



Functional implications of variation in lumbar vertebral count among hominins

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ABSTRACT

As early as the 1970s, Robinson defined lumbar vertebrae according to their zygapophyseal orientation. He identified six lumbar elements in fossil Sts 14 *Australopithecus africanus*, one more than is commonly present in modern humans. It is now generally inferred that the modal number of lumbar vertebrae for australopiths and early *Homo* was six, from which the mode of five in later *Homo* is derived. The two central questions this study investigates are (1) to what extent do differences in human lumbar vertebral count affect lordotic shape and lumbar function, and (2) what does lumbar number variation imply about lumbar spine function in early hominins? To address these questions, I first outline a biomechanical model of lumbar number effect on lordotic function. I then identify relevant morphological differences in the human modal and extra-modal variants, which I use to test the model. These tests permit evaluation of the human L6 variant as a model for reconstructing early hominin modal number and spine function. Application of the biomechanical model in reconstructing australopith/early *Homo* lumbar spines highlights shared principles of Euler column strength and sagittal spine flexibility among early and modern hominins. Within modern humans, the extra-modal L6 variant has an extended series of three cranially positioned kyphotic vertebrae and strongly oblique zygapophyseal facets at the last lumbar level. Although they share the same radius and length of lumbar curvature, the L6 variant differs functionally from the L5 mode in its expanded range of sagittal flexion/extension and enhanced resistance to shear. Given the modal number of six lumbar vertebrae in australopiths and early *Homo*, lumbar spine mobility and strength would have been key properties of vertebral function in early bipeds whose upper and lower body segments were coupled by close approximation of the thorax and iliac crests.

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Introduction

As early as the 1970s, Robinson identified six lumbar vertebrae in fossil Sts 14 *Australopithecus africanus*, one more than is commonly present in modern humans (Robinson, 1972). A second *A. africanus* individual, Stw 431, probably also had six lumbar vertebrae (Ogilvie et al., 1998; Sanders, 1998; Tobias, 1998; Pilbeam, 2004; Lovejoy, 2005). A single specimen of *Homo erectus* (KNM WT 15000) indicates that early *Homo* also had six lumbar vertebrae (Latimer and Ward, 1993; Walker and Leakey, 1993). Thus, it is generally inferred that the modal number for australopiths and early *Homo* was six, from which the mode of five in later *Homo* is derived (e.g., Latimer and Ward, 1993; Sanders, 1998; Pilbeam, 2004). However, not all paleoanthropologists support this reconstruction of hominin lumbar evolution. On the one hand, counting prezygapophyses facing the sagittal midline, as Robinson and others prefer (Washburn and Buettner-Janusch, 1952; Shapiro, 1993a; Whitcome et al., 2007), indicates the presence of six

vertebrae in the lumbar spines of early hominins. On the other hand, lumbar identification according to the absence of rib facets indicates only five, calling into question the notion of evolutionary change in modal number between australopiths and humans (Haeusler et al., 2002).

Biomechanically, there is good reason to define thoraco-lumbar vertebrae according to zygapophyseal orientation. For example, because the lumbar and thoracic zygapophyses align in fundamentally perpendicular planes, their facets generate dissimilar patterns of vertebral rotation (Slijper, 1946; Washburn and Buettner-Janusch, 1952; Erikson, 1963; Adams and Hutton, 1983; Bogduk, 1997). Thoracic facets that lie fully in the coronal plane enhance axial rotation, and lumbar facets, by facing the spinal midline, allow for greater sagittal flexion and extension (Hildebrand, 1974; Guan et al., 2007). Haeusler et al. (2002) reason that the functionally-based facet classification is flawed given that lumbar facets “allow only a moderately higher degree of flexion and extension” and there is no “abrupt change” in rotation at the shared boundary of thoracic and lumbar regions (Haeusler et al., 2002: 625). Yet, because intervertebral joints generate the greatest movement in series (Pearcy et al., 1984; Harada et al., 2000), spinal

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motion is best assessed along the entire length of the lumbar column rather than solely at single joints within segments or at the regional boundaries between them. Furthermore, these criticisms arise from findings of lumbar movement obtained from rib-defined vertebrae (Virchow, 1911; White and Panjabi, 2000) and therefore, through methodological design, lack potential to fully characterize facet function in zygapophyseal determined segments.

