as well. The position of anapophyses in the lumbar vertebrae of *Proconsul nyanzae* and *P. heseloni* is as in cercopithecoids; however, in *Proconsul* these structures are small, non-projecting tubercles (Kelley, 1986; Ward, 1991, 1993*a*; Ward *et al.*, 1993).

Neural spine orientation

The inclination of lumbar neural spines corresponds with the degree of sagittal mobility of the lower spine. Dorsomobile mammals such as felids and canids have anterior to middle thoracic vertebrae with caudally-inclined neural spines and posterior thoracic and lumbar vertebrae with cranially-inclined neural spines that converge on an anticlinal vertebra. This arrangement is suggestive of "powerful dynamic control of the vertebral column from the centers of suspension" (Howell, 1965:125). Although the condition of anticliny may also be found in some stiff-backed mammals, such as large bovids, absence of this arrangement always parallels reduction of dorsoventral mobility in the lower back (Slijper, 1946; Gambaryan, 1974). Among catarrhine primates, only cercopithecoids display vertebral neural spines converging on an anticlinal vertebra. In common with extant hominoids, and contrasting with the cercopithecoid condition, UMP 67-28 appears to have a caudally-angled neural spine. Unfortunately, because of damage to the neural spine of UMP 67-28, it is impossible to confirm this observation with certainty. The orientation of the lumbar neural spines is unknown at present for *Proconsul heseloni*. The neural spines of the lower lumbar vertebrae of *Proconsul nyanzae* are caudally-directed.

Keeling

Cercopithecoid lumbar centra are usually ventrally keeled (Ankel, 1967*a*), laterally-hollowed, and spool-shaped. Ventral keels are present as ridges or broad pillars, and serve as attachment sites for the anterior longitudinal ligament, which is markedly developed in cercopithecoids (pers. obs., WJS). It is possible that these bony superstructures act as beams to help resist longitudinal bending stresses along the ventral faces of vertebral bodies. The vertebral bodies of hominoids are not subjected to the same functions, ranges of flexion (Ward, 1991), or bending stresses as cercopithecoid vertebral bodies, and are instead probably better adapted to bear loads in orthograde postures. Thus, the short lumbar vertebrae of hominoids have a more

columnar appearance, without hollowing or pronounced spooling, and lack ventral keels. UMP 67-28 is moderately spooled, but not laterally hollowed, and exhibits only the hint of a ventral keel (Figure 1). In comparison, the lumbar centra of *Proconsul nyanzae* and *P. heseloni* are distinctly keeled and moderately-spooled (Kelley, 1986; Ward *et al.*, 1993). In *Proconsul nyanzae*, lumbar centra are mildly hollowed laterally.

Neural canal size

Among extant non-human catarrhines, there is a strong relationship between the cross-sectional area of lumbar vertebral foramina and body weight (Table 3). Neural canal size scales to body weight with negative allometry, such that bigger catarrhines exhibit vertebral foramina that seem relatively small compared to overall vertebral size. Because of their great reliance on the hindlimb in locomotion, humans are exceptions to this trend. There is good evidence to suggest that variation in neural canal size is associated with motor control of different anatomical regions of the body. Cervical and lumbar enlargements of the neural canal at levels of nerve branchings that provide motor control for the limbs has been noted for humans and other mammals (Sisson & Grossman, 1938; Elliot, 1945; Thomas & Combs, 1962, 1965). There is also a strong correlation between neural canal dimensions and limb use among avian and reptilian taxa (Giffin, 1990). Proportions of the spinal cord and spinal nerve roots appear to correspond directly with size and activity of regional muscle masses, and with requirements for coordinated muscular movements. In catarrhines, the spinal cord ends above the level of the lower lumbar vertebrae (Thomas & Combs, 1965; Postacchini & Rauschnig, 1989), and the canal is occupied by spinal nerve roots collectively known as the *cauda equina*. In humans and other catarrhines, cross-sections of lumbar vertebral foramina vary closely in conjunction with the size of spinal nerve roots and their surrounding tissue (pers. obs., WJS), and pathological narrowing of the neural canal compromises these nerve roots and causes deleterious conditions (Eisenstein, 1977; Postacchini *et al.*, 1983; Porter, 1990). Humans possess immense lumbar spinal nerves and spinal nerve roots, and hence by absolute and relative standards have capacious lumbar neural canals (Sanders, 1991, in preparation). This is especially true at the last two lumbar levels, where the L4 and L5 spinal nerve roots exit laterally from intervertebral foramina and branch out to the femoral and sciatic nerves (Danforth & Wilson, 1925; O'Rahilly, 1986). At spinal levels L4 and L5 in humans, immense spinal nerve roots crowd tubular nerve root canals located laterally within the neural canal (pers. obs., WJS; Bose & Balasubramaniam, 1984). These nerve root canals contribute to the characteristic trefoil shape of L4 and L5 vertebral foramina in humans. Cross-sectional areas of the human neural canal are larger at these vertebral levels than they are in upper lumbar vertebrae, in contrast to the condition observed for all other catarrhine primates (Sanders, 1991). As the contributions of lumbar nerve roots to the femoral and sciatic nerves in catarrhines and other mammals are positionally homologous to the human distribution pattern (Sonntag, 1924a; Hartman & Straus, 1933; Sisson & Grossman, 1938; Raven & Hill, 1950), relative differences in size of the neural canal and inferred differences in size of spinal nerve roots at the lower levels of the lumbar column imply contrasts between humans and other catarrhines in the functional importance of lumbar nerves for muscular control of the lower limbs.

