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Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41

Lower spinal structure correlates well with positional behavior among mammals. Nonetheless, the functional morphology of the axial post-crania of australopithecines has received less attention than their appendicular skeletons. This paper presents a detailed description and comparative morphometric analysis of the australopithecine thoracolumbar vertebral series Stw-H8/H41, and examines spinal mechanics in early hominids. Stw-H8/H41 is an important specimen, as the australopithecine vertebral sample is small, and vertebral series are more useful than isolated elements for the interpretation of spinal function. Results of the study support the interpretation that australopithecine species are highly sexually dimorphic. The study also reveals a considerable amount of morphometric variation other than size among australopithecine vertebrae, though the sample is too small and incomplete to ascertain whether this indicates significant interspecific differences in spinal function. Most importantly, structural and metric observations confirm that the morphology of the lower spine in australopithecines has no modern analogue in its entirety. Aspects of zygapophyseal structure, numerical composition of the lumbar region, and centrum wedging suggest that the australopithecine vertebral column was adapted to human-like intrinsic lumbar lordosis and stable balance of the trunk over the pelvis in sustained bipedal locomotion. However, relative centrum size in australopithecines indicates that either they had a different mechanism for channeling vertical forces through the vertebral column than humans, or differed behaviorally from humans in ways that produced smaller increments of compression across their centra. These findings have important implications for hypotheses of australopithecine positional behavior, and demonstrate that larger samples and more complete vertebral series are needed to improve our understanding of australopithecine spinal function.

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Introduction

Bipedal adaptations in the postcranial skeleton of australopithecines date to at least the early Pliocene (Leakey *et al.*, 1995). However, there is no consensus about the effectiveness or relative importance of bipedal stance and progression in their positional repertoires (see McHenry, 1982; Stern & Susman, 1983; Susman *et al.*, 1985; Berge & Kazmierczak, 1986; Berge, 1994). In one view, it is hypothesized that australopithecines were obligate terres-trial bipeds mechanically and kinematically similar to modern humans (Lovejoy *et al.*, 1973; Lovejoy, 1974, 1988; Tague & Lovejoy, 1986; Latimer *et al.*, 1987; Latimer & Lovejoy, 1989, 1990*a,b*; Latimer, 1991). Proponents of this view explain variations in postcranial anatomy between australo-pithecines and humans as a consequence of differences in obstetric mechanisms, or as (in australopithecines) functionally-unimportant retentions of ancestral traits (Tague & Lovejoy, 1986; Lovejoy, 1988; Latimer & Lovejoy, 1989; Tague, 1991).

Alternatively, it is suggested that australopithecines were either more quadrupedal and arboreal or employed a different, less proficient form of bipedalism than humans, or both (Oxnard, 1975; Zihlman, 1978; Jungers, 1982; Stern & Susman, 1983; Susman *et al.*, 1984; Susman *et al.*, 1985; McHenry, 1986, 1991*a*; Tompkins, 1986; Rak, 1991; Schmid, 1991; Heinrich *et al.*, 1993; Berge, 1994; Duncan *et al.*, 1994; Hunt, 1994; Spoor *et al.*, 1994; Abitbol, 1995; Clarke & Tobias, 1995; Berger & Tobias, 1996; MacLatchy, 1996). Undoubtedly, the unique morphology of their postcrania, which exhibits mosaics of primitive features common to apes, derived traits shared with humans, and autapomorphies (McHenry, 1991*a*, 1994; Susman & Stern, 1991; McHenry & Berger, 1996), has complicated attempts to reconstruct australopithecine positional behavior. It is evident that more comprehensive surveys of information about individual skeletal elements and joint complexes are required to better clarify the locomotor and postural abilities of australopithecines (see Stern & Susman, 1991).

It is well established that among modern mammals, structural variations in the spine correspond closely with differences in columnar function and positional behavior (Hatt, 1932; Slijper, 1946; Hildebrand, 1959; Howell, 1965; Gambaryan, 1974; Curtis, 1995; Shapiro, 1993*a*, 1995). Nonetheless, disproportionately less attention has been given to the functional morphology of the axial postcranial skeleton of australopithecines than to their appendicular elements, despite the evident utility of vertebral anatomy for evaluating posture and locomotion in fossil taxa (e.g., Zhou *et al.*, 1992; Sanders & Bodenbender, 1994; Giffin, 1995). A number of recent studies (Sanders, 1990, 1994, 1995, 1996; Schmid, 1991; Shapiro, 1991, 1993*b*; Ward & Latimer, 1991) have sought to address this disparity by focusing on architectural and

biomechanical aspects of the australopithecine vertebral column, complementing prior investigations by Robinson (1972), Rose (1975), and Velte (1984, 1987). These studies demonstrate the significance of vertebrae for appraising bipedal abilities in australopithecines.

This paper presents a comparative morphological and metrical analysis of the thoracolumbar vertebral series Stw-H8/H41 (Figure 1), assigned to *Australopithecus africanus* (Tobias, 1973, 1978, 1980; Howell, 1978). Stw-H8 is comprised of four articulated lumbar vertebrae from the hominid-bearing locality of Sterkfontein, South Africa (Tobias, 1973). Oakley *et al.* (1977, p. 131) noted that while these vertebrae were ''removed [by Tobias in 1969] from R. M. Cooper's display cabinet,'' they had been ''excavated many years earlier.'' Although their exact provenience is uncertain, adherent matrix shows that the Stw-H8 vertebrae derive from Member 4 (Oakley *et al.*, 1977), which is dated by biochronological correlation and geomorphological and geophysical methods to ca. 2·6–2·8 Myr (Delson, 1984, 1988; Vrba, 1985; Berger & Tobias, 1996). The Stw-H41 vertebrae (two articulated lower thoracics) were found by Tobias in 1975 in Dump 18 at Sterkfontein (Oakley *et al.*, 1977), and are thought to form a continuous series (T11-L4) with Stw-H8, based on ''concordance of size, shape, state of preservation, colouration and matching areas of damage'' (Tobias, 1978, p. 385). It is likely that Stw-H8/H41 was placed in *Australopithecus africanus* (Tobias, 1973, 1978, 1980; Howell, 1978) because it is the only hominid species usually recognized in Sterkfontein Mbr. 4 (Partridge, 1982; Day, 1986; Berger & Tobias, 1996; but see Clarke, 1994).

Besides Stw-H8/H41, the only other australopithecine vertebral series are from *A. africanus* partial skeletons Sts-14 and Stw-431, *A. afarensis* individual A.L. 288-1
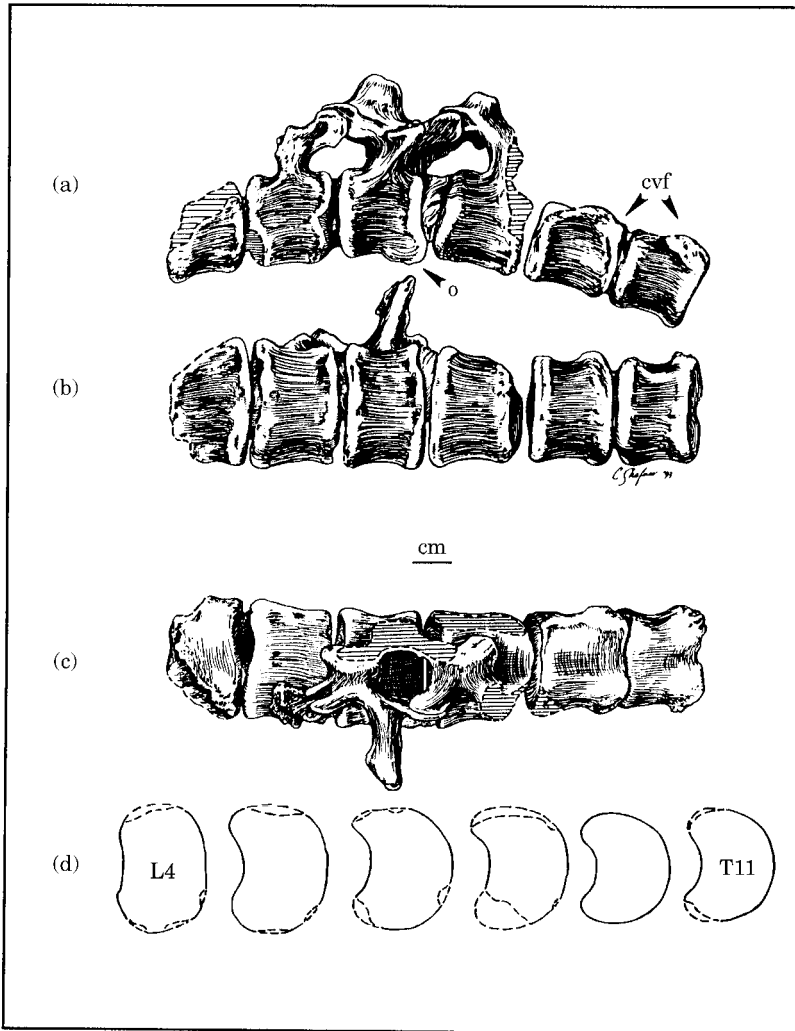
Figure 1. Thoracolumbar vertebrae of *Australopithecus africanus*, specimens Stw-H41 (T11–T12) and Stw-H8 (L1–L4). Abbreviations: cvf=costovertebral facet; o=osteophyte. (a) Right lateral view. Dorsal is to the top of the page and cranial is to the right. Arrows point to costovertebral facets in T11–T12, and an osteophyte on the ventral face of L2. (b) Ventral view. Cranial is to the right. (c) Dorsal view. Cranial is to the right. (d) Outlines of cranial centrum surfaces. Reconstructed portions are indicated by dotted lines.

("Lucy"), and *Paranthropus robustus* individual SKW 14002. Sts-14 preserves thoracics T4–T12, lumbars L1–L6, and parts of sacrals S1–S2 (Robinson, 1972). Vertebrae T9–T12, L1–L6, and a sacrum are present in the Stw-431 skeleton, which is undescribed (McHenry, 1994; McHenry & Berger, 1996). Vertebral fragments from A.L. 288-1 represent portions of seven thoracics and two lumbars, along with a sacrum (Johanson *et al.*, 1982). A small number of isolated vertebrae are also known for *A. afarensis* (Lovejoy *et al.*, 1982) and *A. africanus* (Robinson, 1972). The vertebral series of SKW 14002 is also undescribed, and represents either L1–L4 or L2–L5 from an immature individual (personal communication, H. McHenry; Susman & Stern,

1991). These vertebrae supplement an otherwise meager vertebral sample for *Paranthropus robustus* (Brain, 1970; Robinson, 1970, 1972; Rose, 1975) and *P. boisei* (Grausz *et al.*, 1988).

There are no detailed published accounts of Stw-H8/H41, and a previous study of these vertebrae by Ankel & Tobias (Oakley *et al.*, 1977) was apparently abandoned. It is an important specimen because few australopithecine vertebrae have been collected, and serial patterns in associated vertebrae are more informative than isolated elements for investigations of spinal function, particularly in assessing columnar potentials for managing stresses associated with bipedal behaviors (see Sanders, 1990, 1995; Ward & Latimer, 1991; Latimer & Ward, 1993; Shapiro, 1993*b*). Along with providing the first thorough description of Stw-H8/H41, the present study contributes new comparative morphometric information about australopithecine vertebrae. This information has implications for hypotheses of australopithecine spinal function and positional adaptations.

Materials and methods

The extant sample selected for comparative study of lumbar vertebrae is comprised of 344 individuals from 43 catarrhine species, including humans (Table 1). The non-human individuals are all adults and wild-caught. Human vertebrae examined are from individuals 25–30 years of age at the time of death. Vertebral measurements from the extant sample are compiled in Sanders (1995). Metric data from extant hominoids used in Table 2 are taken from Clauser (1980) and Ward (1991).

The fossil sample includes *A. afarensis* specimens A.L. 288-1ac (T11), A.L. 288-1aa/ak/al (L3), and A.L. 333-73 (L3); *A. africanus* specimens Stw-H8/H41 (T11–L4), Sts-14 a–h (T11–L6), and Sts-73 (L1?);

Paranthropus robustus specimens SK 3981a (T12), SK 3981b (L6), and SK 853 (middle? lumbar); and *Homo erectus* vertebrae KNM-WT 15000Y, AR+BA, AA+AV, Z+BW, AB, BM, and AC (T11, L1–L6). Observations made on original specimens (Sts-14; Stw H8/H41) and from photographs and good quality casts (Sts 14; Stw-H8/H41; A.L. 288-1; A.L. 333-73; KNM-WT 15000) were supplemented by, and checked for accuracy against, notes and measurements taken by other researchers on original specimens of all individuals in the fossil sample.

Figure 2 shows the vertebral dimensions measured for the study. Linear measurements were taken on vertebrae using Brown and Sharpe digital calipers accurate to ± 0·02 mm. Angles and areas were calculated from scaled photographs using an Optimas video digitizing system (Bioscan Inc., 1988). Latex impressions were made of curved facet surfaces and then cut and flattened to facilitate measurement of their areas. In order to establish the contours of cranial centrum surfaces in Stw-H8/H41, casts were made in polyester resin from silicone molds, and separated with a jeweler's diamond saw.

Figure 3 depicts the labeling system for comparing lumbar elements from individuals with different numbers of vertebrae in their lumbar series. In this system, vertebrae with similar roles in columnar force transmission (Sanders, 1990), homologous positions relative to the branching patterns of their lumbar spinal nerves (Sanders, 1991, 1995), and equivalent placement relative to the last vertebral level of the lumbar column are grouped together and labeled with Roman numerals from L I to L VII. Thus, for example, antepenultimate lumbar vertebrae in humans (L3), in great apes (L2), and in cercopithecoids (L4 or L5) are all labeled "L V" (see Figure 3). As dimensional differences between adjacent vertebrae in a series are

Table 1 Extant catarrhine sample used in the study*

Species	Abbreviations	*n* (male/female)	Mean body weight† (kg) Male	Female
Homo sapiens	HS	40 (20/20)	70·7	56·5
Pan troglodytes troglodytes	PT	26 (13/13)	60·0	47·4
Gorilla gorilla gorilla	GG	33 (20/13)	169·5	71·5
Pongo pygmaeus	PP	19 (10/9)	86·3	38·7
Hylobates concolor	HC	11 (6/5)	5·6	5·8
Hylobates muelleri	HM	14 (7/7)	5·8	5·7
Papio hamadryas‡	PH	12 (7/5)	28·2	13·6
Mandrillus sphinx	MS	8 (4/4)	26·9	11·5
Mandrillus leucophaeus	ML	1 (1/0)	20·0	—
Theropithecus gelada	TG	1 (1/0)	19·0	—
Lophocebus albigena	CA	8 (6/2)	9·0	6·4
Lophocebus aterrimus	CAt	2 (1/1)	—	—
Cercocebus galeritus	CG	4 (3/1)	10·2	—
Cercocebus torquatus	CT	6 (3/3)	8·0	5·5
Macaca fascicularis	MF	6 (3/3)	4·9	3·1
Macaca arctoides	MA	3 (2/1)	9·1	6·2
Macaca speciosa	MSp	4 (3/1)	9·2	8·0
Macaca hecki	MH	2 (2/0)	—	—
Macaca tonkeana	MT	3 (2/1)	—	—
Macaca nemestrina	MN	10 (7/3)	10·2	6·4
Macaca fuscata	MFu	1 (0/1)	11·7	9·1
Macaca mulatta	MM	3 (3/0)	6·2	3·0
Macaca nigra	MNi	1 (1/0)	10·4	6·6
Erythrocebus patas	EP	7 (4/3)	11·1	—
Allenopithecus nigroviridis	AN	1 (1/0)	—	—
Cercopithecus mitis	CM	12 (7/5)	7·6	4·4
Cercopithecus aethiops	CAe	15 (8/7)	5·4	3·4
Cercopithecus mona	CMo	4 (2/2)	4·4	2·5
Cercopithecus hamlyni	CH	2 (1/1)	—	—
Cercopithecus ascanius	CAs	4 (3/1)	4·2	2·9
Cercopithecus neglectus	CN	2 (2/0)	7·0	4·0
Colobus polykomos	CoP	10 (4/6)	10·0	7·7
Colobus guereza	CoG	17 (8/9)	9·6	8·0
Colobus angolensis	CoA	4 (2/2)	9·8	9·1
Piliocolobus badius	CoB	5 (5/0)	8·3	—
Presbytis pileata	PrP	2 (1/1)	—	—
Presbytis melalophos	PrM	2 (1/1)	6·7	6·6
Presbytis cristata	PrC	8 (3/5)	6·9	6·0
Presbytis entellus	PrE	4 (3/1)	18·4	11·4
Nasalis larvatus	NL	11 (8/3)	20·4	9·8
Simias concolor	SC	1 (0/1)	8·8	7·1
Rhinopithecus roxellana	RR	12 (4/8)	—	—
Pygathrix nemaeus	PN	3 (2/1)	10·9	—

*Specimens comprising the sample are housed in collections at the American Museum of Natural History (New York City), the Field Museum (Chicago), the National Museum of Natural History (Washington, DC), and the Cleveland Museum of Natural History (Cleveland).

†Body weights are taken from the literature (Gingerich *et al.*, 1982; Jungers & Susman, 1984; Harvey & Clutton-Brock, 1985; Fleagle, 1988; Markham & Groves, 1990) except for *Homo sapiens* (weights calculated from autopsy reports) and *Colobus guereza* and *Colobus angolensis* (weights derived from field records).