Zygapophyses play a major role in spine function because they not only guide but also limit rotation and translation between vertebrae. McGregor et al. (1995) calculated that total sagittal lumbar rotation among adult females is on average 8° less than in males, yet female axial lumbar rotation exceeds that of males by 6–7°. Recent analyses of mass induced spinal loading during human pregnancy showed that along the entire lumbar spine the zygapophyses of females are oriented more coronally by an average of 13% ± 5% than those of males (Whitcome et al., 2007). As facets become sagittally oblique they increase vertebral resistance to anterior displacement (Sharma et al., 1995; Bogduk, 1997; Lu et al., 2005), an inherent risk in the derived lumbar curve of hominins and one that is further exacerbated by fetal loading (Whitcome et al., 2007). Given that the orientation of lumbar facets inversely affects the sagittal and axial rotations of the spine, sex differences in lumbar motion are not surprising. The lumbar anatomy of males and females coupled with the positional kinematics of pregnancy and the biomechanics of fetal load evince the fundamental role of zygapophyses in human spine function. Comparative study of extinct hominins including australopith and early *Homo* fossils shows that the lumbar zygapophyses of bipeds become sequentially more coronally oriented from the cranial to the caudal boundaries (Latimer and Ward, 1993; Sanders, 1998; Whitcome et al., 2007).

If we define lumbar vertebrae according to the zygapophyseal criterion, modern humans and early hominins differ in lumbar modal number (i.e., five and six, respectively) and a key question becomes, should we expect the lumbar curve of early bipeds to differ functionally from modern humans? While vagaries of the fossil record impede analysis of lumbar spine function in early hominins, human lumbar variants provide us a good experimental test. Moreover, comparison of numeric variants within a single species is reasoned because such intraspecific examination reduces the probability of confounding variables in body proportions and positional biomechanics across species, allowing explicit tests of hypotheses relating lumbar vertebral number to functional morphology of the unique hominin lumbar curve.

Therefore, the two central questions this study investigates are 1) to what extent do differences in lumbar vertebral count within humans affect lordotic shape and lumbar function, and 2) what does lumbar number variation imply about lumbar spine function in early hominins? In order to address these questions, I first outline a model of the effect of lumbar number on lordotic function. I then identify relevant morphological differences in the lumbar vertebrae of human modal and extra-modal variants that I use to test the model. Finally, these tests permit me to evaluate the human L6 variant as a model for reconstructing australopith modal number and spine function. The study examines numeric variation within modern humans for the following reasons: 1) *Homo sapiens* is the only living species within the hominin clade on which to test hypotheses of numeric variation; 2) the human numeric variants provide a good analog for comparison of early versus modern lumbar mode because the intraspecific comparison holds other functional complexes constant, thus avoiding confounding variables; and 3) the extra-modal variant (L6) is present at relatively high frequency within human populations (de Beer Kaufman, 1974; Shapiro, 1993a) providing statistical power for testing hypotheses.

Model of lumbar curvature and loading

By positioning the body's center of mass in vertical alignment with the biacetabular axis, lumbar lordosis eliminates gravity-induced hip torque in bipedal stance and walking gait (Latimer and Ward, 1993; Shapiro, 1993a). Lordosis is described as a dorsal concave curve derived ontogenetically from a primary, convex cervicosacral curve (e.g., Cunningham, 1886; Aello and Dean, 1990). However, this sagittal contour of the lumbar spine is more complex than generally appreciated, reflecting a regional span of linked convexity and concavity united by a neutral or nearly non-wedged vertebra (Rose, 1975; Latimer and Ward, 1993; Sanders, 1998; Whitcome et al., 2007). The latter concept pertains because vertebrae that lie cranial to the neutral element are ventrally wedged, and therefore kyphotic, while those positioned caudal to the neutral vertebra are dorsally wedged, thus lordotic (Pal and Routal, 1986, 1987).