Walker & Rose (1968:981) noted that the vertebral foramen of UMP 67-28 is quite small, but thought this feature to "resemble the condition seen in *Homo* rather than in the pongids." In fact, the reverse is true. The cross-sectional area of the vertebral foramen in the Moroto vertebra is matched by areas found in some individuals of *Pan*, *Pongo* and *Papio* (Table 2), and

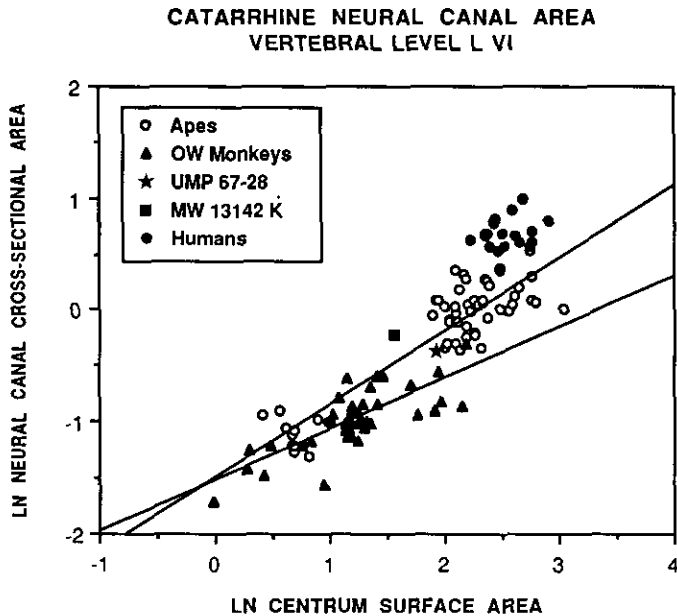


Figure 10. Bivariate plot of cross-sectional area of the vertebral foramen and vertebral body surface area at vertebral level L VI for catarrhine primates. Data points represent individual values for the following taxa: HS, PT, GG, PP, HC, HM, MS, PH, CoP, CoG, CAe (abbreviations in Table 1). The straight lines represent correlative trends between neural canal cross-sectional area and body size, as inferred from vertebral body surface area, for hominoids and cercopithecoids. UMP 67-28 plots both with large male cercopithecoids, and female pongids. The position of KNM-MW 13142 K indicates that it has a relatively oversized vertebral foramen compared with other non-human catarrhines sampled. Data points for humans indicate that relative to body size they have the largest neural canal cross-sectional areas of any catarrhine.

is greatly exceeded by absolute values recorded for *Homo*. Relative to inferred body size, the capacity of the vertebral foramen in UMP 67-28 is typical of similar-sized modern catarrhines, whereas humans have relatively “outsized” lumbar vertebral foramina (Figure 10). Though also of relatively smaller magnitude than those of humans, relative cross-sectional areas of vertebral foramina in lumbar vertebrae of *Proconsul nyanzae* are slightly larger than mean areas of comparable-sized modern catarrhines (Figure 10; Sanders, in preparation). The neural canal area of penultimate lumbar vertebra KNM-MW 13142K of *Proconsul nyanzae* is not only relatively larger than the cross-sectional area of the neural canal of UMP 67-28, it is absolutely larger as well (Table 2). Our preliminary impression of lumbar vertebral foramina *P. heseloni* individual KNM-RU 2036 is that they are relatively large but close to what one would expect for a diminutive catarrhine.

Discussion

Craniodental remains have provided most of the evidence used thus far to reconstruct the evolutionary relationships of afropithecins and other early to middle Miocene catarrhines. The relative proportions of the premolars of the Moroto palate are similar to those of *Afropithecus* and to those of the genus *Heliopithecus* from the Arabian site of Ad Dabtiyah, and are more derived than *Proconsul* towards the condition present in the great ape + human clade. From this

and other dental evidence, the constituent members of the Afropithecini have been regarded as the earliest recognizable branchings of that clade (Andrews & Martin, 1987*a,b*; Andrews *et al.*, 1987). *Proconsul* is considered either the last common ancestor of all great apes and humans (Walker & Teaford, 1989: Figure, p. 79), the sister group to all hominoids (Andrews & Martin, 1987*a,b*), or an "undifferentiated basal catarrhine of modern aspect" sharing no derived craniodental traits with the extant superfamilies of the Catarrhini (Harrison, 1987, 1988).

Finer resolution of catarrhine phylogeny requires consideration of postcranial evidence. The appendicular postcranial skeleton of *Proconsul* differs from, and is considerably more primitive than, that of any extant hominoid (McHenry & Corruccini, 1983; Rose, 1983, 1988; Harrison, 1987; Ward, 1991, 1993*a*; Ward *et al.*, 1993), although this genus apparently exhibits a number of synapomorphies common to the Hominoidea (Andrews & Martin, 1987*a*; Rose, 1988; Andrews, 1992). Appendicular elements of the postcranial skeleton preserved for *Afropithecus*, from Kalodirr, resemble comparable remains from *Proconsul heseloni* and especially those from *P. nyanzae* (Leakey *et al.*, 1988). However, as some of the more diagnostic parts of the appendicular skeleton, such as the distal humerus, have not been recovered for *Afropithecus* for comparison with *Proconsul*, it would be premature to assume complete postcranial identity for these two genera. At present, the scant remnants of the appendicular skeleton of *Afropithecus* from Kalodirr offer little in the way of morphological clues to recommend membership in the Hominoidea. *There are no appendicular remains known for the Moroto hominoid.*