‡Various species of *Papio* are grouped as one "superspecies," *Papio hamadryas* (see Szalay & Delson, 1979; see also Jolly, 1993).
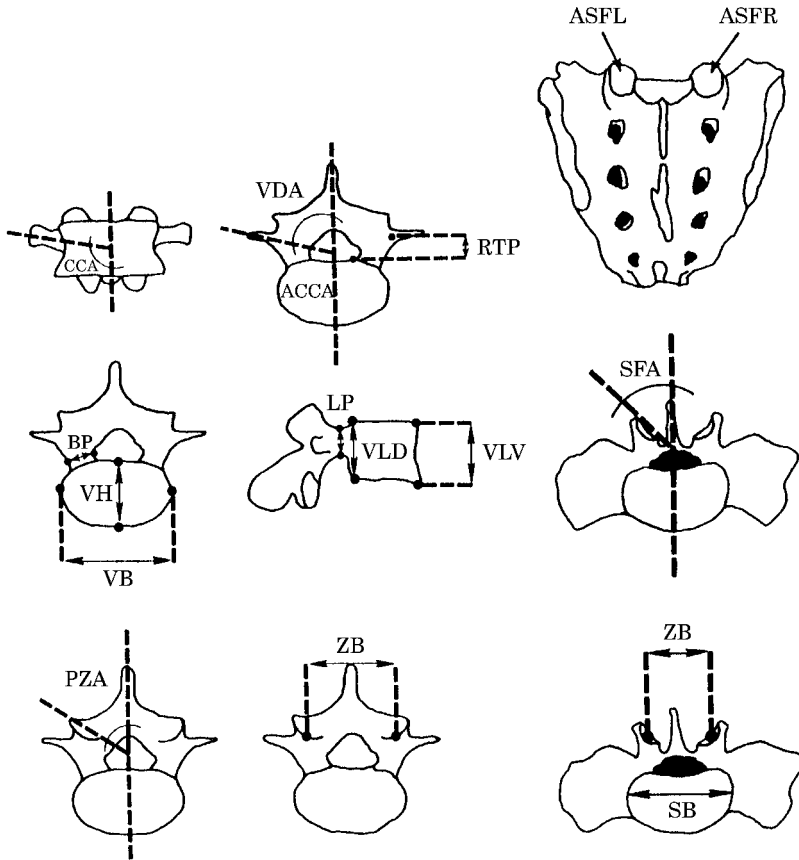
Figure 2. Vertebral measurements used in the study. Abbreviations: VB=vertebral body width, cranial end; VH=vertebral body height, cranial end; VLV=vertebral body length, ventral margin; VLD=vertebral body length, dorsal margin; BP=minimum pedicular width; LP=minimum pedicular length; ACCA=caudal surface area of the vertebral body; 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; ZB=distance between midpoints of right and left prezygapophyses or sacral facets; PZA=angle formed by a straight line along the medial and lateral edges of a prezygapophyseal facet, right side, as it intersects a sagittal midline through the centrum; SB=greatest width, cranial end of first sacral centrum; SFA=angle formed by a straight line along the medial and lateral edges of a sacral facet, right side, as it intersects a sagittal midline through the first sacral centrum; ASFR=sacral facet area, right side; ASFL=sacral facet area, left side.

usually slight, except between the penultimate and last lumbar vertebrae, the results of the analyses *do not differ materially* if upper-to-middle fossil lumbars are compared to modern catarrhine specimens several levels craniad or caudad in the lumbar region (see Sanders & Bodenbender, 1994). Without discounting the validity of alternative methods of making comparisons of unequal vertebral series (see, for example, Rose, 1975; Shapiro, 1993*b*), the present system is preferred especially because it recognizes and maintains the importance of the additive effects of weight bearing caudally through the column, and the unique structural transformation of the last
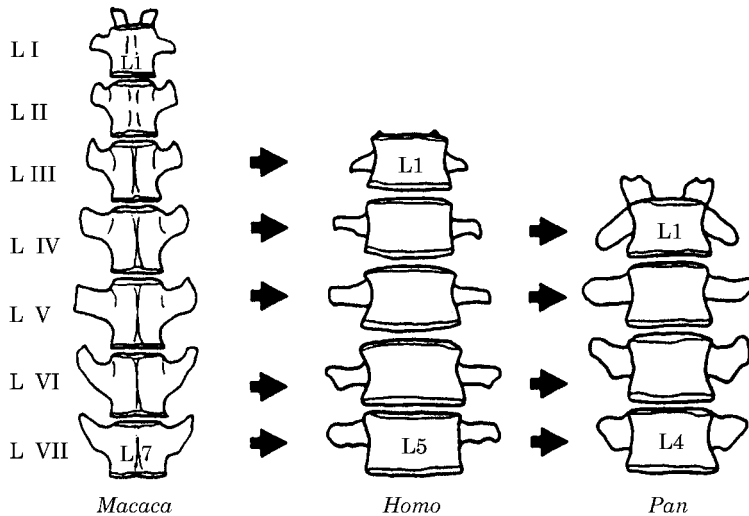
Figure 3. Labeling system for comparing equivalent vertebrae among individuals having lumbar series with different numbers of vertebrae. Equivalent lumbar spinal levels are designated with the same Roman numerals. In this system, for example, vertebrae L6 of *Macaca*, L4 of *Homo*, and L3 of *Pan* are considered equivalent for the purposes of morphological comparison and are labeled "L VI."

three lumbars and functional relationship of the last two lumbars vis-à-vis the pelvis (Sanders, 1995).

In the present study, quantitative assessment of structural differences among sample taxa is based on detailed comparative analyses of raw, indexed, and angular data. Further, regression analysis is used to examine the effect of body size on vertebral dimensions. Both least squares linear regression and reduced major axis regression are used to generate scaling coefficients of log-transformed vertebral dimensions against body weight for extant taxa. While least squares regression is the most frequently used technique to study the scaling of skeletal dimensions (y) in relation to body size (x), it does not assume variance in measurements of the independent variable, body size, and low correlations between x and y may produce misleading best-fit line slopes (Aiello, 1981; Sokal & Rohlf, 1987). These problems are addressed in reduced major axis regression and consequently it is seen by some as a better line-fitting technique (Rayner, 1985; Aiello, 1992). When

correlation coefficients are high, however, these models "tend to produce almost identical results and have little, if any, impact on interpretations" (Jungers, 1985, p. 352). Percentage deviations are used to determine the extent and direction that vertebral dimensions of fossil individuals and sex-specific samples depart proportionally from overall scaling trends, and are calculated as: observed value-predicted value × 100/predicted value (Jungers, 1982).

Results

Thoracic vertebrae
The Stw-H41 vertebrae are identified as the lowermost two thoracics by the remnants of cranially-placed costovertebral facets, for support of "floating" ribs, unaccompanied by caudal demifacets for rib articulations [Figure 1(a)]. These costovertebral facets are large and protuberant. When complete, each facet would have extended onto its corresponding pedicle. The centra are locally hollowed out immediately ventral and caudal to the rib facets.

While the modal number of thoracics in australopithecines is unknown, the Stw-H41 vertebrae probably represent either T11 and T12, or T12 and T13, as hominoids typically have either 12 (*Homo*, *Pongo*) or 13 (*Pan*, *Gorilla*, *Hylobates*) thoracics (Schultz, 1961; Sanders, 1995). For convenience, the Stw-H41 elements are referred to here as T11 and T12. They are cemented together by sediment, and have lost their neural arches. T11 lacks its cranial endplate. In T12, the surface cortex is damaged at the left caudo-lateral margin, corresponding closely to abrasion of the left cranio-lateral surface of vertebra L1 (=L II) in Stw-H8, and dorsally and caudally the right side of the centrum is chipped.

The structural affinity of the Stw-H41 thoracics with those of extant hominoids is marked by the dorsal position of their costovertebral facets, lack of ventral keeling, and ''blocky'' appearance (Figure 1 and Figure 4). In proportions of centrum width-to-height, the Stw-H41 vertebrae are similar to great ape and human lowermost thoracics, but differ from lowermost thoracics in *Pongo* and representative cercopithecoid species, which have dorsoventrally higher or lower centra, respectively (Table 2). Cranially, the Stw-H41 vertebrae are reniform in shape, and more round than oblong [Figure 1(d)], which is normal for hominoid vertebrae at this level (Aiello & Dean, 1990). However, the ratios of centrum width-to-length in the Stw-H41 vertebrae differ considerably from average ratios for lowermost thoracic vertebral bodies in great apes and humans (Table 2). Although the Stw-H41 thoracics have smaller transverse and sagittal dimensions than their human and great ape homologues, their centrum lengths are absolutely longer than mean centrum lengths of the extant sample (Table 2). Thus, the lowermost thoracics of Stw-H41 are elongate in comparison with those of large-bodied hominoids.

Shape differences between the centra of Stw-H41 and large-bodied hominoids may in part be allometric. This would not be surprising, given that among hominoids, vertebral body lengths scale with negative allometry in close correlation with increasing body size (Sanders & Bodenbender, 1994; Sanders, 1995). Resistance to bending moments is in inverse proportion to length in columnar structures (Slijper, 1946; Gordon, 1978), and therefore relative shortening of hominoid vertebral elements as body mass increases probably helps to maintain bony integrity against bending stresses, as well as shearing and buckling (Sanders, 1995). Analyses of australopithecine body sizes, especially for smaller, presumably female individuals, produce weight estimates suggesting that they were considerably lighter than extant large-bodied hominoids, including most humans (Reed & Falk, 1977; Suzman, 1980; Jungers, 1988a; McHenry, 1991b, 1992a,b; Hartwig-Scherer, 1993; see Table 1 and Table 5). As a result, centrum shapes in Stw-H41 are closer to those in smaller living catarrhines, such as gibbons and cercopithecoids (Table 2).

Proportionally, the Stw-H41 thoracics are nearly identical with corresponding elements in the Sts-14 *A. africanus* skeleton (Table 2). Prominent costovertebral facets are also observed in the lowermost thoracics of Sts-14, though in this individual the rib articulations are smaller and the penultimate thoracic has demifacets instead of complete costovertebral facets (Robinson, 1972). The Stw-H41 vertebrae are slightly larger than lowermost thoracic SK 3981a (*P. robustus*), and are much bigger than A.L. 288-1ac (*A. afarensis*) and the last thoracics in Sts-14 (*A. africanus*) (Figure 4 and Table 2). The dimensions of T12 in Stw-H41 and the presumed female Sts-14 (Robinson, 1972) have a size ratio of 1·32, equivalent to the sex-specific size differential for last thoracics in the highly dimorphic species *Gorilla gorilla* (calculated from Ward, 1991).
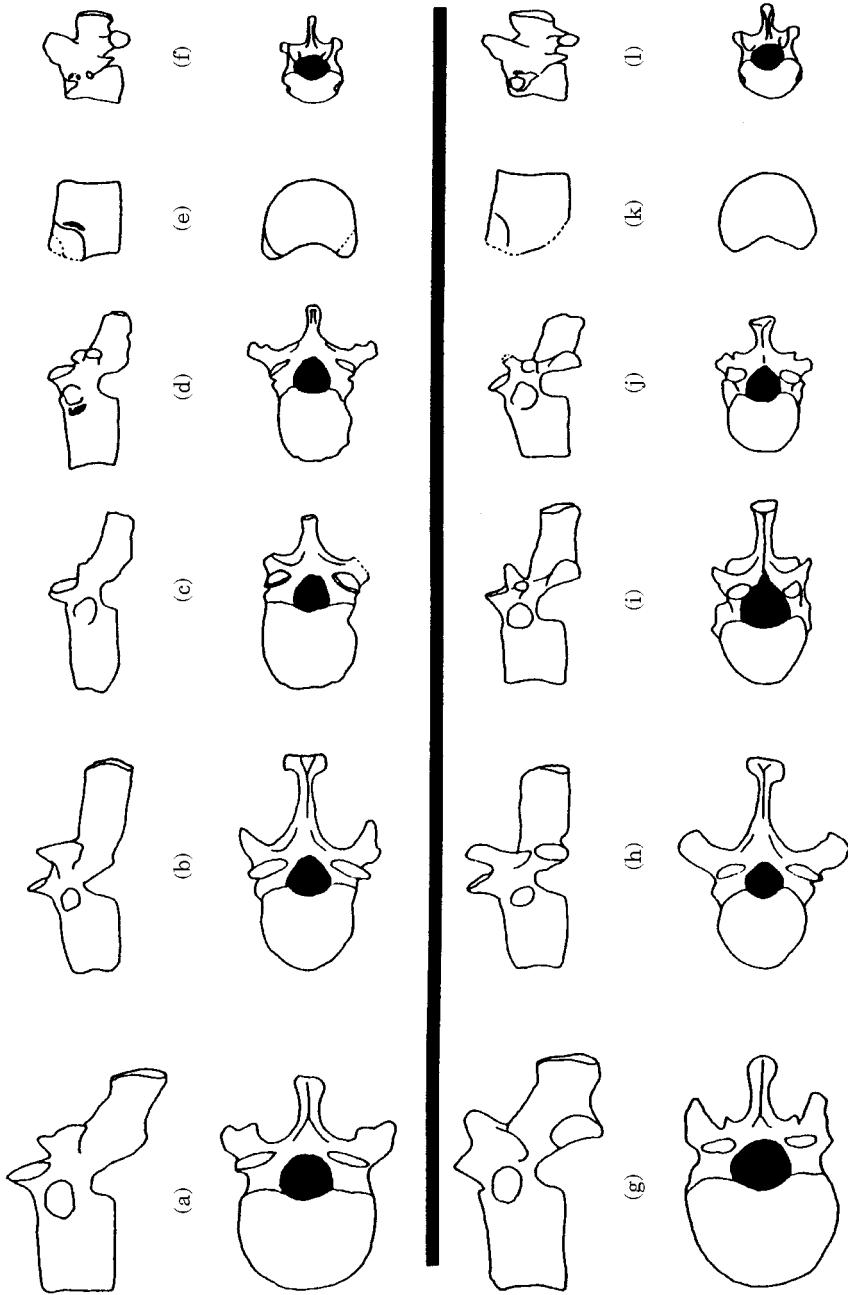
Figure 4. Lateral and cranial views of lowermost thoracic vertebrae of selected fossil hominids and extant catarrhines. a–f, penultimate thoracic vertebrae; g–l, last thoracic vertebrae. Vertebrae are to the same scale. Ventral is to the left for all vertebrae except those of Stw-H41. (a) *Homo sapiens*. (b) *Pan troglodytes*. (c) *Homo erectus* (KNM-WT 15000y). (d) *Australopithecus afarensis* (A.L. 288-1ac). (e) *A. africanus* (Stw-H41). (f) *Cercopithecus aethiops*. (g) *Homo sapiens*. (h) *Pan troglodytes*. (i) *Paranthropus robustus* (SK 3981a). (j) *A. africanus* (Stw-H41). (k) *A. africanus* (Sts-14g). (l) *Cercopithecus aethiops*.

Table 2 Comparative dimensions and indices of penultimate (T11 or T12) and last (T12 or T13) thoracic vertebrae in selected extant catarrhines and fossil hominids

Taxon/specimen	Vertebra	n	Centrum length, ventral (VLV)	Centrum length, dorsal (VLD)	Centrum width, cranial (VB)	Centrum height, cranial (VH)	Centrum cranial surface shape index VB × 100/VH	Centrum shape index VB × 100/VLV	Centrum wedging index VLV × 100/VLD
Homo sapiens[C]	T11	29	19·9 (1·6)	22·2 (1·7)	37·0 (3·9)	27·6 (2·8)	134	186	90
Pan troglodytes[C]	T12	14	15·0 (0·9)	17·7 (1·0)	29·9 (2·1)	22·4 (1·9)	133	199	85
Gorilla gorilla[C]	T12	10	17·5 (1·9)	20·9 (2·1)	38·8 (4·6)	28·2 (3·3)	138	222	84
Pongo pygmaeus[C]	T11	10	14·7 (1·9)	18·8 (1·6)	29·1 (3·2)	24·2 (2·9)	120	198	78
Lophocebus albigena[C]	T11	34	11·5 (0·9)	14·4 (1·2)	14·6 (1·2)	10·1 (1·2)	145	127	80
A. afarensis A.L. 288-1ac	T11	1	13·9	16·1	22·5	20·2	111	162	86
A. africanus Sts-14h	T11	1	15·2[M]	17·3[M]	18·4[M]	—	—	121	88
Stw-H41	T11	1	+20·3	+21·6	27·7	19·5	142	<136	94
H. erectus KNM-WT 15000y	T11	1	+13·6	+15·6	29·4	22·5	131	<216	87

Table 2 Continued

Taxon/ specimen	Vertebra	n	Centrum length, ventral (VLV)	Centrum length, dorsal (VLD)	Centrum width, cranial (VB)	Centrum height, cranial (VH)	Centrum cranial surface shape index VB × 100/VH	Centrum shape index VB × 100/VLV	Centrum wedging index VLV × 100/VLD
Homo sapiens[C]	T12	29	21·6 (2·0)	23·4 (1·6)	40·9 (4·2)	28·3 (3·1)	145	189	92
Pan troglodytes[C]	T13	14	16·3 (1·1)	19·7 (1·3)	32·7 (2·5)	22·8 (1·7)	143	201	83
Gorilla gorilla[C]	T13	10	20·7 (2·2)	23·6 (1·8)	41·7 (4·2)	29·0 (3·0)	144	201	88
Pongo pygmaeus[C]	T12	10	17·0 (1·8)	21·0 (1·6)	32·1 (3·5)	24·4 (3·0)	132	189	81
Hylobates lar[W]	T13	20	11·8	13·1	16·1	10·7	150	136	90
Lophocebus albigena[C]	T12	34	12·7 (0·9)	16·0 (1·2)	16·5 (1·5)	10·1 (1·2)	163	130	79
Papio hamadryas[W]	T12	20	17·2	19·4	25·0	15·4	163	145	89
A. africanus									
Sts-14g	T12	1	17·0[M]	19·1[M]	22·1[M]	15·3[M]	144	130	89
Stw-H41	T12	1	22·5	25·2	29·1	20·0	146	129	89
P. robustus									
SK 3981a	T12	1	19·2[M]	20·2[M]	27·3[M]	16·0[M]	171	142	95

Mean values are provided for each extant species; standard deviations are given in parentheses. Dimensions are given in mm. "+" indicates missing endplate(s), and that the original length was greater. "<" indicates that the centrum shape index would be lower if the endplate(s) were intact.
[C]Dimensions from Clauser, 1980.
[M]McHenry, unpublished data.
[W]Dimensions from Ward, 1991; standard deviations unavailable; dimensions of penultimate thoracic vertebrae in *Papio* and *Hylobates* unavailable.