In a strict geometric sense, the lumbar region itself is sinusoidal, comprised of two spinal curves, a cranial kyphosis that is continuous with the primary thoracic curve and a lordosis, a secondarily derived feature of the biped lumbar column. This curvilinear complexity gives rise to fundamental mechanisms of strength and stability in the spine; despite an increase in spinal loading associated with bipedal posture and gait, the hominin torso remains fully upright and consistently balanced (e.g., Thorstensson et al., 1984; Schache et al., 1999). Its longitudinal axis is vertically stable without deflection. Meakin et al. (1996) explain that this is possible because the sinusoidal spine, achieved through evolution of the lumbar lordosis, behaves according to Euler Buckling Theory (Fig. 1). Its conformation is determined by the inequality:

$$L(Mg/EI)^{1/2} \geq \pi(2n - 1)/2 \quad (1)$$

where L is the length of the column, Mg the supporting weight, EI the flexural stiffness of the column (product of Young's modulus and the second moment of the cross-sectional area about the neutral axis) and the integer n which describes the mode of buckling (Meakin et al., 1996). When modeled as an Euler column, spinal

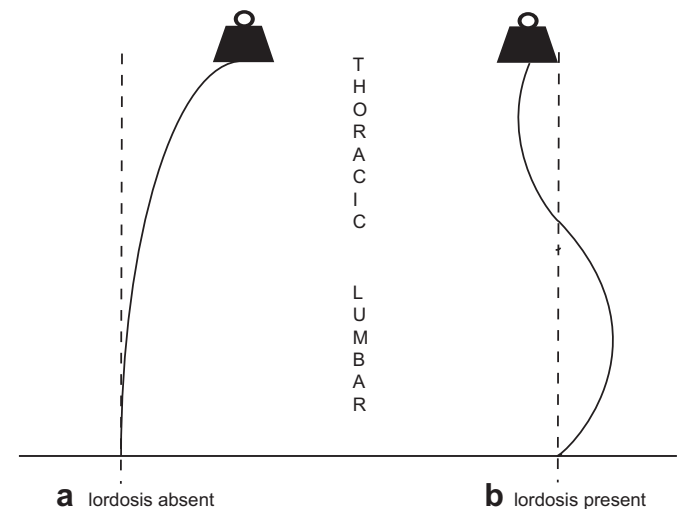


Figure 1. Thoraco-lumbar spine characterized as an Euler column comparing (a) a simple deflection curve in which lordosis is absent and (b) a complex sinusoidal curve in which lordosis is present, generating two arcs, one thoracic and one lumbar (modified from Meakin et al., 1996 and Timoshenko and Gere, 1961). The dashed line represents the spine's natural longitudinal axis in upright posture; the solid line represents the spine's thoraco-lumbar conformation in the sagittal plane under increased loading; the parallelogram indicates the vertical component of the added mass.

loading properties become evident and the critical load (P_{cr}) is formalized as:

$$P_{cr} = \frac{4\pi^2 EI}{L^2} \quad (2)$$

The length variable has a smaller value in a buckled column like the human spine because reciprocal curves shorten the distance between inflection points (Fig. 1b). That is, lumbar lordosis enhances load capacity because its functional length, the distance between points of column inflection, is short (Timoshenko and Gere, 1961) relative to the inflection points of the primary spinal curve retained by all African apes (Sanders, 1998; Lovejoy, 2005) and by inference, the last common ancestor. For the australopiths, whose muscular torsos, relatively long forelimbs and massive faces preceded the slighter proportions of later *Homo* (McHenry and Coffing, 2000), the loading strength and dynamic stability of a deep lumbar spine conferred a key biomechanical advantage.