The morphology of UMP 67-28 is evidence that the lower spine of the Moroto hominoid is more derived from the primitive catarrhine condition than the same region in *Proconsul*. This information supports the idea that the taxon it represents is phyletically closer than is *Proconsul* to the origin of the great ape+human clade. The lumbar vertebrae from *Proconsul nyanzae* resemble those of extant cercopithecoids in centrum shape, keeling, presence of anapophyses, pedicular shape, and, at some vertebral levels, in angulation of transverse processes (Table 4; Ward, 1990, 1991, 1993*a*; Ward *et al.*, 1993). The diaphragmatic vertebra is cranial to the last thoracic element in *P. nyanzae*, which is also a cercopithecoid trait. In addition, *P. nyanzae* probably had a relatively long lumbar region comprised of six lumbar vertebrae (Ward, 1991), which is the number found in the lumbar series of many extant cercopithecoids. Since the proportions and construction of lumbar vertebrae in cercopithecoids probably represent the primitive condition for catarrhine primates (Martin, 1986; Harrison, 1987), nothing in the lower spine of *P. nyanzae* links this species phylogenetically with cercopithecoids. The position of origin for transverse processes in the lumbar vertebrae of *P. nyanzae* are intermediate between those of hylobatids and cercopithecoids. An apparent lack of anticlivity is the only derived feature of the lumbar region shared in common with modern hominoids. *Proconsul heseloni* also displays lumbar vertebral body and pedicular proportions and keeling similar to cercopithecoids, although the anapophyses are reduced to slight "traces" (Walker & Pickford, 1983; Kelley, 1986; Velte, 1987). *The lumbar vertebrae of P. heseloni resemble the Moroto specimen and some hominoids in the orientation of their transverse processes (but not in position of origin, contra Walker & Pickford, 1983, and Walker & Teaford, 1989).* The tapering of an apparent last sacral vertebra from *Proconsul heseloni* suggests the lack of a tail (Ward *et al.*, 1991, 1993*b*), a feature derived in common among all extant hominoids. Except for the lattermost trait, the overall morphology of the lower spine in *Proconsul* is not likely to be present in a close relative of extant great apes and humans, or even of extant lesser apes. However, the retention of features primitive for the Catarrhini in the lower spine of *Proconsul* should not be thought unexpected for an early, basal member of the Hominoidea (see Harrison, 1993).

The overall morphological affinities of UMP 67-28 are not restricted to the lumbar vertebrae of any one species of modern hominoid. Instead, the lumbar vertebra from Moroto exhibits clear synapomorphies with extant large-bodied hominoids in several morphological aspects: (1) origin of the transverse processes from the pedicles; (2) dorsal and caudal orientation of the transverse process(es); (3) apparent caudal inclination of the neural spine; (4) reduction of ventral keeling; and (5) pedicular shape. Quantitatively, UMP 67-28 overlaps with great apes and differs significantly from cercopithecoids in expression of these features. In common with great apes and humans, and some lesser apes, anapophyses are absent in this specimen. UMP 67-28 cannot be distinguished from cercopithecoids and hominoids of inferred equivalent body size in a number of other traits: (1) outline shape of the caudal vertebral body surface; (2) relative size of the cross-sectional area of the vertebral foramen; (3) endplate morphology; and (4) degree of centrum wedging. Vertebral body shape of UMP 67-28, as expressed by its width-to-length ratio, is most like the proportions of vertebral bodies from large baboons, which are fairly stiff-backed for cercopithecoids. Overall, the morphology of UMP 67-28 approximates that expected for a lumbar vertebra from a generalized large-bodied hominoid. While no characters observed for UMP 67-28 link the Moroto hominoid exclusively with any particular modern great ape or with humans, on the basis of vertebral evidence it is reasonable to consider the Moroto hominoid a closer sister taxon to modern large-bodied hominoids than is *Proconsul*. The appearance in a member of the Afropithecini of derived vertebral morphology shared in common with the modern great ape+human clade supports the systematic implications of dental remains from this extinct tribe.

Despite significant size differences between *Proconsul nyanzae* and the smaller *P. heseloni*, the array of features seen in the appendicular skeleton of these species is remarkably similar and appears primarily adapted for arboreal, palmigrade quadrupedalism (Morbeck, 1975; McHenry & Corruccini, 1983; Walker & Pickford, 1983; Kelley & Pilbeam, 1986; Senut, 1988; Ward, 1993a). Schön & Ziemer (1973) felt that the arrangement of wrist bones would have allowed *Proconsul heseloni* to engage in some suspensory behaviors as well. Because of limb bone robusticity, these species are thought to have progressed "powerfully and slowly" (Walker & Pickford, 1983; Kelley & Pilbeam, 1986). The resemblances between the preserved limb elements of *Afropithecus* from Kalodirr and *Proconsul* also suggest similarity in positional behavior (Leakey *et al.*, 1988). However, if UMP 67-28 is found to belong to *Afropithecus*, the notion that *Afropithecus* and *Proconsul* were positionally alike would be contradicted. Differences in vertebral morphology between *Proconsul* and the Moroto hominoid indicate clear distinctions in locomotor capabilities.

The lower back region of mammals is adapted primarily to either dorsostable or dorsomobile functions (Slijper, 1946, 1947; Gambaryan, 1974). In dorsomobile animals, movements of the lumbar spine are correlated with pelvic and hindlimb activity during running to increase stride length (Hildebrand, 1959; English, 1980). Flexibility of the lumbar spine is also important in leaping and hopping behaviors (Hatt, 1932; Howell, 1965). Old World monkeys are capable of running, bounding, and leaping behaviors requiring active flexion and extension of the lower spine (Mittermeier & Fleagle, 1976; Fleagle, 1977; Morbeck, 1977; Rose, 1977, 1978, 1979; Wells *et al.*, 1977; Hurov, 1982, 1985, 1987; Cant, 1988), and they concomitantly share many of the structural adaptations in lumbar morphology present in other dorsomobile mammals (Benton, 1967, 1974). In contrast, the lower spine of hominoids (particularly the great apes) functions to limit lower spinal movements and is better adapted for orthograde posture. The lumbar centra and lumbar region in hominoids are relatively short

(Jungers, 1984; Sanders, 1990), and the sacrospinalis muscles of hominoids are relatively reduced while the transversospinalis muscles are relatively enlarged in comparison with cercopithecoids (Benton, 1974). The stiff vertebral columns of apes presumably serve to counteract spinal extension during vertical climbing and to provide truncal stability during suspension and in upright postures, and in at least some hominoids may link the thorax with the pelvis as a single unit during bridging behaviors (Benton, 1974; Cartmill & Milton, 1977; Filler, 1981; Jungers, 1984; Hunt, 1991).