Table 3 Dimensions of fossil hominid lumbar and sacral vertebrae

Species/ accession number	Vertebra	VB	VH	VLV	VLD	BP	LP
Australopithecus afarensis							
A.L. 333-73	L3?	34·0[L]	22·7[L]	25·0[L]	24·5[L]	8·3	16·2
A.L. 288-1 aa/ak/al	L2 or L3	29·9	16·5	19·9	21·7	6·0	11·6
Australopithecus africanus							
Sts-14 f	L1	—	—	—	19·6[R]	5·0	11·3
e	L2	23·2[M]	17·5[M]	19·3[R]	19·9[R]	4·5	11·3
d	L3	25·0[M]	17·7[M]	19·7[R]	19·5[R]	5·1	10·0
c	L4	26·2[M]	18·4[M]	19·4[R]	19·1[R]	6·5	10·3
b	L5	—	17·2[M]	18·4[R]	17·3[R]	5·9	8·3
a	L6	27·7[M]	19·0[M]	18·8[R]	16·8[R]	7·9	8·4
Sts-73	L1?	31·7[R]	22·2[R]	19·7[Z]	20·1[R]	—	—
Stw-H8 A	L1	—	21·2	23·2	24·8	—	—
B	L2	33·0	22·5	22·7	24·4	9·2	12·8
C	L3	32·2	23·2	20·0	21·5	8·5	11·8
D	L4	34·2	21·6	—	—	—	—
Paranthropus robustus							
SK 3981b	Last lumbar vertebra	39·7[R]	23·7[R]	21·3[R]	19·0[R]	11·5	9·6
SK 853	Lumbar vertebra	27·4[M]	15·8[M]	15·5[M]	16·5[M]	5·0	—
Homo erectus							
KNM-WT 15000							
AR+BA	L1	30·6	22·5	15·9	17·2	—	—
AA+AV	L2	31·2	—	15·4	17·2	6·7	10·4
Z+BW	L3	—	—	—	—	9·5	—
AB	L4	37·6	27·0	—	17·7	10·1	8·9
BM	L5	38·6	26·7	19·5	17·6	13·3	9·1
AC	L6	40·9	27·3	20·1	15·6	15·2	9·4

		ACCA	VDA	CCA	PZA	ZB	RTP
Australopithecus afarensis							
A.L. 333-73	L3?	7·2	—	—	—	—	—
A.L. 288-1 aa/ak/al	L2 or L3	4·5	—	—	33	24·5	−7·5
Australopithecus africanus							
Sts-14 f	L1	2·4	70	71	29	16·1	−2·4
e	L2	3·2	67	97	31	17·2	−4·9
d	L3	4·0	69	113	37	17·4	−3·4
c	L4	4·5	74	114	50	19·1	−2·8
b	L5	—	80	86	52	20·3	−2·9
a	L6	4·1	75	111	62	30·0	−0·6
Sts-73	L1?	5·9	—	—	—	—	—
Stw-H8 A	L1	6·0	—	—	—	—	—
B	L2	6·3	77	113	40	26·0[e]	−4·7
C	L3	6·4	—	—	45[e]	28·0[e]	−4·1
D	L4	—	—	—	—	—	—
Paranthropus robustus							
SK 3981b	Last lumbar vertebra	5·2[e]	67	104[e]	—	—	0·0
SK 853	Lumbar vertebra	4·3	64	—	33	19·1	−9·0

Table 3 *Continued*

Species/accession number	Vertebra	VB	VH	VLV	VLD	BP	LP
Homo erectus							
KNM-WT 15000							
AR+BA	L1	6·5[e]	—	—	—	—	—
AA+AV	L2	—	—	—	36	—	—
Z+BW	L3	—	—	—	—	20·7	—
AB	L4	7·7	—	—	35	26·2	− 8·1
BM	L5	9·6	76	92	54	29·5	− 7·2
AC	L6	8·7	78	91	60	31·2	− 4·3

		ASFR (cm^2)	ASFL (cm^2)	SFA	SB	ZB
Australopithecus afarensis						
A.L. 288-1 an	S1	0·9	0·8	55	37·7	36·2[e]
Australopithecus africanus						
Sts-14	S1	—	0·7	62	27·0[R]	30·0[e]
Homo erectus						
KNM-WT 15000						
AD/BY/BB/BC/AE/AF	S1	0·9[e]	1·4	87	41·0[e]	41·0[e]

Linear measurements are in mm, areas are in cm^2, and angles are in degrees. Abbreviations and explanations of measurements are given in Figure 2. Dimensions of original specimens are from [Z]Zihlman (1971), [R]Robinson (1972), [W]Wolpoff (1973), [L]Latimer (unpublished data), and [M]McHenry (unpublished data).
[e]Estimated dimension.

Although observed size ranges in fossils and average dimorphism in extant taxa are not directly comparable (Richmond & Jungers, 1995), nonetheless this ratio supports the view of Tobias (1980, p. 9) that these vertebrae "point to a strong degree of sexual dimorphism in body size . . . in *A. africanus*."

SK 3981a, assigned to *Paranthropus robustus* (Robinson, 1972), resembles last thoracic vertebrae of *A. africanus* in the relative elongation of its centrum [Figure 4(h) and Table 2]. While its superior surface is also kidney-shaped [Figure 4(h)], it is more compressed dorsoventrally and consequently has a higher cranial surface shape index than last thoracics in extant hominoids and other australopithecines (Table 2). Conversely, the centrum of A.L. 288-1ac (*Australopithecus afarensis*) has a low cranial surface shape index (Table 2), reflecting its nearly circular contour [Figure 4(d)]. However, the cranial outline of this specimen has been altered by pathological bone formation along the ventral margin of the centrum (Cook *et al.*, 1983). The centrum shape index for A.L. 288-1ac (Table 2) seems to indicate that it is also relatively shorter than lowermost thoracics in other australopithecines. An alternative explanation is that it is relatively broader, as there is some pathological expansion of the ring apophyses transversely in this specimen, suggesting that normal proportions of lowermost thoracic vertebrae in *A. afarensis* are similar to those in *A. africanus*. In contrast, even with the addition of endplates the T11 centrum of *Homo erectus* juvenile KNM-WT 15000 would be shaped like those of extant large-bodied hominoids, relatively much broader and shorter than corresponding elements in australopithecines (Figure 4 and Table 2).

Lumbar vertebrae

Dimensions for lumbar vertebrae in Stw-H8 and other fossil hominids are given in Table 3. In overall size, the Stw-H8 lumbars are comparable to A.L. 333-73 (*A. afarensis*) and Sts-73 [from a presumed male of *A. africanus* (Robinson, 1972)], and larger than lumbars from A.L. 288-1aa/ak/al (*A. afarensis*) and subadult *P. robustus* individual SK 853. The size disparity between thoracic elements in Stw-H41 and Sts-14 is also expressed in the Stw-H8 and Sts-14 lumbars, and is paralleled by A.L. 333-73 and A.L. 288-1aa/ak/al (Figure 5), whose dimensions produce an average size ratio of 1·33. Although there is no known adult *P. robustus* homologue to Stw-H8 lumbars L1–L4 (=L II–L V), in size last lumbar SK 3981b would fit well at the lower end of the Stw-H8 vertebral series.

It is unknown how many lumbars were originally present in the Stw-H8 individual. However, it may be argued from the presence of six lumbar vertebrae in Sts-14 (Robinson, 1972), Stw-431 (McHenry & Berger, 1996), and KNM-WT 15000 (Latimer & Ward, 1993) that it is the primitive condition for modal number of lumbar elements in hominids, and therefore that Stw-H8 probably had six lumbar vertebrae. Cranial centrum outlines in Stw-H8 gradually transform in shape between L1 (=L II) and L4 (=L V) from reniform with a strong dorsal concavity to nearly ovoid with a shallow dorsal concavity [Figure 1(d)]. This is consistent with the notion that at least one more lumbar was formerly present in the Stw-H8 series, as last lumbar vertebrae in hominoids frequently have straight or convex dorsal centrum margins. The modal number of lumbars in modern humans is five, and the variant of six lumbars occurs at low frequency in most human populations (Schultz, 1961).

The Stw-H8 lumbars are fixed in a ventrally-concave lateral profile by sediment [Figure 1(a)]. This kyphosis was probably caused by post-mortem shrinkage of the anterior longitudinal ligament. In L1 (=L II), the centrum is damaged craniolaterally on the right side, the neural arch is incomplete on the left side [Figure 1(c)], the spinous process is reduced by weathering or breakage [Figure 1(a)], and only the right postzygapophysis is preserved. L2 (=L III) also lacks the left side of the neural arch and has a truncated spinous process [Figure 1(a),(c)], but retains pre- and postzygapophyses on the right side. In addition, it has an osteophytic bump on the right ventral face of the vertebral body [Figure 1(a)]. A rugose lesion is found in a similar position on the ventral face of the centrum of middle lumbar A.L. 288-1aa/ak/al (*A. afarensis*) (Johanson *et al.*, 1982; Cook *et al.*, 1983). These osteophytic growths are formed by ossification of anterior longitudinal ligament attachments and are associated with either arthritis or mechanical trauma (Cook *et al.*, 1983). L3 (=L IV) has a smaller osteophyte ventrally. While L3 preserves the right prezygapophysis and pedicle, the rest of its neural arch is missing [Figure 1(a),(c)], and it has suffered some minor abrasions of its centrum. L4 (=L V) has completely lost its neural arch, and is sheared in such a way that it is without most of the caudal and dorsal part of its vertebral body [Figure 1(a),(b),(c)].

Vertebral bodies. The vertebral bodies of Stw-H8 are like those of extant hominoids, squat in ventral view, with no keeling or hollowing [Figure 1(b)]. Although there is some overlap between hominoids and cercopithecoids in lumbar centrum proportions, apes tend to have relatively mediolaterally wider, craniocaudally shorter lumbars than monkeys, and even the diminutive gibbons have, on average, wider centra than the largest monkeys (Table 4). These differences reflect craniocaudal shortening and mediolateral broadening of hominoid centra in functional association with the need for
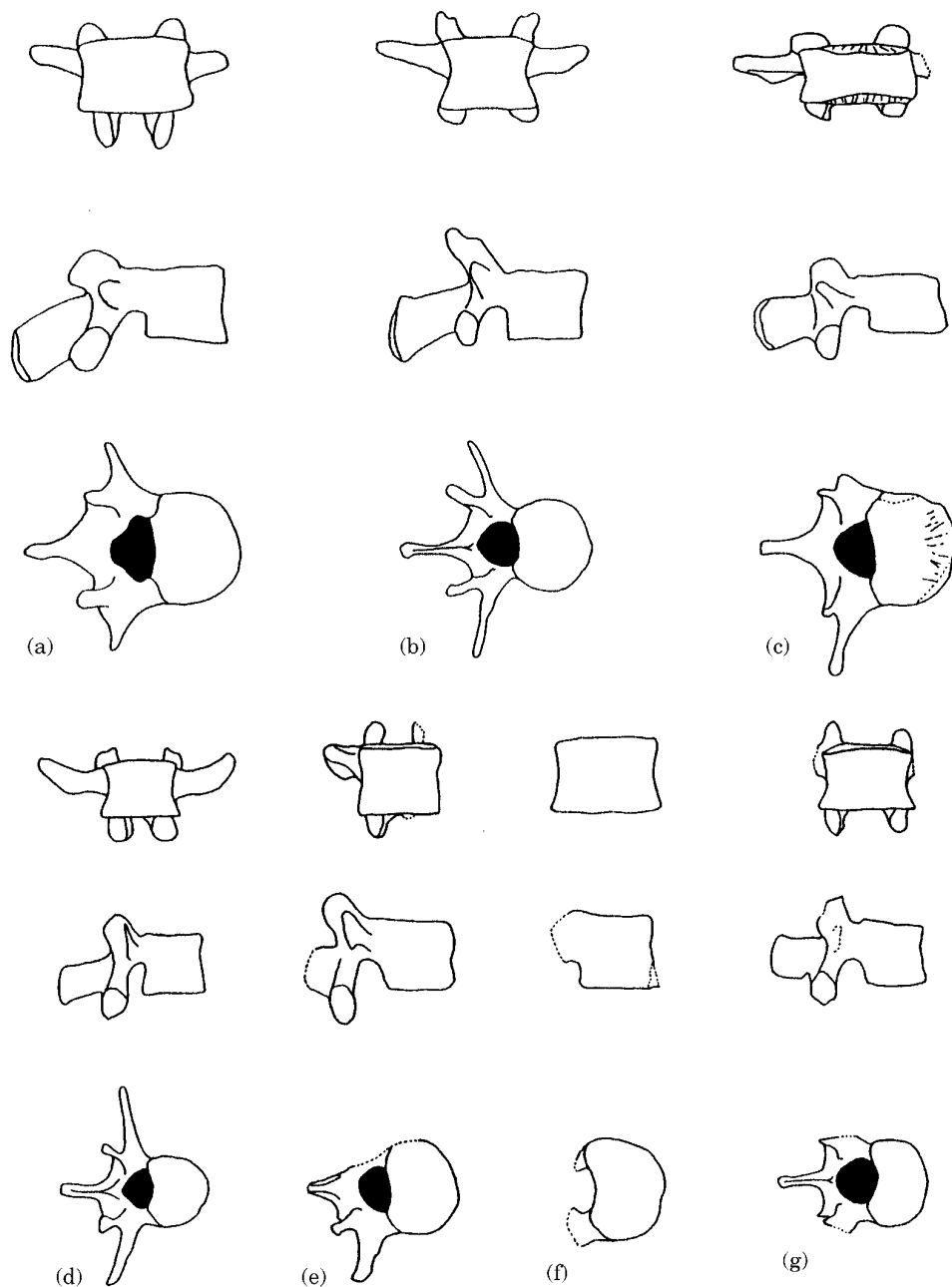
Figure 5. Middle lumbar vertebrae of selected fossil hominids and extant hominoids. Vertebrae are to the same scale. Each vertebra is shown in ventral (top), right lateral (middle), and cranial (bottom) view. For lateral and cranial views, ventral is to the right. For ventral views, cranial is to the top of the page. (a) *Homo sapiens*, L3. (b) *Pan troglodytes*, L2. (c) *Homo erectus* (KNM-WT 15000bm), L5. (d) *Australopithecus africanus* (Sts-14d), L3. (e) *A. africanus* (Stw-H8), L2. (f) *A. afarensis* (A.L. 333-73), L2 or 3. (g) *A. afarensis* (A.L. 288-1aa/ak/al), L2 or 3.

Table 4 Centrum shape indices of lumbar vertebrae for selected catarrhine taxa and fossil hominid individuals

Taxon	Sex	n		LI	LII	LIII	LIV	LV	LVI	LVII
Papio hamadryas	F	5	Mean	139	134	126	118	117	116	135
			S.D.	15	18	14	11	8	7	9
			Range	122–152	108–154	109–145	103–132	107–125	108–125	125–149
Papio hamadryas	M	5		150	144	132	128	126	128	141
				13	7	6	9	5	4	5
				141–159	136–154	122–139	116–138	121–133	124–132	137–149
Other cercopithecoid species	All	189	Range	85–149	82–161	79–136	75–124	76–120	75–138	87–150
Hylobates spp.	F	4				148	130	129	135	153
						—	11	12	14	17
						147–148	118–138	112–141	117–145	137–175
Hylobates spp.	M	8				144	144	136	143	156
						13	10	10	7	6
						128–163	129–160	123–152	134–150	150–164
Pongo pygmaeus	F	5					145	140	144	155
							12	14	12	16
							130–153	126–154	130–154	134–170
Pongo pygmaeus	M	8					158	158	162	167
							18	15	19	13
							138–178	140–180	139–181	146–182
Pan troglodytes	F	13					153	152	154	154
							13	14	16	14
							140–182	135–174	129–188	138–183
Pan troglodytes	M	12					166	165	161	166
							15	13	17	15
							147–198	149–185	138–206	137–195

Table 4 Continued

Taxon	Sex	n				Vertebral levels			
			LI	LII	LIII	LIV	LV	LVI	LVII
Gorilla gorilla	F	10				154 10	150 14	153 12	159 12
Gorilla gorilla	M	10				141–166 155 13	127–169 163 14	136–177 166 11	139–182 168 11
Homo sapiens	F	20			155 13	138–177 155 11	146–190 159 11	146–179 165 14	151–186 177 18
Homo sapiens	M	20			120–175 174 14	130–176 174 14	138–179 175 14	145–196 177 15	144–211 177 15
Homo erectus WT 15000 (subadult)	M	1		<192	156–201	156–213	153–206	159–199	154–214
A. africanus Sts-14	F	1		—	<203	—	—	<198	<203
A. africanus Stw-H8	M?	1		—	121	124	128	139	139
A. africanus Sts-73	M?	1		161	147	151	—	—	—
A. afarensis A.L. 288-1 aa/ak/al	F	1		—	—	150	—	—	—
A. afarensis A.L. 333-73	M?	1		—	—	135	—	—	—
P. robustus SK 853 (subadult)	?	1		—	—	<177	—	—	—
P. robustus SK 39981b	?	1		—	—	—	—	—	186

Shape indices are calculated as VB × 100/VLV (abbreviations are explained in Figure 2). Index values >100 indicate vertebrae wider than long. Index values <100 indicate vertebrae longer than wide. "<" indicates that the shape index would be lower if the endplate(s) were intact.

increased lower spinal stability during climbing, bridging, and transferring behaviors, and for greater orthogrady (Cartmill & Milton, 1977; Jungers, 1984). Humans constantly support their upper body weight vertically on their vertebral column and consequently have proportionally the widest centra among hominoids, especially at the lower end of the lumbar series (Table 4).