Our results confirm that the lumbar vertebrae of *Proconsul* are adapted for dorsoventral flexion of the lower back in pronograde postures (Ward, 1993a,b), though perhaps not to the same degree as modern cercopithecoids. Lack of anticlivity, reduction in the size of anapophyses, and positioning of the lumbar transverse processes more dorsally on the vertebral body than in modern Old World monkeys are evidence that the long epaxial muscles of *Proconsul* were relatively less massive and were capable of generating less power than those of modern cercopithecoids. *Proconsul* probably engaged in leaping, bounding, and running behaviors less frequently or with less efficiency than do extant members of the cercopithecoidea. Nonetheless, it may be inferred that *Proconsul* had a positional repertoire more typical of living monkeys than living apes (see also Ward, 1993a), and that the species of *Proconsul* considered here differed significantly from the Moroto hominoid in this aspect of its behavior.

The morphology of UMP 67-28 suggests that the Moroto hominoid used its lower back in more orthograde postures, and perhaps may have climbed more like extant apes or engaged in some below-branch movements and quadrumanous bridging and transferring behaviors (see also Filler, 1981; Ward, 1993a). Paralleling the situation for modern catarrhines, differences in vertebral proportions and associated contrasts in inferred spinal function and positional behavior between the Moroto hominoid and *Proconsul* are probably also linked in part with the effects of body size. It is clear that the musculoskeletal arrangement of the lower spine in the Moroto hominoid was adapted for stabilizing the lower back during positional behaviors, though perhaps not as well as modern hominoids of similar body size. Our results for transverse process position and relative vertebral body length in UMP 67-28 suggest that the long back muscles of the Moroto hominoid may have been less effective in resisting spinal flexion in orthograde posture, and that the length of the lumbar region in relation to overall trunk length may have been greater than in extant apes. It is not possible, however, given the limitations of analysing a single vertebral element, to use the results of our study to link the Moroto hominoid with the set of behaviors found in any particular extant species of hominoid, or even to place this extinct ape in a predominantly arboreal milieu. We do not, for instance, know how many vertebrae were present in the lumbar region of this fossil ape, so we cannot at present reconstruct the relative length of the lumbar column for comparison with modern hominoids. In addition, lower spinal adaptations for dorsostability cannot be taken as automatic predictors of substrate preference, because African apes are primarily terrestrial while hylobatids and orang-utans utilize arboreal settings more frequently, even though they all have limited spinal mobility. Despite these limitations to interpretation, UMP 67-28 is an important specimen because it is the first indication that at least by the early part of the middle Miocene, an evolutionary reorganization of the axial skeleton in the direction of modern hominoid morphology had begun. Alterations in the axial skeleton of early hominoids, as evinced by the Moroto lumbar, may have occurred as a result of new strategies of substrate utilization. The derived dentition characterizing afropithecines from other early-middle

Miocene catarrhines suggests that these changes were adaptively driven by a major shift in diet, perhaps toward an increased emphasis on hard fruits (Andrews, 1992).

Summary

Detailed morphometric analysis of the lumbar vertebra from Moroto II, in comparison with vertebrae from a large sample of extant catarrhines, reveals that it shares no special proportional or structural affinities with lumbar vertebrae from African apes or humans. UMP 67-28 is the same size as lower middle lumbar vertebrae from female chimpanzees and orang-utans, or from large male baboons. Based on this similarity, the individual that UMP 67-28 represents is estimated to have weighed approximately 37.6 kg (95% C.I. 33.8–43.4 kg). The close scaling of some vertebral dimensions with body weight makes it difficult to characterize UMP 67-28 as either cercopithecoid- or hominoid-like on the basis of overall shape of its vertebral body or size of its vertebral foramen. The relative length of the vertebral body, however, is slightly elongate for a hominoid, yielding a vertebral body width/length ratio similar to ratios for some specimens of *Papio* and *Mandrillus*. Other features of UMP 67-28 are more hominoid- or even great ape-like: the neural spine is angled in a caudal direction; ventral keeling is reduced; the surviving transverse process arises from the pedicle and is oriented dorsally and caudally; anapophyses are absent; and pedicular width and the pedicular robusticity index are greater than values recorded for any extant cercopithecoid.

Considered together, the characteristics of UMP 67-28 are more derived towards the morphotype for extant large-bodied hominoids than are the lumbar vertebrae of *Proconsul heseloni* and *P. nyanzae*. In contrast, the lumbar region of the genus *Proconsul* appears to have retained an overall morphology close to the primitive condition for catarrhines. These findings support the suggestion that the Moroto hominoid is phyletically closer to the great ape + human clade than is *Proconsul*. The structure and proportions of UMP 67-28 also indicate that the lower back of the Moroto hominoid had limited mobility. The presence of dorsostable adaptations in the lower back of the Moroto hominoid may be ecologically associated with evolutionary derivations in the dentition of afropithecins, relative to the primitive condition hypothesized for catarrhines. Significant differences between the Moroto hominoid and *Proconsul* in lumbar vertebral morphology make it likely that they had divergent functional capabilities of the lower back and dissimilar locomotor patterns.