Lumbar centrum shape indices are also given for fossil hominids in Table 4. Indices calculated for Stw-H8 vertebrae L2–L3 (=L III–L IV) are similar to average ratios of width-to-length for middle lumbars in female great apes (as is A.L. 288-1aa/ak/al), but are low compared with mean sex-specific indices for humans. The centrum of Sts-73 is more human-like in this regard. Conversely, the lumbar centra of Sts-14 and A.L. 333-73 are below or at the low end of index ranges for apes and are proportionately closest to those of extant large-bodied cercopithecoids (Rose, 1975; Sanders, 1995). These differences do not reveal a clear sex-specific pattern of variation for australopithecines. Lumbar centrum shape indices for KNM-WT 15000 and *P. robustus* are most similar to those of humans.

Regression analyses more clearly sort out the contributions of individual dimensions to variations in centrum shape among australopithecines, and between australopithecines and extant sample taxa. For example, in ratio to width, australopithecine lumbars appear relatively long compared with those of other hominoids (Figure 6). However, percentage deviations for the Sts-14 lumbars (Table 5) in regressions of centrum dimensions against body weight (Appendix 1) show that they are close to predicted lengths for an ape of its estimated body weight (see also Velte, 1984, 1987), and instead are relatively narrow and dorso-ventrally compressed. In contrast, these regressions indicate the middle lumbar of individual A.L. 288-1 to be the expected length and relatively wide, but low, com-

pared with an ape of its estimated size (Table 5). Humans have relatively very wide, high, and slightly elongate lumbar centra, and KNM-WT 15000 uniquely has lumbar centra that are relatively *short* and wide compared with ape homologues (Table 5). In addition, in comparison with humans and *Homo erectus* individual KNM-WT 15000, Sts-14 and A.L. 288-1 have relatively small lumbar centrum articular surfaces (Table 5). Without non-vertebral estimates of body weight, it is impossible to make similar determinations for Stw-H8 (and other australopithecine individuals). Nonetheless, compared with humans, its lumbars are either relatively narrow or elongate, or both.

Lumbar centrum wedging indices for extant catarrhines and fossil hominids are compiled in Table 6. These indices represent the ratio of ventral to dorsal centrum length. Vertebral wedging helps determine spinal curvatures and is associated with orientation of the trunk and range of intervertebral joint motion (Cunningham, 1886; Jenkins, 1974; Rose, 1975; Clauser, 1980). In non-human catarrhines, lumbar vertebral bodies are characteristically ventrally-wedged (longer dorsally), although index values may approach or slightly exceed 100 (indicating greater ventral length, or dorsal wedging) at the level of the last lumbar, and their lumbar columns are typically kyphotic, or ventrally concave. The human lumbar spine must make a transition between a ventrally-tilted sacral platform and an upright thorax, and therefore is uniquely lordotic, or ventrally convex. Lumbar lordosis is achieved in humans by dorsal wedging of the centra and intervertebral discs.

The last four vertebrae in the lumbar column of Sts-14 are dorsally wedged (Table 6). This has been interpreted as evidence for lordosis of the lower spine and habitual bipedality (Robinson, 1972; Rose, 1975; Aiello & Day, 1982; Ward & Latimer,
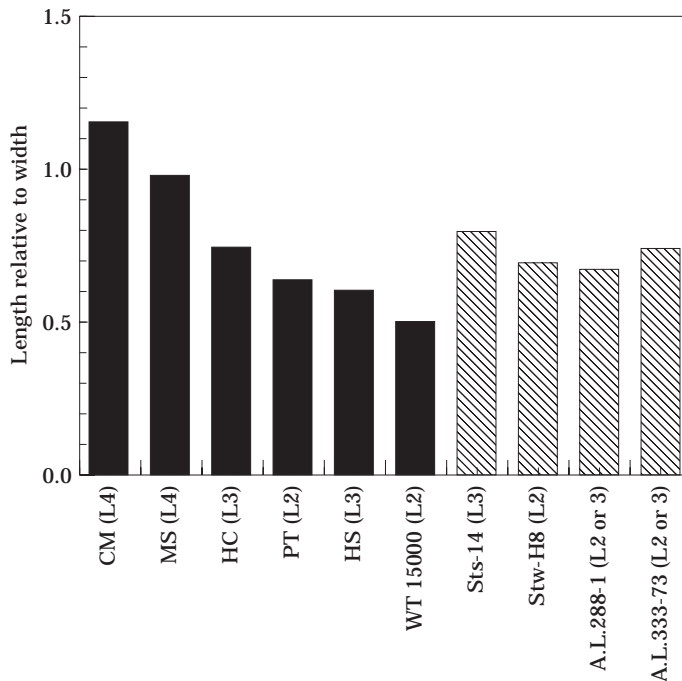
Figure 6. Length of lumbar vertebral bodies, in ratio to width, in selected fossil hominids and extant catarrhines. Mean values are given for extant species. Abbreviations for extant species are explained in Table 1. Fossil species represented are *Homo erectus* (KNM-WT 15000), *Australopithecus africanus* (Sts-14 and Stw-H8), and *A. afarensis* (A.L. 288-1 and A.L. 333-73). Black columns show relative length of centra in extant species and KNM-WT 15000. Cross-hatched columns show relative length of centra in australopithecine individuals.

1991). In addition, dorsal wedging is observed in middle lumbar A.L. 333-73, last lumbar SK 3981b, and at least in the L5 and L6 (=L VI and L VII) vertebrae of KNM-WT 15000 (Table 6). First lumbar (=L II) Sts-73 has a wedging index of 98, and as wedging indices usually progressively increase through the lumbar series in catarrhines, it is likely that its lower lumbars were dorsally wedged.

In contrast with humans and *Homo erectus* individual KNM-WT 15000, which accomplish dorsal wedging by serially increasing ventral centrum length at a greater rate than dorsal length through the lumbar column (Anderson, 1883; Sanders, 1995), dorsal wedging is attained in the Sts-14 lumbar series by serially *decreasing* dorsal centrum length more than ventral

length from L1–L6 (L II–L VII) (Table 3). Serial decrease in ventral and dorsal centrum lengths is shared by Stw-H8, and is apparently peculiar to australopithecines. Nevertheless, there is no sign of dorsal wedging in the first three lumbars (=L II–L IV) of Stw-H8, or in middle lumbars A.L. 288-1aa/ak/al and SK 853 (Table 6). However, lumbar lordosis cannot be ruled out for these individuals as some or all of their last three lumbar centra (assuming that they had six lumbars) could have been dorsally-wedged. In humans, there is considerable variation in the pattern of centrum wedging and in the expression of lumbar curvature (Cunningham, 1886; Sullivan & Miles, 1959; Knussman & Finke, 1980). While human vertebrae are usually dorsally wedged at least at the level of the

Table 5   Percentage deviations from least square regressions of lumbar centrum dimensions to body weight in non-human hominoids (see Appendix 1)

Taxon	BW (kg)	Sex	L IV	L V	L VI	L VII
				Vertebral levels		
				Ventral length		
Apes		All	− 4 to +3	− 3 to +2	− 2 to +3	− 2 to +3
Humans		F	+5	+4	+4	+3
		M	+3	+2	+3	+3
WT 15000	48·0*	M	—	—	− 5	− 5
Sts-14	27·4†	F	+1	− 1	− 3	− 2
A.L. 288-1	30·0‡	F	0	—	—	—
				Width		
Apes		All	− 1 to +2	− 1 to +2	− 1 to +3	− 1 to +3
Humans		F	+5	+5	+6	+6
		M	+6	+6	+7	+6
WT 15000	48·0*	M	—	+2	− 3	+2
Sts-14	27·4†	F	− 4	− 4	—	+6
A.L. 288-1	30·0‡	F	+5	—	—	—
				Height		
Apes		All	− 2 to +2	− 3 to +2	− 3 to +4	− 4 to +3
Humans		F	+4	+4	+5	+6
		M	+5	+5	+6	+6
WT 15000	48·0*	M	—	+2	− 2	+3
Sts-14	27·4†	F	− 4	− 5	− 4	− 2
A.L. 288-1	30·0‡	F	− 6	—	—	—
				Surface area		
Hylobatids		All	− 8 to +7	− 6 to +5	− 6 to +4	− 22 to +26
African apes		All	− 2 to +2	− 2 to +1	− 1 to +2	− 1 to +3
Orang-utans		All	− 3 to +7	− 2 to +7	− 2 to +7	− 2 to +11
Humans		F	+12	+12	+10	+16
		M	+18	+17	+16	+21
WT 15000	48·0*	M	—	+1	+10	+13
Sts-14	27·4†	F	− 14	− 10	—	− 10
A.L. 288-1	30·0‡	F	− 10	—	—	—

Percentage deviations are calculated as observed − predicted × 100/predicted (Jungers, 1984). Ape taxa used in the regressions are PT, GG, PP, HC, and HM (abbreviations are explained in Table 1). Dimensions: ventral length=VLV; width=VB; height=VH; surface area=ACCA (measurements are explained in Figure 2).
    *Calculated by Ruff & Walker (1993).
    †Calculated by McHenry (1988).
    ‡Calculated by McHenry (1988) and Jungers (1990).

last two lumbars, dorsal wedging may occur at all lumbar levels, or only in the last lumbar (Sanders, 1995).

Transverse processes. In Stw-H8, the only transverse process preserved is on the right side of L2 (=L III). This process is moderately long, angled slightly cranially, and has a prominent inferior tubercle [Fig. 1(b)] for the insertion of m. longissimus. As in extant great apes and humans, the surviving Stw-H8 lumbar transverse process has a

pedicular origin (Table 7), and is dorsally reflected (Figure 7).

Among mammals, position and orientation of lumbar transverse processes are closely correlated with functional differences of the lower back associated with contrasts in typical positional behaviors (Hatt, 1932; Howell, 1965; Gambaryan, 1974; Hildebrand, 1988). In cercopithecoids and other dorsomobile mammals, lumbar transverse processes are laterally rooted on the vertebral bodies and are angled cranially and

Table 6 Centrum wedging indices of lumbar vertebrae for extant catarrhine taxa and fossil hominid individuals

Taxon	Sex	n	Statistic	LI	LII	LIII	LIV	LV	LVI	LVII
Cercopithecoid species (PH, MS, CA, CG, CT, MN, MA, MF, CAe, CM, CN, EP, CoP, CoA, CoG, CoB, NL, PrC, PrM, PrE)[1]	All	105	Range	70–96	72–97	78–99	78–98	82–98	84–102	84–106
			Mean			90	92	94	94	95
			S.D.			3	3	3	2	2
Hylobates spp.	F	5	Range			87–93	88–95	90–99	93–97	92–98
			Mean			88	89	91	92	90
			S.D.			5	5	4	7	4
Hylobates spp.	M	8	Range			78–96	81–96	84–97	85–94	84–96
			Mean			96	92	90	92	96
			S.D.			3	3	4	5	3
Pongo pygmaeus	F	5	Range				87–95	84–94	87–97	93–100
			Mean				93	92	92	98
			S.D.				6	5	4	6
Pongo pygmaeus	M	8	Range				82–103	83–100	86–97	91–110
			Mean				93	92	93	100
			S.D.				4	6	6	5
Pan troglodytes	F	13	Range				86–99	84–101	83–104	91–108
			Mean				90	88	93	98
			S.D.				6	3	7	6
Pan troglodytes	M	12	Range				76–95	83–93	77–99	88–106
			Mean				95	99	99	102
			S.D.				3	3	3	5
Gorilla gorilla	F	10	Range				92–100	93–106	96–103	91–109
			Mean				97	96	95	100
			S.D.				5	5	4	4
Gorilla gorilla	M	10	Range				91–106	86–104	88–99	97–110
			Mean				100	103	106	114
			S.D.				3	5	5	7
Homo sapiens	F	20	Range			90–103	92–105	96–113	98–114	100–127
			Mean			93	95	100	104	116
			S.D.			3	4	4	4	8
Homo sapiens	M	20	Range			88–98	87–102	90–105	98–113	108–138
Homo erectus WT 15000 (subadult)	M	1			92	90	—	—	111	129
A. africanus Sts-14	F	1			—	97	101	102	106	112
A. africanus Stw-H8	M?	1			94	93	93	—	—	—

Shape indices are calculated as VLV × 100/VLD (abbreviations are explained in Figure 2). Index values <100 indicate ventral wedging (vertebral body is longer dorsally). Index values >100 indicate dorsal wedging.

[1] Abbreviations are given in Table 1.

ventrally (Table 7 and Figure 7; Mivart, 1865; Ankel, 1967, 1972). This arrangement creates a large ''trough'' to accommodate thick erector spinae muscles (Benton, 1967, 1974). Cranial angulation of transverse processes allows the lower spine to be laterally flexed without bony impingement of adjacent vertebrae (Gambaryan, 1974). In addition, cephalad elongation and ventral orientation of lumbar transverse processes shift the insertions of iliocostalis away from the point of rotation, or fulcrum of each lumbar vertebra at the center of its caudal end, thereby heightening the effectiveness of this muscle by lengthening its lever arm, and increase the distance that these muscles may extend the lumbars. Such spinal adaptations are advantageous for powerful recovery of the flexed spine and for hyperextending the lower back (and concomitant increase of stride length) during running, bounding, and leaping (see Morbeck, 1976; Fleagle, 1977; Rose, 1977; Wells et al., 1977; Hurov, 1982, 1985, 1987).

In small-bodied hylobatids, lumbar transverse processes arise from the centro-pedicular junction and are laterally set, while in great apes these processes take their origin more dorsad, on the pedicles, and are dorsally oriented (Table 7 and Figure 7; Mivart, 1865; Ankel, 1967, 1972). These configurations correspond with reduced cross-sectional areas for erector spinae muscles (Vallois, 1928; Benton, 1967, 1974; Donisch, 1973). However, shifting epaxial muscles posterior to centers of vertebral rotation limits their range of contraction and enhances their ability to resist forward flexion of the lumbar column (Ward, 1993; Sanders, 1995, 1996). The rheostatic quality of lower back muscles in apes is mechanically consistent with maintaining orthograde posture and controlling movement between the thorax and pelvis during suspensory and bridging behaviors.

As well as resisting ventral rotation of the trunk, in humans the erector spinae muscles must also sustain lordosis of the lumbar column. Consequently, humans have relatively thicker, more differentiated and more complex erector spinae muscles than other hominoids (Vallois, 1928; Winckler, 1948; Bogduk, 1980; Bogduk & Twomey, 1987; MacIntosh & Bogduk, 1987). In addition, the leverage of these muscles is increased in humans by a tendency for their transverse process to arise more dorsally on the pedicles than in other hominoids (Table 7; Mivart, 1865; Sanders, 1995). T-tests for samples of unequal size comparing sex-specific means for indices of transverse process position show that human means differ significantly from nearly all non-human catarrhine means at comparable vertebral levels (Table 7), though these results should be considered preliminary given small sample sizes. Leverage of the erector spinae muscles is further increased by the dorsal reflection of their posterior superior iliac spines (Aiello & Dean, 1990; Schmid, 1991), which provide their origin.

Transverse process position indices for Stw-H8, calculated for L2 and L3 (=L III and L IV), are close to mean index values for great apes and outside the range of human indices (Table 7). Index values for the Sts-14 lumbars are also closer to those of apes, while those for A.L. 288-1aa/ak/al, SK 853, and the KNM-WT 15000 lumbars indicate more dorsal, human-like, origins for their transverse processes (Table 7), suggesting greater mechanical advantage for resisting forward flexion of the trunk in individuals sampled of *A. afarensis* and *H. erectus* than of *A. africanus*. Despite these differences, expansion of the postero-medial portion of the iliac crest and strong development and dorsal reflection of the posterior superior iliac spine (which provide origin for erector spinae muscles) in A.L. 288-1, Sts-14, SK 3155 and SK 50, and KNM-WT 15000 (Robinson, 1972; Johanson et al., 1982; Sigmon, 1986; Walker & Ruff, 1993) are all synapomorphic with the condition in
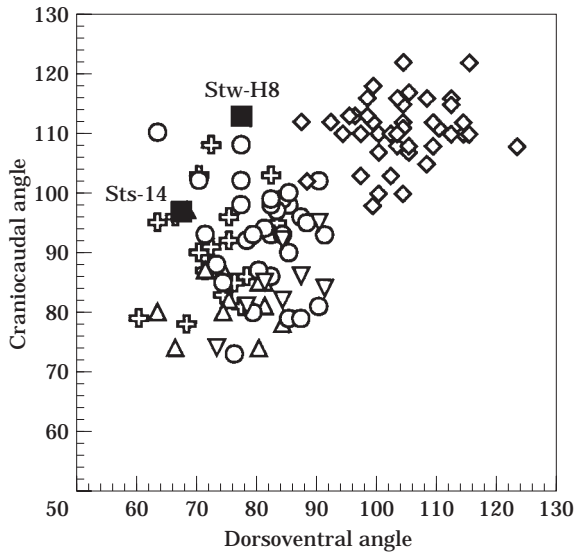
Figure 7. Bivariate plot of craniocaudal and dorsoventral angles of transverse processes at mid-lumbar level (L2 in hominoids and L4 in cercopithecoids) in selected fossil hominids and extant catarrhines. Craniocaudal angles >90° indicate transverse processes oriented cranially. Dorsoventral angles >90° indicate transverse processes oriented ventrally. Symbols: ◇=cercopithecoids; ▼=gibbons; △=orang-utans; ○=African apes; ⊹=humans; ■=fossil hominids. Extant species plotted are HS, PT, GG, PP, HC, HM, PH, MS, CG, CT, CA, CoP, NL, PE, and PC (abbreviations are listed in Table 1).

modern humans, indicating that functional demands for erector spinae muscles in *A. afarensis*, *A. africanus*, *P. robustus*, and *H. erectus* to resist forward flexion of the trunk were similar to those of modern humans. Furthermore, the relatively wide span of lumbar transverse processes in Sts-14 (Figure 5; Robinson, 1972; Aiello & Dean, 1990) corresponds with the relatively broad separation of its ilia (Berge *et al.*, 1984; Sigmon, 1986; Tague & Lovejoy, 1986; Tague, 1991), and would have improved the effectiveness of m. iliocostalis to contralaterally resist lateral columnar flexion by placing its line of action at a distance from vertebral centers of rotation (Sanders, 1995).