Acknowledgements

Generous permission to study collections in their care was given by Drs G. Musser (American Museum of Natural History), R. Thorington and C. Wozencraft (National Museum of Natural History), B. Patterson (Field Museum), and B. Latimer (Cleveland Museum of Natural History). We are grateful to Dr Carol Ward for providing casts and original measurements of *Proconsul* vertebrae, to Dr William Jungers for providing programs to run reduced major axis regression, and to Ms Claudia Grosz for drawing Figure 1. Helpful technical assistance was provided by Mr L. Jellema and Mr A. Grosse. We thank Drs T. Harrison, P. Gingerich, D. Fisher, M. Foote, M. Zelditch, G. Gunnell, D. McShea, and Ms E. Miller for constructive comments. We are also indebted to Drs L. Shapiro and C. Ward for their encouragement and excellent critical advice. Kind hospitality during research travel was extended by the Grosse family. This project was supported by predoctoral grants (to WJS) from the Wenner-Gren

Foundation and the L.S.B. Leakey Foundation, and a Dean's Dissertation Fellowship from New York University.

References

- Aiello, L. C. (1992). Allometry and the analysis of size and shape in human evolution. *J. hum. Evol.* **22**, 127–147.
- Allbrook, D. & Bishop, W. W. (1963). New fossil hominoid material from Uganda. *Nature* **197**, 1187–1190.
- Andrews, P. (1992). Evolution and environment in the Hominoidea. *Nature* **360**, 641–646.
- Andrews, P. & Martin, L. B. (1987a). Cladistic relationships of extant and fossil hominoids. In (F. E. Grine, J. G. Fleagle & L. B. Martin, Eds) *Primate Phylogeny*, pp. 101–118. London: Academic Press.
- Andrews, P. & Martin, L. B. (1987b). The phyletic position of the Ad Dabiyah hominoid. *Bull. Brit. Mus. Nat. Hist. Geol.* **41**, 383–393.
- Andrews, P., Martin, L. & Whybrow, P. (1987). Earliest known member of the great ape and human clade. *Am. J. phys. Anthropol.* **72**, 174–175.
- Ankel, F. (1967a). Morphologie von Wirbelsäule und Brustkorb. *Primatologia* **4**, 1–120.
- Ankel, F. (1967b). Morphologische Spezialisierungen der menschlichen Wirbelsäule. *Bull. Schweiz. Gesell. Anthropol. Ethnol.* **43**, 70–81.
- Ankel, F. (1972). Vertebral morphology of fossil and extant primates. In (R. Tuttle, Ed.) *The Functional and Evolutionary Biology of Primates*, pp. 223–240. Chicago: Aldine-Atherton.
- Badoux, D. M. (1974). An introduction to biomechanical principles in primate locomotion and structure. In (F. A. Jenkins, Jr, Ed.) *Primate Locomotion*, pp. 1–43. New York: Academic Press.
- Benton, R. S. (1967). Morphological evidence for adaptations within the epaxial region of the primates. In (H. Vagtberg, Ed.) *The Baboon in Medical Research*. Vol. 2, pp. 201–216. Austin: University of Texas Press.
- Benton, R. S. (1974). Structural patterns in the Pongidae and Cercopithecoidea. *Ybk phys. Anthropol.* **18**, 65–88.
- BioScan, Incorporated (1988). *BioScan Optimas User's Manual and Reference*. Edmonds, Washington: BioScan, Incorporated.
- Bishop, W. W. (1964). More fossil primates and other Miocene mammals from North-East Uganda. *Nature* **203**, 1327–1331.
- Bishop, W. W., Miller, J. A. & Fitch, F. J. (1969). New potassium-argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *Am. J. Sci.* **267**, 669–699.
- Bishop, W. W. & Whyte, F. (1962). Tertiary mammalian faunas and sediments in Karamoja and Kavirondo, East Africa. *Nature* **196**, 1283–1287.
- Bookstein, F. L., Strauss, R. E., Humphries, J. M., Chernoff, B., Elder, R. L. & Smith, G. R. (1982). A comment upon the uses of Fourier methods in systematics. *System. Zool.* **31**, 85–92.
- Bose, K. & Balasubramaniam, P. (1984). Nerve root canals of the lumbar spine. *Spine* **9**, 16–18.
- Calder, W. A. (1984). *Size, Function, and Life History*. Cambridge: Harvard University Press.
- Cameron, D. W. (1991). Sexual dimorphism in the early Miocene species of *Proconsul* from the Kisingiri Formation of East Africa: A morphometric examination using multivariate statistics. *Primates* **32**, 329–343.
- Cant, J. G. H. (1988). Positional behavior of long-tailed macaques (*Macaca fascicularis*) in northern Sumatra. *Am. J. phys. Anthropol.* **76**, 29–37.
- Cartmill, M. & Milton, K. (1977). The loriform wrist joint and the evolution of “brachiating” adaptations in the Hominoidea. *Am. J. phys. Anthropol.* **47**, 249–272.
- Clauser, D. A. (1972). The Spinal Column and Associated Muscles of *Macaca speciosa*. Masters Thesis, The University of Wisconsin (Milwaukee).
- Clauser, D. A. (1980). Functional and Comparative Anatomy of the Primate Spinal Column: Some Locomotor and Postural Adaptations. Ph.D. Thesis, The University of Wisconsin—Milwaukee.
- Danforth, M. S. & Wilson, P. D. (1925). The anatomy of the lumbo-sacral region in relation to sciatic pain. *J. Bone Joint Surg.* **7**, 109–128.
- Eisenstein, S. (1977). The morphometry and pathological anatomy of the lumbar spine in South African Negroes and Caucasoids with specific reference to spinal stenosis. *J. Bone Joint Surg.* **59B**, 173–180.
- Elliott, H. C. (1945). Cross-sectional diameters and areas of the human spinal cord. *Anat. Record* **93**, 287–293.
- English, A. W. (1980). The functions of the lumbar spine during stepping in the cat. *J. Morph.* **165**, 55–66.
- Ferson, S., Rohlf, F. J. & Koehn, R. K. (1985). Measuring shape variation of two-dimensional outlines. *Syst. Zool.* **34**, 59–68.
- Filler, A. G. (1981). Anatomical specializations in the hominoid lumbar region. *Am. J. phys. Anthropol.* **54**, 218.
- Filler, A. G. (1986). Axial Character Seriation in Mammals: An Historical and Morphological Exploration of the Origin, Development, Use and Current Collapse of the Homology Paradigm. Ph.D. Thesis, Harvard University.
- Fleagle, J. G. (1977). Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-eating monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Am. J. phys. Anthropol.* **46**, 297–308.
- Fleagle, J. G. (1988). *Primate Adaptation and Evolution*. New York: Academic Press.
- Flower, W. H. (1885). *An Introduction to the Osteology of the Mammalia*. London: MacMillan and Co.

- Gadow, H. F. (1933). *The Evolution of the Vertebral Column*. Cambridge: Cambridge University Press.
- Gambaryan, P. P. (1974). *How Mammals Run*. New York: John Wiley and Sons.
- George, R. (1968). The Intrinsic Back Musculature of *Macaca mulatta*. Masters Thesis, Medical College of Virginia (Richmond).
- Giffin, E. (1990). Gross spinal anatomy and limb use in living and fossil reptiles. *Paleobiol.* **16**, 448–458.
- Gingerich, P. D. (1990). Prediction of body mass in mammalian species from long bone lengths and diameters. *Contrib. Mus. Paleont., The University of Michigan* **28**, 79–92.
- Gingerich, P. D., Smith, B. H. & Rosenberg, K. (1982). Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *Am. J. phys. Anthrop.* **58**, 81–100.
- Harrison, T. (1987). The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. In (F. E. Grine, J. G. Fleagle & L. B. Martin, Eds) *Primate Phylogeny*, pp. 41–80. London: Academic Press.
- Harrison, T. (1988). A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatologica* **50**, 59–108.
- Harrison, T. (1993). Cladistic concepts and the species problem in hominoid evolution. In (L. Martin & W. Kimbel, Eds) *Species, Species Concepts, and Primate Evolution*, pp. 345–371. New York: Plenum Press.
- Hartman, C. G. & Straus, W. L., Jr (1933). *The Anatomy of the Rhesus Monkey (Macaca mulatta)*. Baltimore: Williams and Wilkins.
- Harvey, P. H. & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution* **39**, 559–581.
- Hatt, R. T. (1932). The vertebral column of richochetal rodents. *Bull. Am. Mus. Nat. Hist.* **63**, 599–738.
- Hildebrand, M. (1959). Motions of the running cheetah and horse. *J. Mammal.* **40**, 481–495.
- Hildebrand, M. (1988). *Analysis of Vertebrate Structure, Third Edition*. New York: John Wiley and Sons.
- Hill, W. C. O. (1974). *Comparative Anatomy and Taxonomy. Volume VII, Cynopithecinae*. New York: John Wiley and Sons.
- Howell, A. B. (1965). *Speed in Animals*. New York: Hafner Publishing Company.
- Hunt, K. D. (1991). Mechanical implications of chimpanzee positional behavior. *Am. J. phys. Anthrop.* **86**, 521–536.
- Hurov, J. R. (1982). Spinal flexibility as a locomotor adaptation in patas (*Cercopithecus [Erythrocebus] patas*) and vervet monkeys (*Cercopithecus aethiops*). Ph.D. Dissertation, University of Texas, Austin.
- Hurov, J. R. (1985). Monkey locomotion during gait transitions: how do interlimb time intervals, step sequences, and kinematics change? *Am. J. phys. Anthrop.* **66**, 417–427.
- Hurov, J. R. (1987). Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). *Am. J. Primat.* **13**, 297–311.
- Jungers, W. L. (1984). Scaling of the hominoid locomotor skeleton with special reference to lesser apes. In (H. Preuschoft, D. J. Chivers, W. Y. Brockelman & N. Creel, Eds) *The Lesser Apes*, pp. 146–169. Edinburgh: Edinburgh University Press.
- Jungers, W. L. (1985). Body size and scaling of limb proportions in primates. In (W. L. Jungers, Ed.) *Size and Scaling in Primate Biology*, pp. 345–381. New York: Plenum Press.
- Jungers, W. L. (1990). Problems and methods in reconstructing body size in fossil primates. In (J. Damuth & B. J. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 103–118. Cambridge: Cambridge University Press.
- Jungers, W. L. & Susman, R. L. (1984). Body size and skeletal allometry in African apes. In (R. L. Susman, Ed.) *The Pygmy Chimpanzee: Evolution, Morphology and Behavior*, pp. 131–177. New York, Plenum Press.
- Kaessler, R. L. & Waters, J. A. (1972). Fourier analysis of the ostracode margin. *Geol. Soc. Am. Bull.* **83**, 1169–1178.
- Kelley, J. (1986). Paleobiology of Miocene Hominoids. Ph.D. Dissertation, Yale University.
- Kelley, J. & Pilbeam, D. (1986). The dryopithecines: Taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In (D. R. Swindler & J. Irwin, Eds) *Comparative Primate Biology, Vol. 1: Systematics, Evolution, and Anatomy*, pp. 361–411. New York: Alan Liss.
- Kimura, K., Konishi, M., Takahashi, Y. & Iwamoto, S. (1987). The skeletal system of *Macaca fascicularis*. Part IV. *J. Nat. Defense Med. Coll., Japan* **12**, 183–194.
- Kuhl, F. P. & Giardina, C. R. (1982). Elliptic Fourier features of a closed contour. *Comp. Graph. Image Proc.* **18**, 236–258.
- Leakey, R. E., Leakey, M. G. & Walker, A. C. (1988). Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. phys. Anthrop.* **76**, 289–307.
- Leakey, R. E. F. & Walker, A. (1985). New higher primates from the early Miocene of Buluk, Kenya. *Nature* **318**, 173–175.
- Markham, R. M. & Groves, C. P. (1990). Weights of wild orang utans. *Am. J. phys. Anthrop.* **81**, 1–3.
- Martin, L. (1986). Relationships among extant and extinct great apes and humans. In (B. Wood, L. Martin & P. Andrews, Eds) *Major Topics in Primate and Human Evolution*, pp. 161–187. Cambridge: Cambridge University Press.
- McHenry, H. M. & Corruccini, R. S. (1983). In (R. L. Ciochon & R. S. Corruccini, Eds) *New Interpretations of Ape and Human Ancestry*, pp. 353–367. New York: Plenum Press.
- McMahon, T. A. (1973). Size and shape in biology. *Science* **179**, 1201–1204.
- Mittermeier, R. A. & Fleagle, J. G. (1976). The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. *Am. J. phys. Anthrop.* **45**, 235–255.