Pedicles. The lumbar series in Stw-H8 preserves a partial right pedicle in L1 (=L II) and complete right pedicles in L2–L3 (=L III–L IV). These are bounded caudally by deep intervertebral notches and

consequently enclose, along with adjoining laminae and zygapophyses, capacious intervertebral foramina (Figure 1a). Proportionally, the L2–L3 (=L III–L IV) pedicles are relatively short and stout. Craniolaterally, these pedicles are concave, and in L2 (=L III) there is a prolongation of a deep sulcus from the transverse process onto the caudo-lateral aspect of the pedicle, for insertion of an intertransverse ligament.

Pedicles have important functions in force distribution and stress resistance within vertebrae (Davis, 1961; Bogduk & Twomey, 1987; Pal *et al.*, 1988; Sanders, 1990, 1992, 1995, 1996; Shapiro, 1990, 1991, 1993*b*; Sanders & Bodenbender, 1994), and thus vary in size and shape in relation to the effects of different loading regimes and allometric scaling. Hominoid lumbar pedicles are relatively shorter and relatively wider than those of cercopithecoids (except for the pedicles of the last lumbar vertebra in some

Table 7 Transverse process position indices of lumbar vertebrae for extant catarrhine taxa and fossil hominid individuals

Taxon	Sex	n		L I	L II	L III	L IV	L V	L VI	L VII
								Vertebral levels		
Cercopithecoid species (CoP, CoG, CAe, CG, CT, MS, PH)[1]	All	51	Range	28–70	28–69	29–68	23–68	20–50	7–46	(−15)–26
			Mean			8	10	11	12	−4
			S.D.			5	2	2	2	9
Hylobates spp.	F	4	Range			4–14	9–12	9–13	10–14	(−12)–10
			Mean			4	7	7	4	−7
			S.D.			10	6	5	6	4
Hylobates spp.	M	8	Range			(−9)–15	(−31)–(−11)	(−23)–(−14)	(−21)–(−14)	(−18)–(−5)
Pongo pygmaeus	F	4	Range				(−11)–16	(−7)–13	0–11	(−13)–0
			Mean				−23	−14	−14	−20
			S.D.				6	3	5	7
Pongo pygmaeus	M	9	Range				(−32)–(−18)	(−18)–(−10)	(−21)–(−9)	(−29)–(−12)
			Mean				−22	−13	−12	−21
			S.D.				6	4	4	6
Pan troglodytes	F	9	Range				(−29)–(−10)	(−20)–(−7)	(−19)–(−6)	(−29)–(−11)
			Mean				−28	−22	−19	−12**
			S.D.				7	7	7	6
Pan troglodytes	M	9	Range				(−36)–(−15)	(−34)–(−14)	(−28)–(−10)	(−20)–(−5)
			Mean				−21	−20*	−18*	−12*
			S.D.				7	7	4	4

Table 7 Continued

Taxon	Sex	n	L I	L II	L III	L IV	L V	L VI	L VII
						Vertebral levels			
Gorilla gorilla	F	5				−19 3	−20 4	−19 4	−10** 3
Gorilla gorilla	M	5				(−24)−(−16) −17 4	(−25)−(−15) −16 5	(−23)−(−13) −14* 6	(−14)−(−7) −8 1
Homo sapiens	F	10			−44 7	(−20)−(−13) −39 7	(−24)−(−11) −36 7	(−24)−(−7) −26 7	(−9)−(−6) −12 10
Homo sapiens	M	10			(−57)−(−34) −36 6	(−48)−(−28) −31 5	(−43)−(−28) −26 6	(−33)−(−16) −20 5	(−23)−(−11) −12 5
Homo erectus WT 15000 (subadult)	M	1	—	—	(−45)−(−25)	(−39)−(−21)	(−33)−(−16)	(−27)−(−12)	(−21)−0
A. africanus Sts-14	F	1	—	—	−28	−19	−30	−27	−16
A. africanus Stw-H8	M?	1	—	—	−21	−18	−15	−17	−3
A. afarensis A.L. 288-1 aa/ak/al	F	1	—	—	—	−45	—	—	—
P. robustus SK 853 (subadult)	?	1	—	—	—	−57	—	—	—
P. robustus SK 3981b	?	1	—	—	—	—	—	—	0

Indices are calculated as the ratio of the distance of the transverse process origin from the dorsalmost margin of the centrum to vertebral height, ±RTP × 100/VH (abbreviations are explained in Figure 2). Index values >0 indicate transverse processes rooted on vertebral bodies; the higher the value, the more ventral the point of origin. Index values =0 indicate transverse processes arising from the centro-pedicular junction. Index values <0 indicate transverse processes arising from pedicles; the lower the value, the more dorsal the point of origin.

[1]Abbreviations are given in Table 1.

*Mean not significantly different from that of *Homo sapiens* (male sample) at $t_{.05}$ in Student's *t*-test (see Sokal & Rohlf, 1981).

**Mean not significantly different from that of *Homo sapiens* (female sample) at $t_{.05}$ in Student's *t*-test (see Sokal & Rohlf, 1981).

Table 8   Pedicle shape indices of lumbar vertebrae for selected catarrhine taxa and fossil hominid individuals

Taxon	Sex	n		Vertebral levels						
				LI	LII	LIII	LIV	LV	LVI	LVII
Papio hamadryas	F	5	Mean	21	18	17	17	20	21	40
			S.D.	7	5	4	4	5	2	8
			Range	15–28	12–26	14–24	14–24	14–27	18–24	31–48
Papio hamadryas	M	6		28	23	22	20	24	30	47
				7	6	7	5	6	5	9
				23–33	16–30	13–30	14–26	17–31	24–35	39–62
Mandrillus sphinx	F	4		20	18	13	13	14	18	35
				4	3	2	4	6	7	10
				17–22	14–21	10–15	9–18	9–23	12–28	28–50
Mandrillus sphinx	M	4		22	19	17	15	17	27	45
				3	1	3	3	1	4	6
				20–24	18–21	13–19	12–18	16–19	26–32	40–53
Other cercopithecoid species (NL, PrC, CoA, CoP, CoG, CoB, CM, CAe, CA, CT, CG, MN, MF, MT, MA)[1]	All	79	Range	9–32	8–26	7–23	6–22	6–25	8–33	16–50
Hylobates spp.	F	5				32	32	33	37	65
						5	5	6	7	20
						27–37	26–37	24–38	28–47	36–78
Hylobates spp.	M	8				32	29	31	37	67
						10	5	5	8	14
						23–54	23–37	21–39	26–45	40–85
Pongo pygmaeus	F	5					50	56	53	56
							3	6	5	9
							46–54	50–62	48–61	43–63
Pongo pygmaeus	M	8					62	62	62	77
							10	9	12	15
							44–77	44–73	55–77	63–109
Pan troglodytes	F	9					44	52	52	58
							10	10	8	7
							32–65	39–67	42–70	44–68
Pan troglodytes	M	9					59	54	57	62
							8	10	11	12
							45–70	37–70	39–73	38–77

Table 8 Continued

Taxon	Sex	n				Vertebral levels			
			LI	LII	LIII	LIV	LV	LVI	LVII
Gorilla gorilla	F	10				58	53	63	77
						4	12	11	18
						53–62	34–73	44–80	51–108
Gorilla gorilla	M	10				62	65	76	88
						9	11	16	19
						51–75	50–78	54–88	56–110
Homo sapiens	F	19			47	51	65	79	141
					11	11	14	16	22
					37–61	33–68	49–88	61–110	105–176
Homo sapiens	M	18			51	56	67	85	136
					9	10	11	10	28
					33–67	33–71	44–82	65–100	99–161
Homo erectus WT 15000 (subadult)	M	1			64	—	113	146	162
A. africanus Sts-14	F	1		44	40	51	63	71	94
A. africanus Stw-H8	M?	1		—	72	72	—	—	—
A. afarensis A.L. 288-1 aa/ak/al	F	1		—	—	52	—	—	—
A. afarensis A.L. 333-73	M?	1		—	—	51	—	—	—
P. robustus SK 3981b	?	1		—	—				120

Shape indices are calculated as BP × 100/LP (abbreviations are explained in Figure 2). Index values >100 indicate pedicles wider than long. Index values <100 indicate pedicles longer than wide.
[1] Abbreviations are given in Table 1.

of the largest monkeys) (Figures 8 and 9; *contra* Shapiro, 1993*b*, who found no separation in relative pedicular width between small-bodied *Cercopithecus aethiops* and apes at the last lumbar level, L VII), resulting in greater ''robustness'' (Table 8; Sanders & Bodenbender, 1994; Sanders, 1990, 1992, 1995, 1996). While pedicular length in catarrhines correlates with differences in centrum length (Sanders, 1995), the relatively greater breadth of lumbar pedicles in hominoids may be a response to the application of epaxial muscular force via transverse processes rooted on or near them (Sanders, 1990, 1992, 1995, 1996; Sanders & Bodenbender, 1994). Catarrhines tend to scale with negative allometry for pedicular length and positive allometry for pedicular width; the correlation between pedicular dimensions and body size is particularly strong among non-human hominoids (Appendix 2; Sanders, 1995). Consequently, among both cercopithecoids and apes, larger species generally have higher pedicular robustness indices (Table 8; Sanders & Bodenbender, 1994; Sanders, 1995). As with centrum dimensions, relative decrease in length and increase in width of pedicles as catarrhines become larger is reasonably interpreted as an adaptation to reducing bending moments, induced by the interposition of the pedicles between compression-bearing structures (Sanders, 1990, 1995).

The critical role of pedicles in handling columnar stresses is also evidenced by serial changes in pedicular robustness through the lumbar column. In association with greater loads sustained at the caudalmost lumbar levels, particularly in orthograde posture, pedicular robustness increases at these levels in all catarrhines sampled (Table 8), as does pedicular cross-sectional area (except in orang-utans) (Sanders, 1990, 1995, 1996; Shapiro, 1993*b*). However, the marked increase in pedicular width and robustness at the level of the last lumbar vertebra

(=L VII) in gibbons (Table 8) is likely influenced more by the dorsal shift of transverse processes onto their pedicles at that vertebral level and concomitant resistance to the pull of iliolumbar ligaments and epaxial muscles (Sanders, 1990, 1995). At more cranial levels of the gibbon lumbar column, the transverse processes arise from the lateral sides of the centra, close to the centro-pedicular junction.

Humans exhibit uniquely exceptional ''jumps'' in pedicular robustness and cross-sectional area between the penultimate and last lumbar vertebrae (Table 8; Sanders, 1990, 1995, 1996; Shapiro, 1990, 1991, 1993*b*). In humans, however, transverse processes are rooted on the pedicles at each lumbar level, and so cannot be used to explain these phenomenal changes (Shapiro, 1993*b*). The pattern of pedicular shape transformation in humans is achieved by progressive increases in pedicular width and decreases in length from the first to last lumbar element (Clauser, 1980; Amonoo-Kuofi, 1982; Berry *et al.*, 1987; Zindrick *et al.*, 1987; Scoles *et al.*, 1988; Moran *et al.*, 1989; Sanders, 1995). As human percentage deviations from ape regression lines for lumbar pedicular lengths fall within the range of values for ape species (Table 9), contrasts in pedicular shape between humans and other hominoids must be accounted for by differences in relative pedicular width.

Compared with apes, pedicles in human upper-middle lumbar vertebrae (L IV, L V) are not especially wide relative to body weight (Table 9). At the level of the penultimate and last lumbar vertebrae (L VI, L VII), however, humans have slightly to extremely wide pedicles, respectively, as indicated by mean percentage deviations from ape regression lines for this dimension (Table 9). The impressive robustness and cross-sectional area of pedicles in the last lumbar vertebrae of humans is due solely to the
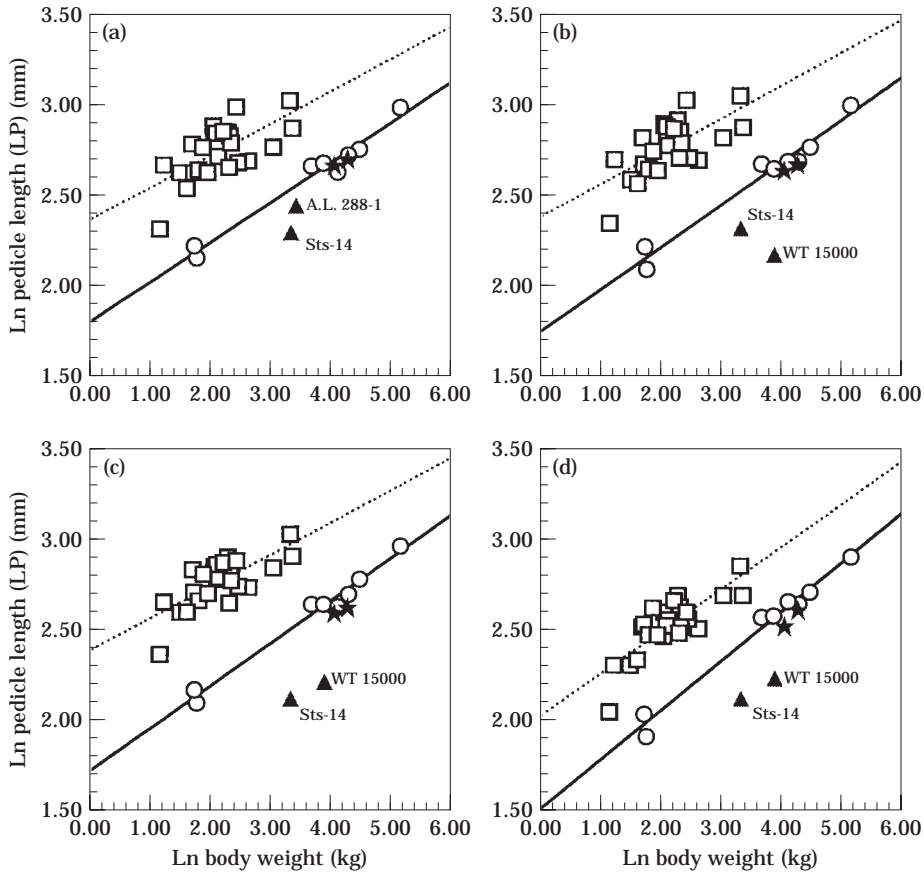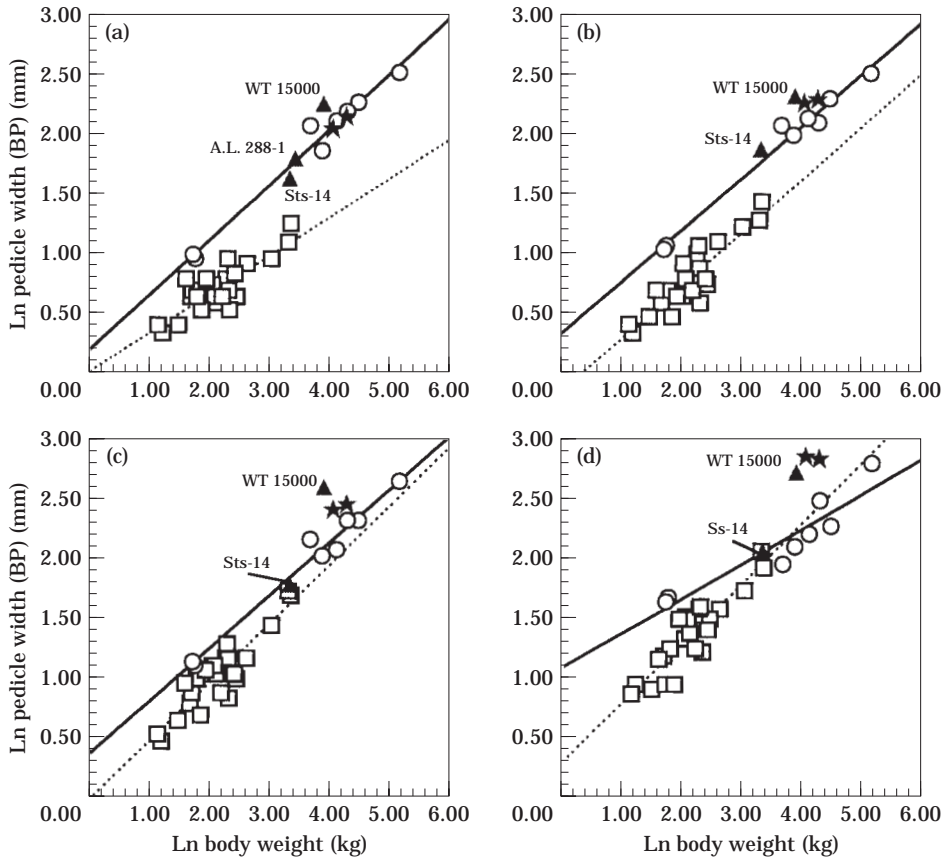
Figure 8. Least squares regression of pedicular length (LP) to body weight in extant non-human catarrhines. Although humans and fossil hominids were not used to generate the regressions, their data points are plotted for comparative purposes. Data are logarithmatically (ln) transformed. □=cercopithecoid sex-specific means; ○=ape sex-specific means; ★=*Homo sapiens* sex-specific means; ▲=fossil hominid individuals. Solid lines=ape scaling trends; dotted lines=cercopithecoid scaling trends (slopes given in Appendix 2). (a) Vertebral level L IV (see Figure 3). (b) Vertebral level L V. (c) Vertebral level L VI. (d) Vertebral level L VII. Extant taxa plotted are HS, PT, GG, PP, HC, PH, MS, CT, CA, CG, MF, CAe, CM, EP, CoG, CoP, CoB, NL, and PC (abbreviations are listed in Table 1). Fossil taxa represented are *Australopithecus afarensis* (A.L. 288-1), *A. africanus* (Sts-14), and *Homo erectus* ([KNM-]WT 15000).

substantial increase in pedicular width between vertebral levels L VI and L VII (Sanders, 1990, 1995, 1996; Shapiro, 1990, 1991, 1993*b*), and suggest a special mechanical role for lower lumbar pedicles in human bipedality.