- Mivart, St. G. (1865). Contributions towards a more complete knowledge of the axial skeleton in the primates. *Proc. Zool. Soc. London* 545–592.
- Morbeck, M. E. (1975). *Dryopithecus africanus* forelimb. *J. hum. Evol.* **4**, 39–46.
- Morbeck, M. E. (1977). Positional behavior, selective use of habitat substrate and associated non-positional behavior in free-ranging *Colobus guereza* (Ruppel, 1835). *Primates* **18**, 35–58.
- O'Rahilly, R. (1986). *Anatomy. A Regional Study of Human Structure*. Philadelphia: W. B. Saunders Company.
- Pickford, M. (1986). The geochronology of Miocene higher primate faunas of East Africa. In (J. G. Else & P. C. Lee, Eds) *Primate Evolution*. Vol. 1, pp. 19–33. Cambridge: Cambridge University Press.
- Pilbeam, D. (1972). *The Ascent of Man. An Introduction to Human Evolution*. New York: MacMillan Publishing Company.
- Porter, R. (1990). Development of the vertebral canal. In (J. N. Weinstein & S. W. Wiesel, Eds) *The Lumbar Spine*, pp. 589–594. Philadelphia: W. B. Saunders Company.
- Postacchini, F. & Rauschnig, W. (1989). Anatomy of the vertebral canal and the neural structures in the lumbar spine. In (F. Postacchini, Ed.) *Lumbar Spinal Stenosis*, pp. 21–48. New York: Springer-Verlag.
- Postacchini, F., Ripani, M. & Carpano, S. (1983). Morphometry of the lumbar spine. *Clin. Orth.* **172**, 296–303.
- Raven, H. C. & Hill, J. E. (1950). Regional anatomy of the gorilla. In (W. K. Gregory, Ed.) *The Anatomy of the Gorilla*, pp. 15–188. New York: Columbia University Press.
- Rockwell, H. F., Evans, E. & Pheasant, H. C. (1938). The comparative morphology of the vertebral spine column: Its form as related to function. *J. Morph.* **63**, 87–117.
- Rohlf, F. J. (1990). Fitting curves to outlines. In (F. J. Rohlf & F. L. Bookstein, Eds) *Proceedings of the Michigan Morphometrics Workshop: Special Publication Number 2, The University of Michigan Museum of Zoology*, pp. 167–177. Ann Arbor: The University of Michigan Museum of Zoology.
- Rohlf, F. J. & Archie, J. W. (1984). A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Syst. Zool.* **33**, 302–317.
- Rohlf, F. J. & Ferson, S. (1988). Program EFA.
- Rose, M. D. (1975). Functional proportions of primate lumbar vertebral bodies. *J. hum. Evol.* **4**, 21–38.
- Rose, M. D. (1977). Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* **18**, 59–116.
- Rose, M. D. (1978). Feeding and associated positional behavior of black and white colobus monkeys (*Colobus guereza*). In (G. G. Montgomery, Ed.) *The Ecology of Arboreal Folivores*, pp. 253–262. Washington, D.C.: Smithsonian Institution Press.
- Rose, M. D. (1979). Positional behaviour of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In (M. E. Morbeck, H. Preuschoft & N. Gomberg, Eds) *Environment, Behavior, and Morphology: Dynamic Interactions in Primates*, pp. 75–93. New York: Gustav Fischer.
- Rose, M. D. (1983). Miocene hominoid postcranial morphology: Monkey-like, ape-like, neither, or both? In (R. L. Ciochon & R. S. Corruccini, Eds) *New Interpretations of Ape and Human Ancestry*, pp. 405–417. New York: Plenum Press.
- Rose, M. D. (1988). Another look at the anthropoid elbow. In (E. Strasser & M. Dagosto, Eds) *The Primate Postcranial Skeleton. Studies in Adaptation and Evolution*, pp. 193–224. London: Academic Press.
- Rose, M. D., Leakey, M. G., Leakey, R. E. F. & Walker, A. C. (1992). Postcranial specimens of *Simiolus enjessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. *J. hum. Evol.* **22**, 171–237.
- Ruff, C. B. (1990). Body mass and hindlimb bone cross-sectional and articular dimensions in anthropoid primates. In (J. Damuth & B. J. MacFadden, Eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, pp. 119–149. Cambridge: Cambridge University Press.
- Ruff, C. B., Walker, A. & Teaford, M. F. (1989). Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Island, Kenya. *J. hum. Evol.* **18**, 515–536.
- Sanders, W. J. (1990). Weight transmission through the lumbar vertebrae and sacrum in australopithecines. *Am. J. phys. Anthropol.* **81**, 289.
- Sanders, W. J. (1991). Comparative study of hominoid lumbar neural canal dimensions. *Am. J. phys. Anthropol. Supplement* **12**, 157.
- Sanders, W. J. (In preparation). Function, Allometry, and Evolution of the Australopithecine Lower Precaudal Spine. Ph.D. Dissertation, New York University.
- Schön, M. A. & Ziemer, L. K. (1973). Wrist mechanism and locomotor behavior of *Dryopithecus (Proconsul) africanus*. *Folia Primatologica* **20**, 1–11.
- Schultz, A. H. (1930). The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* **2**, 303–438.
- Schultz, A. H. (1938). The relative length of the regions of the spinal column in Old World primates. *Am. J. phys. Anthropol.* **24**, 1–22.
- Schultz, A. H. (1961). Vertebral column and thorax. *Primatologia* **4**, 1–66.
- Senut, B. (1988). Taxonomie et fonction chez les Hominoidea Miocènes Africains: Exemple de l'articulation du coude. *Annls Paléont. (Vert.-Invert.)* **74**, 129–154.
- Simons, E. L. (1972). *Primate Evolution. An Introduction to Man's Place in Nature*. New York: MacMillan Publishing Company.