The position of pedicles between load-bearing ventral pillars, formed by centra and intervertebral discs, and dorsal pillars, comprised of zygapophyses and laminae (see Kapandji, 1974; Pal & Routal, 1986, 1987; Sanders, 1990; Shapiro, 1990, 1993*a*,*b*), places them under constant bending stress (Figure 10; see Bogduk & Twomey, 1987). In upright posture, the lordotic curve of the human lumbar column situates the zygapophyses closer to the center of vertical compression than is the condition in other catarrhines; correspondingly, human lumbar zygapophyses bear a more substantial

Figure 9. Least squares regression of pedicular width (BP) to body weight in extant non-human catarrhines. Although humans and fossil hominids were not used to generate the regressions, their data points are plotted for comparative purposes. Data are logarithmatically (ln) transformed. □=cercopithecoid sex-specific means; ○=ape sex-specific means; ★=*Homo sapiens* sex-specific means; ▲=fossil hominid individuals. Solid lines=ape scaling trends; dotted lines=cercopithecoid scaling trends (slopes given in Appendix 2). (a) Vertebral level L IV (see Figure 3). (b) Vertebral level L V. (c) Vertebral level L VI. (d) Vertebral level L VII. Extant taxa plotted are HS, PT, GG, PP, HC, PH, MS, CT, CA, CG, MF, CAe, CM, EP, CoG, CoP, CoB, NL, and PC (abbreviations are listed in Table 1). Fossil taxa represented are *Australopithecus afarensis* (A.L. 288-1), *A. africanus* (Sts-14), and *Homo erectus* ([KNM-]WT 15000).

portion of the intervertebral compressive load (see Adams & Hutton, 1980; Yang & King, 1984; Dietrich & Kurowski, 1985), especially at the level of the last lumbar vertebra. In humans, the last lumbar zygapophyses passively carry as much as 23% of the load borne by the spine (Pal & Routal, 1987). The amount of compressive force applied to the lumbar zygapophyses is even greater during walking and running (Putz, 1985). Because the proportion of overall body weight to be supported expands incrementally from L1–L5 (=L III–L VII) (Nachemson, 1966), pedicular bending stress is almost certainly significantly greater at the caudal end of the lumbar series, accounting for some of the "jump" in pedicular width, cross-sectional area, and robustness seen in the human L5 (=L VII) vertebra.

More importantly, in humans resistance to the pull of iliolumbar ligaments on the pedicles of the last lumbar vertebra, via the transverse processes, probably has a greater impact on shape change and size increase in pedicular dimensions at that vertebral level than in other extant catarrhines (Sanders, 1990, 1995, 1996; Shapiro, 1990, 1991, 1993b). In habitual bipedal posture, the last lumbar vertebra of humans is positioned oblique to the vertical, and as a result compressive force acting on this vertebra can be resolved into two components: one that drives the last lumbar and sacrum together, and another that threatens to slide the last lumbar ventral to the sacrum (Figure 11; Mitchell, 1934; Davis, 1961; Weis, 1975; Giles, 1989). In consequence, in humans the occurrence of spondylolysis (separation of neural arch elements) and spondylolisthesis (forward slip of a vertebra) are most common in the lowermost lumbar vertebrae (Thieme, 1950; Weis, 1975; Wiltse et al., 1976). Human iliolumbar ligaments run from the transverse processes of the last lumbar(s) to the iliac crests and sacral alae, resisting the tendency of the last lumbar to slide ventrally on the sacrum (Mitchell, 1934; Shellshear & MacIntosh, 1949; Davis, 1961; Weis, 1975; Farfan, 1978; Luk et al., 1986; Bogduk & Twomey, 1987; Cartmill et al., 1987). Thus, although all catarrhines have iliolumbar ligaments attached to the transverse processes of their last lumbar vertebra (and occasionally to the transverse processes of the penultimate lumbar element) (personal observation; Hartmann, 1886; Sonntag, 1923, 1924; Pun et al., 1987), humans have iliolumbar ligaments that are considerably thicker and more complex (personal observation; Shellshear & MacIntosh, 1949; Bogduk & Twomey, 1987; Leong et al., 1987; Chow et al., 1989), and therefore more robust L5 (=L VII) pedicles. The effectiveness of this adaptation is evidenced by the much greater incidence of spondylolysis in the interarticular area of the neural arch than in the pedicles of L5 (=L VII) (Dietrich & Kurowski, 1985).

Upper and middle lumbar pedicles in Sts-14 and specimens A.L. 288-1aa/ak/al and A.L. 333-73 have robustness indices close to mean values for human pedicles (Table 8). In contrast, the L2 and L3 (=L III and L IV) pedicles in Stw-H8 are more robustly shaped than those in most hominoids, with index values greater than mean indices for human middle lumbar pedicles (Table 8). Nonetheless, the differences in pedicular proportions between Sts-14 and Stw-H8 are within the range of variation observed in modern hominoid species. Regression analyses show that the pedicles of Sts-14 and A.L. 288-1 are comparable to the upper-to-middle lumbar pedicles of extant hominoids in width, but that they are relatively short (Table 9; Figures 8 and 9). Consistent with the odd proportions of its centra, the upper-middle lumbar pedicles in KNM-WT 15000 are relatively short and broad (Table 9; Figures 8 and 9), making them ''hyper''-human in shape (Table 8). Without an independent estimate of body weight for Stw-H8, it is difficult to assess the relative size of its pedicular dimensions. However, as the lumbar pedicles in Stw-H8 are similar in length but almost twice as wide as those in Sts-14 (Table 3), it is reasonable to conclude that its pedicles are relatively much broader.

Given the functional association in modern humans between habitual bipedal posture, lumbar lordosis, and the tremendous robustness of their last lumbar pedicles, the relative size and shape of pedicles in the lowermost vertebrae of australopithecines is of particular interest. Sts-14 lacks the ''jump'' in pedicular robustness, width, and cross-sectional area characteristic of humans (Tables 8 and 9; Figures 8 and 9; Sanders, 1990, 1995, 1996; Shapiro, 1990, 1991, 1993b). Compared with humans, the pedicles of the last two lumbar vertebrae in

Table 9 Percentage deviations from least square regressions of lumbar pedicle dimensions to body weight in non-human hominoids (see Appendix 2)

Taxon	BW (kg)	Sex	L IV	L V	L VI	L VII
			Pedicle length			
Hylobatids		All	− 1 to +1	− 3 to +3	− 1 to +2	− 4 to +2
African apes		All	− 3 to +2	− 1 to +2	− 6 to +2	− 5 to +8
Orang-utans		All	+1 to +11	+1 to +12	− 2 to +1	− 2 to 0
Humans	F		0	− 2	− 5	− 4
	M		− 2	− 2	− 4	− 3
WT 15000	48·0★	M	—	− 18	− 16	− 13
Sts-14	27·4†	F	− 9	− 7	− 15	− 13
A.L. 288-1	30·0‡	F	− 4	—	—	—
			Pedicle width			
Hylobatids		All	− 2 to +1	− 5 to 0	− 3 to 0	+2 to +5
African apes		All	− 5 to +2	− 4 to +1	− 6 to +2	− 5 to +8
Orang-utans		All	+1 to +11	+1 to +12	− 2 to +8	− 9 to − 5
Humans	F		0	+8	+11	+26
	M		0	+5	+8	+21
WT 15000	48·0★	M	+14	+15	+24	+23
Sts-14	27·4†	F	− 4	+6	− 4	0
A.L. 288-1	30·0‡	F	+2	—	—	—

Percentage deviations are calculated as observed − predicted × 100/predicted (Jungers, 1984). Ape taxa used in the regressions are PT, GG, PP, HC, and HM (abbreviations are explained in Table 1). Dimensions: pedicle length=LP; pedicle width=BP; (measurements are explained in Figure 2).
★Calculated by Ruff & Walker (1993).
†Calculated by McHenry (1988).
‡Calculated by McHenry (1988) and Jungers (1990).

Sts-14 are relatively narrower and considerably shorter (Figures 8 and 9). These differences are seen as possibly indicating lesser adaptation to bipedality in the spine of australopithecines (Shapiro, 1993b). Alternatively, it may be that because the last lumbar vertebra of Sts-14 is more deeply "captured" within the pelvic frame than in humans (Sanders, 1994, 1995, 1996), there was less potential for this vertebra to slide forward, and therefore less danger of spondylolysis. It is reasonable to assume that the lumbar pedicles of Stw-H8 followed the same pattern of serial shape change seen in other catarrhines. Thus, although the last lumbar vertebrae of Stw-H8 are not preserved, it is likely that their pedicles were more robust than the pedicles of the lower lumbars in Sts-14. This would suggest that the modest size of the lowermost lumbar

pedicles in Sts-14 is not necessarily the modal condition for australopithecines. Indeed, the pedicles of last lumbar specimen SK 3981b, attributed to *P. robustus*, are as robust as those of modern humans (Table 8). Its remaining transverse process is distinguished by a massive accessory tuberosity (Robinson, 1970, 1972: Figures 68 and 69), undoubtedly for the attachment of powerful iliolumbar ligaments.

Zygapophyses. The preserved zygapophyses in Stw-H8 are flat and simple in contour. They are unadorned by bony flanges and exhibit only small metapophyseal tuberosities at their dorso-lateral edges, for insertion of mm. multifidus and rotatores. The prezygapophyses are set oblique to the sagittal plane, with their articular surfaces facing medially and dorsally in equal
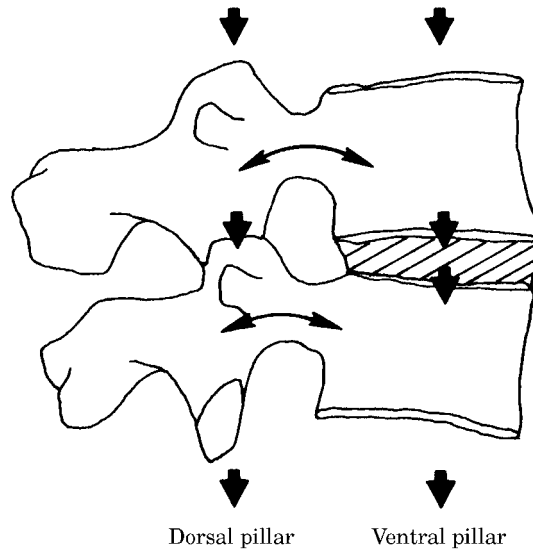
Dorsal pillar   Ventral pillar

Figure 10. Two-pillar model of force distribution in the human vertebral column. Vertebral centra and intervertebral discs form a ventral pillar, which supports most of the vertical load applied to the lumbar spine. Some of the vertical load is also supported by a dorsal pillar, comprised of laminae and zygapophyses (see Pal & Routal, 1986, 1987). The pedicles are positioned between these compressive members and subjected to bending stress.

measure (measurement PZA in Table 3), and project moderately above the level of the cranial articular surface of the centra (Figure 5). The postzygapophyses are also obliquely oriented and flat, but extend more below the level of the caudal centrum surfaces and are slightly dorsally tilted (Figure 5). Zygapophyseal widths (see Figure 2) were estimated for Stw-H8 by doubling the distance measured from the right zygapophysis to the vertebral midline in each, and suggest a sequential increase in zygapophyseal spacing caudally through the lumbar column (measurement ZB in Table 3). Relative to centrum width, the zygapophyses in Stw-H8 are unremarkable in comparison with their serial homologues in other catarrhines (Sanders, 1995).

Zygapophyses function to guide or restrict intervertebral motion and assist the centra in transmitting force through the vertebral column. For example, a number of stiff-backed mammals independently evolved interlocking, S-shaped zygapophyses that promote spinal rigidity by prohibiting dorsoventral and lateral movements between vertebrae (Flower, 1885; Cope, 1889; Denison, 1938; Halpert et al., 1987; Zhou et al., 1992). Catarrhines exhibit no zygapophyseal traits of such extreme derivation, although in some gorillas the size and dorsal deflection of metapophyses lock them against suprajacent postzygapophyses, permitting only minimal lateral intervertebral movement (personal observation; Clauser, 1980; Filler, 1981). The lumbar zygapophyses of chimpanzees and gorillas sampled for this study seem to be more curved and form tighter embrasures than those of other catarrhines. It should be noted, however, that elsewhere gorilla zygapophyses are reported to be flatter than those of other hominoids (Struthers, 1892; Shapiro, 1993a). Obviously, this aspect of catarrhine vertebral morphology needs to be quantified and studied in greater detail (Shapiro, 1993a). On average, cercopithecoid lumbar zygapophyses are more ''open'' (angled further
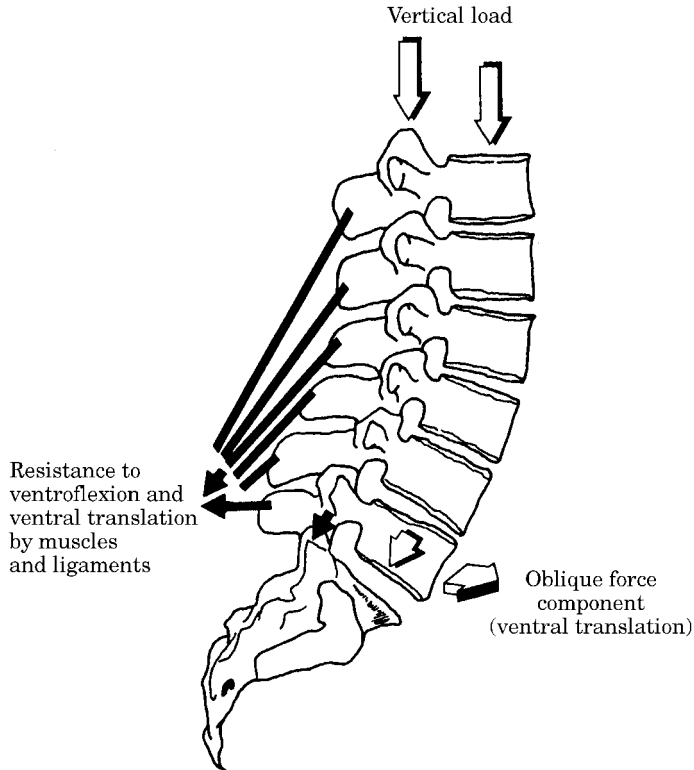
Figure 11. Human lumbar column, set in normal lordotic configuration. Compressive force generated by vertical loads is channeled through the centra (ventral pillar) and zygapophyses (dorsal pillar). The angulation of the last lumbar vertebra on the sacrum causes compressive force applied to the ventral pillar to be divided into downward and ventrally oblique components. Ventral translation of the last lumbar vertebra on the sacrum is resisted by epaxial muscles, powerful iliolumbar ligaments, and the dorsoventral orientation of the sacral facets and last lumbar postzygapophyses.

away from the sagittal plane) than those of apes, allowing a greater degree of lateral flexion of the lower spine, but there is much overlap between them in this feature (Sanders, 1995). More striking are contrasts in zygapophyseal morphology between humans and non-human catarrhines.

In conjunction with habitual bipedality and lumbar lordosis, human lumbosacral zygapophyses are distinguished from those of other extant catarrhines in relative size and serial patterns of orientation and spacing. Schultz (1961) observed that large-bodied apes appear to have small lumbo-sacral joints. Scaling coefficients for sacral facet area-to-body weight in modern apes

confirm this (Appendix 3), showing that as apes become larger, they have relatively smaller facets. The presence of relatively smaller sacral articular areas in apes as body size increases is probably linked with relative shortening of the lumbar region and consequent lessened mobility of the lower spine and reduction of sacral joint stresses. Sacral facet areas of apes correlate closely with body weight (Appendix 3), suggesting that substantial departures of sacral facet size in hominids from this scaling trend are functionally meaningful. Compared with those of extant apes, the lumbar and sacral articular facets of humans are relatively immense (Table 10; Sanders, 1990, 1995,

Table 10 Percentage deviations from least square regressions of combined sacral facet area to body weight in non-human hominoids (see Appendix 3)

Taxon	BW (kg)	Sex	Area ASFR+ASFL
Hylobatids		All	−34 to +29
African apes		All	−23 to +22
Orang-utans		All	−31 to +29
Humans		F	+111
		M	+120
WT 15000	48·0*	M	+81
Sts-14	27·4†	F	+140
A.L. 288-1	30·0‡	F	+179

Percentage deviations are calculated as observed − predicted × 100/predicted (Jungers, 1984). Ape taxa used in the regressions are PT, GG, PP, HC, and HM (abbreviations are explained in Table 1). Dimensions: sacral facet area=ASFR+ASFL (measurements are explained in Figure 2)
*Calculated by Ruff & Walker (1993).
†Calculated by McHenry (1988).
‡Calculated by McHenry (1988) and Jungers (1990).

1996; Latimer & Ward, 1993), in response to their role in supporting upper body weight in bipedal posture. In addition, humans contrast with other catarrhines in the strong increase in zygapophyseal spacing between their upper lumbar and sacral (S1) facets (Figure 12; Fawcett, 1932; Mitchell, 1934; Sanders, 1990, 1995, 1996; Ward & Latimer, 1991; Latimer & Ward, 1993). The ratio of zygapophyseal spacing to centrum width also increases sharply between L4–L5 (=L VI–L VII) and L5–S1 in humans, a feature unique among modern catarrhines (Table 11; Sanders, 1990, 1995, 1996; Latimer & Ward, 1993). As a result, a broad, triangular configuration is created at the base of the lumbosacral column, which serves as a mechanism for stable balance of an habitually upright torso.

Humans also exhibit a pattern of change in zygapophyseal angulation through the lumbosacral vertebral series that is unlike that of virtually all non-human catarrhines and other mammals (Clauser, 1980; Shapiro, 1991, 1993a; Ward & Latimer, 1991; Latimer & Ward, 1993). In humans, upper lumbar prezygapophyses face medially, whereas the angulation of lower lumbar prezygapophyses and S1 facets increases markedly and they face more dorsally (Figure 13; Struthers, 1892; Mitchell, 1934; Cihak, 1970; Van Schaik et al., 1985; Shapiro, 1993a; Sanders, 1995). The more open orientation of prezygapophyses at the base of the lumbar column is an adaptation to counter the tendency for spondylolisthesis of the lowermost lumbar elements (see above; Mitchell, 1934; Davis, 1961; Sanders, 1990, 1995; Shapiro, 1990, 1993a). Orang-utans exhibit a similar serial change in lumbosacral zygapophyseal angulation. While the functional reason for this similarity is presently obscure, the fact that they differ from humans in all other aspects of their lumbosacral facet morphology makes it likely that open lumbosacral zygapophyseal angulation underlies several different types of positional behavior, and therefore cannot be used by itself to diagnose bipedality.

Further associated with habitual bipedality are dorsal angulation and conspicuous projection below the level of the caudal centrum surfaces of human lumbar postzygapophyses (Figure 5; Ward & Latimer, 1991). The dorsal tilt of the postzygapophyses accommodates the hyperextension of one vertebra on another that is essential for achieving lordosis, while the caudal elongation of these processes is thought to keep them from impinging on intervertebral foramina when the lumbar vertebrae are held in lordosis (Ward & Latimer, 1991; Latimer & Ward, 1993).

The scant evidence available indicates that australopithecines closely resemble modern humans in the morphology of their lumbar zygapophyses and sacral facets. For example, Sts-14 and A.L. 288-1 both show the same trends as humans for increasing width and angulation of articular facets in

Table 11 Ratios of prezygapophyseal width to centrum width in lumbar and sacral vertebrae from selected catarrhine taxa and fossil hominid individuals

Taxon and sex	n		Vertebral levels							
			LI	LII	LIII	LIV	LV	LVI	LVII	S1
Colobus polykomos, F	4	Mean	73	75	76	70	71	66	64	65
		S.D.	4	8	6	6	2	5	4	2
		Range	70–77	68–86	70–83	64–78	68–72	62–72	58–67	61–67
Colobus polykomos, M	4	Mean	72	69	68	68	62	61	59	68
		S.D.	11	9	7	4	5	7	8	10
		Range	56–79	58–78	59–75	62–72	55–67	50–66	50–68	57–79
Cercopithecus aethiops, F	4	Mean	72	76	72	67	62	60	61	62
		S.D.	6	7	8	9	8	8	2	3
		Range	65–78	70–86	66–84	62–81	53–71	52–69	58–63	58–65
Cercopithecus aethiops, M	4	Mean	77	74	76	68	62	59	57	62
		S.D.	10	6	7	6	8	3	6	5
		Range	63–84	70–83	71–86	60–75	49–66	56–62	50–64	59–69
Papio hamadryas, F	3	Mean		78	79	77	75	78	72	75
		S.D.		5	7	6	6	7	6	4
		Range		75–84	75–87	72–84	69–81	73–86	66–78	71–79
Papio hamadryas, M	6	Mean		74	75	76	73	70	73	73
		S.D.		11	5	8	7	6	4	5
		Range		55–86	64–82	63–86	63–82	62–79	67–78	67–80
Hylobates spp., F	3	Mean			78	77	76	73	72	72
		S.D.			4	7	8	4	3	4
		Range			78–81	70–83	69–84	71–78	69–74	68–76
Hylobates spp., M	8	Mean			75	73	75	73	70	72
		S.D.			9	9	6	7	8	10
		Range			61–88	63–87	62–81	64–87	61–85	53–83
Pongo pygmaeus, F	6	Mean				71	63	63	59	56
		S.D.				7	4	6	5	6
		Range				63–81	59–69	53–69	52–65	48–63
Pongo pygmaeus, M	9	Mean				66	63	59	56	53
		S.D.				9	5	6	6	7
		Range				54–82	51–69	50–68	49–65	43–64

Table 11 Continued

Taxon and sex	n	LI	LII	LIII	LIV	LV	LVI	LVII	S1
Pan troglodytes, F	7				80	79	75	70	65
					8	6	5	3	6
					65–90	69–87	71–81	67–75	58–75
Pan troglodytes, M	6				79	84	79	72	66
					10	10	13	15	13
					63–93	70–96	65–98	57–96	56–91
Gorilla gorilla, F	5				82	77	77	67	64
					6	8	8	11	13
					76–91	65–86	62–86	55–85	53–79
Gorilla gorilla, M	5				73	77	73	63	57
					7	9	6	10	7
					63–83	67–91	70–84	53–75	62–67
Homo sapiens, F	8			73	69	70	75	84	101
				7	6	7	8	6	11
				64–86	60–77	59–82	61–88	72–92	80–115
Homo sapiens, M	10			70	62	63	68	78	89
				6	5	7	7	7	6
				58–81	55–70	54–75	59–79	66–87	77–97
Homo erectus WT 15000 (subadult), M	1	—	—	—	—	70	76	76	100e
A. africanus Sts-14, F	1	—	—	74	70	73	—	108e	111e
A. africanus Stw-H8, M?	1	—	—	79	87	—	—	—	—
A. afarensis A.L. 288-1 aa/ak/al, F	1	—	—	—	82	—	—	—	96e
P. robustus SK 853 (subadult), ?	1	—	—	—	70	—	—	—	—

Ratios are calculated as ZB × 100/VB for lumbar vertebrae and ZB × 100/SB for sacral vertebra S1 (abbreviations are explained in Figure 2). A ratio <100 indicates that the distance between prezygapophyseal midpoints is narrower than centrum width.
eEstimated.
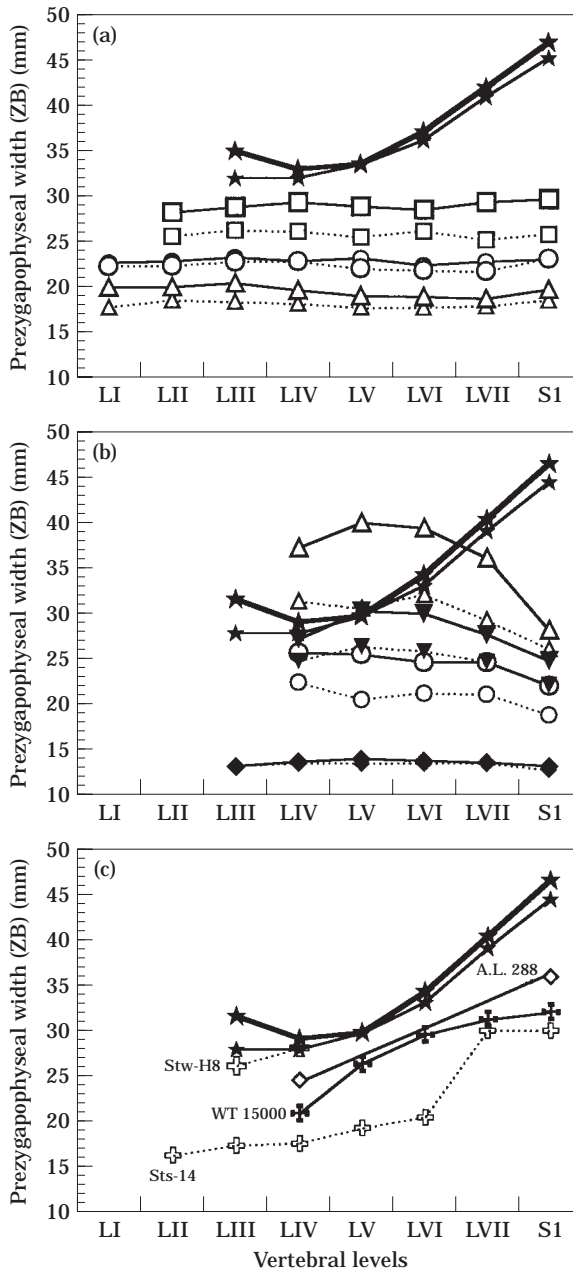
Figure 12. Patterns of lumbosacral prezygapophyseal spacing (ZB) in sex-specific samples of selected catarrhine taxa and fossil hominid individuals. Interzygapophyseal distances are given in mm. ★=*Homo sapiens*, male; ★=*H. sapiens*, female. (a) Cercopithecoid species compared with human samples. △=*Cercopithecus aethiops*, male; △=*C. aethiops*, female; ○=*Colobus polykomos*, male; ○=*C. polykomos*, female; □=*Papio hamadryas*, male; □=*P. hamadryas*, female. (b) Ape species compared with human samples. ○=*Pongo pygmaeus*, male; ○=*P. pygmaeus*, female; △=*Gorilla gorilla*, male; △=*G. gorilla*, female; ▼=*Pan troglodytes*, male; ▼=*P. troglodytes*, female; ◆=*Hylobates* spp., male; ◆=*Hylobates* spp., female. (c) Fossil individuals compared with human samples. Fossil taxa represented are *Australopithecus afarensis* (A.L. 288-1), *A. africanus* (Sts-14, Stw-H8), and *Homo erectus* ([KNM-]WT 15000).
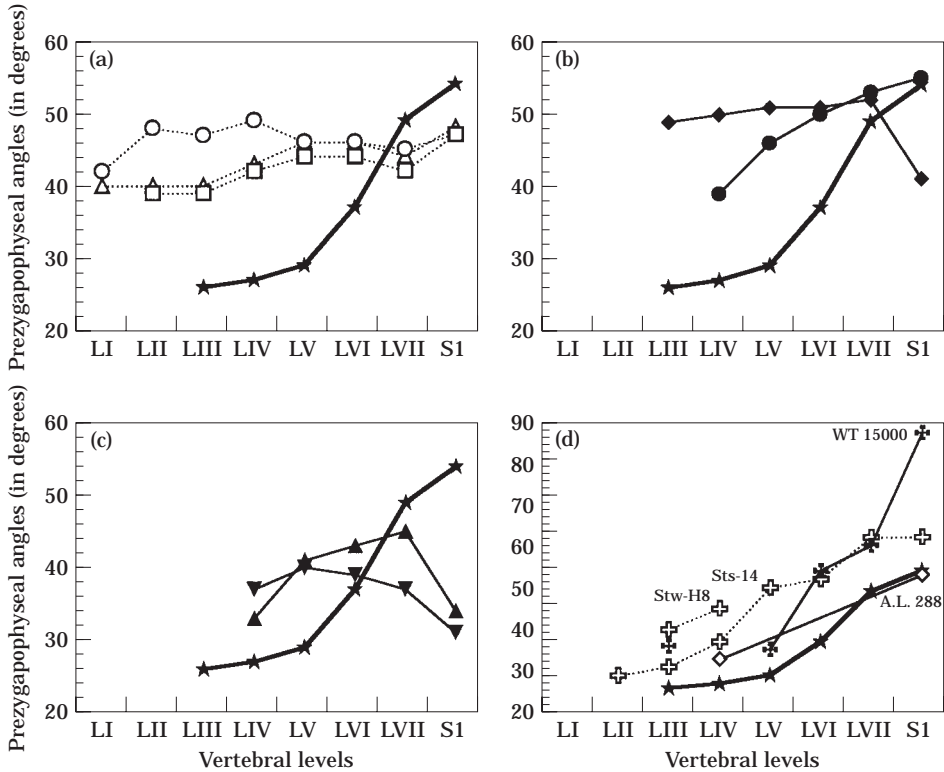
Figure 13. Patterns of lumbosacral prezygapophyseal angulation (PZA+SFA) in selected catarrhine taxa and fossil hominid individuals. Angles are given in degrees. (a) Cercopithecoid species compared with human sample. △=*Cercopithecus aethiops*; ○=*Colobus polykomos*; □=*Papio hamadryas*; ★=*Homo sapiens*. (b) Asian ape species compared with human sample. ◆=*Hylobates*; ●=*Pongo*; ★=*Homo sapiens*. (c) African ape species compared to human samples. ▲=*Gorilla*; ▼=*Pan*; ★=*Homo sapiens*. (d) Fossil individuals compared to human sample. Fossil taxa represented are *Australopithecus afarensis* (A.L. 288-1), *A. africanus* (Sts-14, Stw-H8), and *Homo erectus* ([KNM-]WT 15000).

the lumbar-S1 series (Figure 12 and 13). Also, these individuals have relatively large lumbar zygapophyses and massive sacral facets, even compared with humans (Table 10). From this, it may be inferred that in australopithecines a greater percentage of load bearing force was channeled through dorsal columnar structures in the lumbosacral column than is the case in humans (Sanders, 1990, 1995, 1996). Relative to centrum width, zygapophyseal spacing in australopithecines is even greater than mean values for humans, particularly at the level of the last lumbar vertebra and S1 (Table 11). This provided a stable base for upright

balance of the vertebral column. In addition, lumbar postzygapophyses in australopithecines are angled dorsally relative to vertical and project strongly below the level of caudal centrum surfaces, as in humans (Ward & Latimer, 1991). The implication is that the lumbar zygapophyses and S1 facets of australopithecines were well adapted for lumbar lordosis and columnar support in bipedal posture. These conditions are also documented for *Homo erectus* individual KNM-WT 15000 (Tables 10 and 11; Figures 12 and 13; Latimer & Ward, 1993). Although it is not possible to calculate the size of the Stw-H8 zygapophyses relative to

Table 12 Structural–functional complexes of the lower spine associated with human bipedality (see Sanders, 1995)

Spinal function	Vertebral structure	Presence in australopithecines
Permit/enhance lumbar lordosis (transmission between tilted sacrum and vertical thorax)	Dorsal wedging of some or all lumbar vertebrae	●
	Strong caudal projection of lumbar postzygapophyses	● √
	Low cranial projection of lumbar prezygapophyses	● √
	Dorsal angulation of lumbar postzygapophyses	● √
	Tendency for very dorsal origin of lumbar processes on pedicles	¶
	Dorsal deflection of iliac tuberosities and iliac crests	●
	Subhorizontal orientation of lumbar neural spines	¶
	Large, robust metapophyses	○
	Thick, complex transversospinal muscles	○
	Thick, complex erector spinae muscles (especially longissimus) and lumbar insertion of iliocostalis	● √
	Ventro–dorsal orientation of last lumbar/first sacral articular facets	●
	Secondary increase in modal # of lumbar vertebrae to 5 or 6	●
	Secondary increase in length of lumbar vertebrae relative to body weight	○
Resistance to ventroflexion of lumbar vertebrae/maintenance of constant truncal erectness	Tendency for very dorsal origin of lumbar transverse processes from pedicles	●
	Caudal orientation of lumbar transverse processes	¶
	Dorsal orientation of lumbar transverse processes	● √
	Caudal orientation of lumbar neural spines	●
	Dorsal orientation of sacral alar surfaces for interosseous sacroiliac ligaments	●
	Strong lumbar supraspinous ligaments	●
	Very stout, complex iliolumbar ligaments	● (SK 3981b) ? (Sts-14)
	Dorsal deflection of epaxial muscle attachment areas on iliac tuberosities and iliac crests	●
	Large, robust metapophyses	○
	Thick, complex transversospinal musculature	○
	Thick, complex erector spinae muscles (especially longissimus) and lumbar insertion of iliocostalis	● √

Table 12   *Continued*

Spinal function	Vetebral structure	Presence in australopithecines
Constant vertical load bearing/resistance to buckling, bending moments, and shearing stresses/balance of upright lumbar region	Lumber centra wide and high relative to length	○
	"Pillaring" of lumbar vertebral bodies	● √
	Relatively very wide pedicles at some or all lumbar levels	¶ √
	Tendency for S3 to participate in the formation of the sacroiliac joints	○
	Relatively large lumbar zygapophyses	● √
	Marked enlargement of zygapophyses through lumbar series	●
	Substantial increase in zygapophyseal spacing through lumbar series	● √
	Open angulation of articular facets at lumbosacral junction	●
	Relatively large and widely-spaced sacral facets	●
	At least some expansion of auricular surface areas	●
	Secondary increase of modal # of lumbar vertebrae to 5 or 6	●
	Transverse expansion of the sacrum via hypertrophic development of the lateral masses	●
	Powerful sacrotuberous, dorsal sacroiliac, and interosseous sacroiliac ligaments (corresponding to well-marked pits and salient tuberosities on the sacrum, and sometimes associated with upper lateral sacral angles)	●
Long distance travel/frequent or sustained running/lifting and carrying objects	Relatively large lumbar centrum surface areas	○
	Relatively large sacral bases	○
	Relatively very large auricular surfaces	○
	Marked "jump" in pedicular width and cross-sectional area between the penultimate and last lumbar vertebrae	○ (Sts-14) ? (Stw-H8; SK 3981b; others)
Sagittal and lateral excursions of the lumbar column during walking and running (to keep the trunk balanced over the pelvis)	Secondary increase in the modal # of lumbar vertebrae to 5 or 6	●
	Secondary increase in the length of lumbar centra relative to body weight	○

●=present or probable in australopithecines; ○=absent or improbable in australopithecines; ¶=present in some but not all australopithecines; ?=presence or absence in australopithecines unknown; √=confirmed or probable in Stw-H8.

body mass, nonetheless they also seem large in comparison with overall vertebral size, and are clearly human-like in the combination of their degree of caudal projection (of postzygapophyses) and sequential increase in spacing.