- Sisson, S. & Grossman, J. D. (1938). *The Anatomy of the Domestic Animals*, 3rd edition. Philadelphia: W. B. Saunders Company.
- Slijper, E. J. (1946). Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen*, Tweede Sectie **42**, 1-128.
- Slijper, E. J. (1947). Observations on the vertebral columns of the domestic animals. *Vet. J.* **103**, 376-387.
- Smith, J. M. & Savage, R. J. G. (1955). Some locomotory adaptations in mammals. *Linn. Soc. Lond. Zool. J.* **42**, 603-622.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. 2nd Edition. New York: W. H. Freeman and Company.
- Sokal, R. R. & Rohlf, F. J. (1987). *Introduction to Biostatistics*. New York: W. H. Freeman and Company.
- Sonntag, C. F. (1924a). *The Morphology and Evolution of the Apes and Man*. London: John Bale, Sons and Danielsson.
- Sonntag, C. F. (1924b). On the anatomy, physiology, and pathology of the orang-outang. *Proc. Zool. Soc. Lond.* **1924**, 349-449.
- Szalay, F. S. & Delson, E. (1979). *Evolutionary History of the Primates*. New York: Academic Press.
- Thomas, C. E. & Combs, C. M. (1962). Spinal cord segments. A. Gross structure in the adult cat. *Am. J. Anat.* **110**, 37-48.
- Thomas, C. E. & Combs, C. M. (1965). Spinal cord segments. B. Gross structure in the adult monkey. *Am. J. Anat.* **116**, 205-216.
- Uehara, S. & Nishida, T. (1987). Body weights of wild chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. *Am. J. phys. Anthropol.* **72**, 315-321.
- Velte, M. (1987). A New Biomechanical Model of the Vertebral Column in Anthropoid Primates. Ph.D. Dissertation, The University of Chicago.
- Walker, A. & Pickford, M. (1983). New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In (R. L. Ciochon & R. S. Corruccini, Eds) *New Interpretations of Ape and Human Ancestry*, pp. 325-351. New York: Plenum Press.
- Walker, A. & Rose, M. D. (1968). Fossil hominoid vertebra from the Miocene of Uganda. *Nature* **217**, 980-981.
- Walker, A. & Teaford, M. (1989). The hunt for *Proconsul*. *Sci. Am.* **260**, 76-82.
- Walker, A., Teaford, M. F., Martin, L. & Andrews, P. (1993). A new species of *Proconsul* from the early Miocene of Rusinga/Mfangano Islands, Kenya. *J. hum. Evol.* **25**, 43-56.
- Walker, W. F., Jr (1987). *Functional Anatomy of the Vertebrates: An Evolutionary Perspective*. Philadelphia: Saunders College Publishing.
- Ward, C. V. (1990). The lumbar region of the Miocene hominoid *Proconsul nyanzae*. *Am. J. phys. Anthropol.* **81**, 314.
- Ward, C. V. (1991). Functional Anatomy of the Lower Back and Pelvis of the Miocene Hominoid *Proconsul nyanzae* from Mfangano Island, Kenya. Ph.D. Dissertation, The Johns Hopkins University.
- Ward, C. V. (1993a). Torso morphology and locomotion in *Proconsul nyanzae*. *Am. J. phys. Anthropol.* **92**, 291-328.
- Ward, C. V. (1993b). Function and phylogeny in hominoid trunk and hindlimb evolution. *Am. J. phys. Anthropol. Supplement* **16**, 204.
- Ward, C. V., Walker, A. & Teaford, M. F. (1991). *Proconsul* did not have a tail. *J. hum. Evol.* **21**, 215-220.
- Ward, C. V., Walker, A., Teaford, M. F. & Odhiambo, I. (1993). Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *Am. J. phys. Anthropol.* **90**, 77-111.
- Wells, J. P., Wood, G. A. & Tebbetts, G. (1977). The vertical leap of *Cercopithecus aethiops sabaues*: biomechanics and anatomy. *Primates* **18**, 417-434.
- Young, J. Z. (1962). *The Life of Vertebrates*. London: Oxford University Press.
- Younker, J. L. & Ehrlich, R. (1977). Fourier biometrics: Harmonic amplitudes as multivariate shape descriptors. *Syst. Zool.* **26**, 336-342.