Discussion and conclusions

Non-human primates characteristically have diverse locomotor repertoires and *compromise* postcranial morphologies, while humans are specialized for a single locomotor activity and consequently possess a *committed* postcranial morphology (Rose, 1991). The musculoskeletal commitment to bipedality is especially well expressed in the lumbosacral region of the human vertebral column. Among mammals, this portion of the spine is usually the most useful for investigating the functional relationship of structure to positional behavior (Hatt, 1932; Slijper, 1946, 1947; Smith & Savage, 1955; Hildebrand, 1959; Howell, 1965; Gambaryan, 1974). In humans, adaptation to bipedality is marked by a suite of lumbosacral features that principally correlate with (1) facilitating the transition between a tilted sacrum and vertical thorax via lordosis of the lumbar column; (2) resisting ventroflexion of lumbar vertebrae and maintenance of constant truncal erectness; (3) constant vertical load bearing, and resistance to buckling, bending moments, and shearing stresses; (4) resistance to additional stresses created by lifting and carrying objects, and sustained, active bipedal movement; and (5) allowing sagittal and lateral excursions of the lumbar column adequate to keep the trunk balanced over the pelvis during walking and running (Table 12). Such close concordance of structures and proportions with a particular behavior indicates the utility of the lumbosacral column for assessment of bipedality in fossil hominids.

Some lumbosacral features of humans, such as pedicular origin and dorsal orientation of transverse processes, caudal angulation of neural spines, and "pillaring" of lumbar centra, are shared by other hominoids, presumably to promote dorsostability of the lower spine for support of the trunk in orthograde postures and for arboreal bridging and transferring between branches (Cartmill & Milton, 1977; Jungers, 1984). Nonetheless, when vertebral proportions and spinal traits of humans are considered as a whole, they comprise a morphology that is effective for vigorous bipedal locomotion and sustained upright stance and mechanically inappropriate for some behaviors typical of extant apes. For example, humans have a greater number of lumbar elements, and relatively longer lumbar columns than other large-bodied hominoids (Schultz, 1938; Sanders, 1995). These conditions are hypothesized as secondarily derived to achieve lumbar lordosis without exposing individual lumbar intervertebral joints to high amounts of shear stress (Sanders, 1995), as well as to create sufficient lower spinal mobility to maintain the center of gravity over an alternating eccentric support base during walking and running (Thorstensson et al., 1982; Thorstensson et al., 1984; Thurston & Harris, 1983; Suzuki, 1985; Majoral et al., 1997). Long lumbar regions are thought to be mechanically less competent than short ones for bridging behaviors or climbing large-diameter substrates in the manner of extant apes (see Preuschoft et al., 1992).

Much of what is known or inferred about the anatomy and function of the australopithecine vertebral column is based on two fossil individuals, Sts-14 (*Australopithecus africanus*) and A.L. 288-1 (*A. afarensis*), particularly the former. Information from these individuals is supplemented by details from a sparse collection of mostly isolated vertebrae, although there are several new vertebral series (see above) that should considerably enhance our understanding of australopithecine spinal function, once they are described and available for further study. Due to its completeness, it is tempting to treat the Sts-14 vertebral column as an archetype for spinal morphology in australopithecines. This study, however, shows that there is considerable morphometric variation even in the present small sample of

australopithecine vertebrae, although the fossil evidence is still too incomplete to ascertain whether these structural and proportional differences are interspecifically or mechanically significant. Resolution of this question could have important consequences for hypotheses that posit distinctions in bipedal commitment and capabilities between *Australopithecus* and *Paranthropus* (Robinson, 1972, 1978; Robinson *et al.*, 1972; Berge, 1984; Berge & Kazmierczak, 1986; Susman & Brain, 1988; Susman, 1989; Susman & Stern, 1991) and between *A. afarensis* and *A. africanus* (Berger & Tobias, 1996). Nonetheless, despite the paucity of fossil material, results from this study and presented elsewhere (e.g., Rose, 1975; Sanders, 1990, 1995, 1996; Ward & Latimer, 1991; Shapiro, 1993*b*) are sufficient for preliminary evaluation of spinal function in australopithecines, particularly of the genus *Australopithecus*.

The findings of the present study support several conclusions about the morphology of the australopithecine lower vertebral column: (1) it shows no relationship with pronograde quadrupedalism; (2) there is no specific or exclusive imprint of any climbing, bridging, or suspensory behavior typical of extant apes, and no traits that can be associated directly with alternative modes of these behaviors; (3) it correlates with a dominance of bipedal activity in the positional repertoire, though of lesser commitment or structural soundness than in modern humans; (4) it suggests a somewhat different mechanism of vertical columnar weight bearing than in modern humans; and (5) it does not reveal anything about posited differences from modern humans in the kinematics of bipedality. Australopithecine vertebrae are generally like those of extant hominoids in structure, and lack cercopithecoid adaptations for powerful extension of the spine from a flexed position. Thus, the lumbosacral region of these fossil hominids

seems inadequate for behaviors such as quadrupedal galloping and bounding. Conversely, australopithecines possess many vertebral specializations associated with human-type bipedality (Table 12). Features such as posterior angulation and caudal projection of postzygapophyses, and dorsal wedging of centra, suggest that the australopithecine lumbar column was intrinsically lordotic. In addition, the relatively enormous zygapophyses of australopithecines may be accounted for in part by experimental data showing that lumbar articular facets are under greater compressive stress when lordosis is maintained (Adams & Hutton, 1980). Among extant catarrhines, there is no posture or locomotor behavior other than bipedality that requires such a configuration.

The apparent modal condition of six lumbar vertebrae in australopithecines indicates that the length of their lumbar regions as a percentage of total trunk length is probably at least as great as, if not more than, the average ratio in humans, and proportionately much longer than lumbar regions in extant great apes (Sanders, 1995). This is not a condition expected if australopithecines had engaged in substantial amounts of arboreal activities in the manner of apes of modern aspect, but is correlative with lumbar lordosis and frequent bipedal locomotion. Additionally, the relative breadths across lumbosacral zygapophyses, and serial patterns of prezygapophyseal angulation and spacing through the lumbosacral column in australopithecines are most reasonably interpreted as adaptations for maintaining vertical balance of the trunk, and are not observed in non-human catarrhines.

It may be inferred from this combination of features that bipedality was the most important component of the australopithecine positional repertoire. These observations provide little support for suggestions that australopithecines were only facultative or infrequent bipeds. However,

while the morphology of the australopithecine lower spine is *diagnostic* for bipedality, it would be unwise to use this anatomical region alone to determine whether australopithecines were *committed* bipeds or employed a specifically human form of bipedal locomotion (see Stern & Susman, 1991). There is, for instance, no sound logic for dismissing the functional importance of primitive traits that are associated with climbing found in the appendicular skeleton of australopithecines (Susman & Stern, 1991). These are summarized in McHenry (1991a), and are considerable. However, while it is likely that climbing and other arboreal activities remained important for the survival of early hominids, there is nothing about the lower australopithecine spine that is especially distinctive of any behavior other than bipedality, and thus this anatomical region cannot by itself impart a full understanding of australopithecine positional repertoires. Also, differences in relative hindlimb length and pelvic structure suggest that kinematic equivalence in bipedal gait between australopithecines and humans is unlikely (Jungers, 1982; Rak, 1991; Berge, 1994; Hunt, 1994), but the few observed contrasts between humans and australopithecines in vertebral morphology do not coincide in an obvious way with any aspects of such kinematic dissimilarity.

These considerations suggest that australopithecines, or at least *Australopithecus*, spent considerable time engaged in a unique form of terrestrial bipedality, but had more versatile locomotor abilities and repertoires than modern humans. In this view, australopithecines are compromise instead of committed bipeds, and exchanged bipedal *efficiency* for overall *effectiveness* in their ecological milieu (Rose, 1991). For example, retention of climbing adaptations may have increased the energetic cost of bipedal progression in australopithecines, but bestowed selective advantage for predator avoidance by permitting them to sleep and take refuge in trees (Susman et al., 1984).

Proportional distinctions between human and australopithecine thoracic and lumbosacral centra (Tables 2, 5, 12) indicate that their vertebral columns were not biomechanically identical. It has been noted previously that australopithecine lumbar vertebrae are peculiar in their combination of small vertebral bodies and large neural arches (Robinson, 1970; Johanson et al., 1982; Cook et al., 1983; Schmid, 1991). The findings of this study (Table 6) confirm prior suggestions (Rose, 1975; Leutenegger, 1977; Velte, 1984, 1987; McHenry, 1991a, 1992a; Sanders, 1990, 1995, 1996; Shapiro, 1993b) that the diminutive vertebral bodies and sacral bases of australopithecines are not just scaled down versions of human centra, but are relatively low and/or narrow, and (along with sacral auricular surfaces) have relatively small joint areas.

The coupling of small centrum surfaces with an apparently intrinsically lordotic lumbar region is incongruous, given the correlation of large lumbosacral joint surfaces with sustained bipedal posture in humans, unless australopithecine behaviors produced smaller increments of compression across their centra, or they had a different mechanism for channeling vertical forces through the vertebral column (Velte, 1984; Sanders, 1990). For example, it is possible that australopithecines supported a greater percentage of upper body weight on their relatively immense zygapophyses than do humans (Sanders, 1990, 1995, 1996), though this seems a less sound solution for vertical weight bearing than that of humans. Alternatively, australopithecines may not have engaged as frequently as modern humans in energetic and long-distance bipedal locomotion (see Jungers, 1988b; Berge, 1994), or may have lifted and carried objects less often (see Miller & Stamford, 1987). Another idea, that the small centra in

australopithecines are accounted for by lightly-built upper bodies (Robinson, 1972), seems unlikely, given salient muscle markings on australopithecine scapulae and humeri indicating powerful, heavy forelimbs (Aiello & Dean, 1990; Schmid, 1991; Aiello, 1994). In contrast, vertebral joint sizes and centrum proportions in *Homo erectus* individual KNM-WT 15000 are closer to those in humans, which may denote a shift in spinal function and perhaps greater occurrence of vigorous bipedal behavior and transport of objects during the early Pleistocene.

It is clear that intra- and interspecific structural variation and mechanics of the vertebral column in australopithecines are not completely documented or understood. This problem is the impetus for the present detailed comparative morphometric analysis of the Stw-H8/H41 vertebral series. The results of the study show a large size differential between the vertebrae of this individual and those of Sts-14, and among *A. afarensis* vertebrae, supporting the idea that australopithecine species were highly sexually dimorphic. In addition, the observation of osteophytic lesions on the L2 and L3 (=L III and L IV) centra of Stw-H8 adds to a curiously high incidence of vertebral pathology in australopithecines. Stw-H8/H41 resembles Sts-14 in a number of aspects, including: (1) relative elongation of thoracic centra; (2) disproportionate combination of small centra with robust neural arches; (3) relative narrowness of lumbar centra; (4) serial decrease of dorsal and ventral lumbar centrum lengths; (5) relative large size of zygapophyses; (6) caudal projection of postzygapophyses; and (7) serial increase in zygapophyseal spacing and angulation. The shared occurrence of these features in Stw-H8/H41 with Sts-14 and other australopithecines suggests that they comprise a normal morphology for at least *A. africanus*. Features 1–4 are apparently autapomorphies of *A. africanus* and perhaps

all australopithecines, and bear further study in regard to their implications for columnar function. Features 5–7 are also shared with modern humans, and their presence in Stw-H8/H41 reinforces the notion that the australopithecine vertebral column was adapted to habitual vertical posture.

The australopithecine vertebral column has no modern analogue in the combination of these features. The study also reveals that it has a high degree of morphometric variation. Differences between Stw-H8/H41 and Sts-14 in centrum wedging and pedicular robustness, for example, indicate that ideas of modality for these aspects of vertebral morphology need to be reassessed for australopithecines. These features in particular show high variability among the specimens sampled. Sts-14 exhibits dorsal wedging of the L3–L6 centra, which probably produced a strong lordotic curve, whereas dorsal wedging in Stw-H8 could have occurred only at the lowest levels of the lumbar series and argues against hyperlordosis as the typical configuration of the australopithecine lumbar column. Similarly, the contrast of robust pedicles in Stw-H8 with more slender pedicles in Sts-14 shows that the modal condition of these structures is uncertain for *A. africanus*. These findings suggest that inferences about australopithecine vertebral function will be refined only as species samples are increased and more is known about the serial transformation of individual features in each.

Acknowledgements

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Appendix 1　Scaling of lumbar centrum dimensions to body weight in extant non-human hominoids

Taxon	Analysis		L I	L II	L III	L IV	L V	L VI	L VII
						Vertebral levels			
						Ventral length			
Non-human hominoids	LSR	r^2				0·96	0·95	0·95	0·95
		Y-int.				2·10	2·14	2·08	1·96
		Slope				0·26	0·26	0·27	0·31
	RMA	Y-int.				2·06	2·11	2·04	1·97
		Slope				0·27	0·26	0·28	0·30
		95% CIs				0·23–0·31	0·22–0·30	0·24–0·33	0·26–0·35
						Width			
Non-human hominoids	LSR	r^2				0·99	0·99	0·99	0·99
		Y-int.				2·38	2·39	2·41	2·44
		Slope				0·29	0·30	0·35	0·31
	RMA	Y-int.				2·38	2·38	2·39	2·43
		Slope				0·29	0·30	0·31	0·31
		95% CIs				0·27–0·31	0·28–0·32	0·29–0·32	0·29–0·33
						Height			
Non-human hominoids	LSR	r^2				0·97	0·96	0·95	0·95
		Y-int.				1·81	1·87	1·87	1·90
		Slope				0·35	0·35	0·35	0·34
	RMA	Y-int.				1·81	1·85	1·84	1·88
		Slope				0·35	0·35	0·35	0·34
		95% CIs				0·30–0·40	0·30–0·40	0·30–0·42	0·29–0·40
						Surface area			
Non-human hominoids	LSR	r^2				0·99	0·99	0·99	0·98
		Y-int.				−0·47	−0·41	−0·38	−0·49
		Slope				0·63	0·63	0·63	0·62
	RMA	Y-int.				−0·50	−0·41	−0·39	−0·51
		Slope				0·64	0·63	0·64	0·63
		95% CIs				0·58–0·70	0·57–0·70	0·58–0·70	0·57–0·70

Slope isometry is predicted to be 0·33 for length, width, and height, and 0·67 for surface area in the scaling model of geometric similarity (MacMahon, 1975; Currey, 1984; Schmidt-Nielsen, 1984). Dimensions: ventral length=VLV; width=VB; height=VH; surface area=ACCA (measurements are explained in Figure 2). Abbreviations: LSR=least squares regression; RMA=reduced major axis regression; Y-int.=y-intercept; 95% CIs=± 95% confidence limits to the slope (see Sokal & Rohlf, 1987).

Appendix 2 Scaling of lumbar pedicle dimensions to body weight in extant non-human catarrhines

Taxon	Analysis		LI	LII	LIII	LIV	LV	LVI	LVII
						Vertebral levels			
Non-human hominoids	LSR					Pedicle length			
		r^2				0·97	0·97	0·98	0·98
		Y-int.				1·81	1·76	1·71	1·51
		Slope				0·22	0·23	0·24	0·28
	RMA	Y-int.				1·79	1·73	1·69	1·52
		Slope				0·23NS	0·24NS	0·24NS	0·27NS
		95% CIs				0·19–0·28	0·20–0·29	0·21–0·28	0·24–0·32
Cercopithecoids	LSR					Pedicle length			
		r^2	0·59	0·53	0·42	0·43	0·43	0·52	0·66
		Y-int.	2·16	2·32	2·39	2·38	2·40	2·39	2·03
		Slope	0·25	0·18	0·16	0·18	0·18	0·18	0·24
	RMA	Y-int.	2·01	2·17	2·19	2·18	2·20	2·27	1·92
		Slope	0·32	0·25	0·25	0·27	0·27	0·24	0·29
		95% CIs	0·22–0·46	0·19–0·34	0·18–0·35	0·20–0·38	0·20–0·38	0·18–0·32	0·23–0·37
Non-human hominoids	LSR					Pedicle width			
		r^2				0·98	0·98	0·98	0·86
		Y-int.				0·19	0·31	0·35	1·10
		Slope				0·46	0·44	0·45	0·29
	RMA	Y-int.				0·18	0·29	0·34	1·03
		Slope				0·47NS	0·44NS	0·45NS	0·31*
		95% CIs				0·41–0·54	0·39–0·51	0·39–0·52	0·21–0·44
Cercopithecoids	LSR					Pedicle width			
		r^2	0·48	0·56	0·59	0·69	0·80	0·82	0·80
		Y-int.	0·25	0·32	0·08	0·02	−0·17	−0·03	0·31
		Slope	0·29	0·27	0·31	0·32	0·45	0·50	0·50
	RMA	Y-int.	−0·01	0·12	−0·11	−0·09	−0·26	−0·13	0·18
		Slope	0·43	0·36	0·40	0·38	0·49	0·55	0·56
		95% CIs	0·28–0·64	0·27–0·48	0·30–0·52	0·30–0·48	0·40–0·60	0·46–0·65	0·46–0·69

Slope isometry is predicted to be 0·33 in the scaling model of geometric similarity (MacMahon, 1975; Currey, 1984; Schmidt-Nielsen, 1984). Dimensions: pedicle length=LP; pedicle width=BP (measurements are explained in Figure 2). Abbreviations: LSR=least squares regression; RMA=reduced major axis regression; Y-int.=y-intercept; 95% CIs=±95 percent confidence limits to the slope (see Sokal & Rohlf, 1987).

NS, slope differences between regressions for non-human hominoids and cercopithecoids are not significant.

*Slope differences between regressions for non-human hominoids and cercopithecoids are significant ($P > 0·01$). Clark's (1980) t-test was used to determine significance of slope differences.

Appendix 3   Scaling of combined sacral facet area to body weight in extant non-human hominoids

Taxon	Analysis		Area ASFR+ASFL
Non-human hominoids	LSR	r^2	0·94
		Y-int.	−1·75
		Slope	0·57
	RMA	Y-int.	−1·81
		Slope	0·59
		95% CIs	0·50–0·70

Slope isometry is predicted to be 0·67 for surface area in the scaling model of geometric similarity (MacMahon, 1975; Currey, 1984; Schmidt-Nielsen, 1984). Dimensions: sacral facet area, left side=ASFL; sacral facet area, right side=ASFR (measurements are explained in Figure 2). Abbreviations: LSR=least squares regression; RMA=reduced major axis regression; Y-int.=y-intercept; 95% CIs=±95% confidence limits to the slope (see Sokal & Rohlf, 1987).