Euler Buckling Theory applies to columnar structures that are entirely homogenous (Meakin et al., 1997), and given the trabecular and compact architecture of vertebrae as well as the compliance of the nucleus pulposus and annulus fibrosus within the vertebral discs, spinal columns are structurally heterogeneous. Ultimately, lumbar lordosis and lumbar kyphosis are biomechanically more complex than applied Euler Buckling Theory suggests. Because the points that comprise spinal arcs are articulated vertebrae whose connections are secured through dorsal zygapophyses and ventral vertebral bodies, sinusoidal shear stress increases at intervertebral

joints, particularly the zygapophyseal joint loci where posterior/anterior displacement effects between pairs are concentrated (Lu et al., 2005). A deep spinal curve with its long torque arm generates large bending moments along the arc (Fig. 2a and b). The magnitude and the direction of forces exerted by the upper body onto the spine depend in part on wedging properties of the vertebrae. A non-wedged vertebra experiences pure compression in orthograde postures (Fig. 2c), and a lordotically wedged vertebra experiences the non-coplanar forces of compression and shear (Davis, 1961) (Fig. 2d). Notably, although an increase in number of lordotic lumbar vertebrae may deepen the lumbar curve and shorten its functional length, in doing so it will also increase the bending moment, exacerbating intervertebral shear (Fig. 2). Therefore, the anatomical model of lumbar lordosis presented in this study (Fig. 3a) combines Euler Buckling Theory and spine loading mechanics to explain the principle effects of orthograde lumbar spine lengthening.

I propose that the modal difference between the australopith/early *Homo* six-element lumbar spine and the modern human five-element lumbar spine centers on multiple functional roles of the lumbar zygapophyses. Given the importance of lumbar lordosis to hominin locomotion and the current evidence for multiple modalities in hominin lumbar number, this study tests four hypotheses that relate modal number to spine function. The study model allows for the major prediction that L6 lengthens the mid lumbar region with no lordotic change (Fig. 3b), and therefore conserves the true lumbar lordosis, as well as two alternate

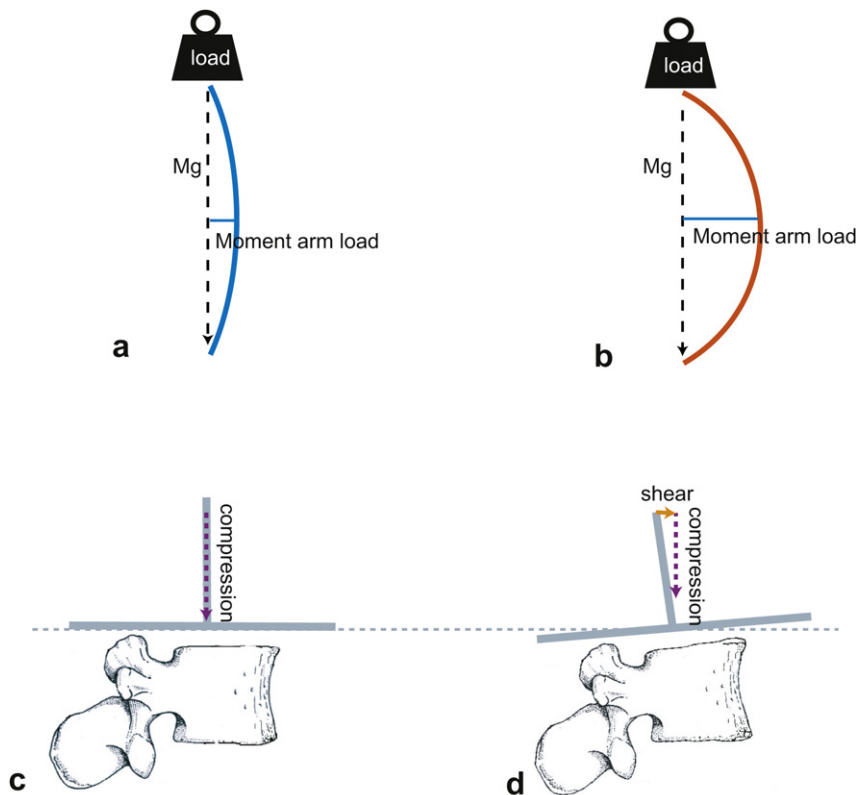


Figure 2. Principal biomechanics of lumbar spine curvature. Simplified curvilinear lordosis with applied load (a) showing how deeper curve (b) increases the bending moment at any point or hypothetical joint along the arc, given equal load. Load applied at the upper origin of the arc will generate a larger bending moment at points along the curve to the right. This is because the torque arm is relatively long. Magnitude and direction of forces exerted by the upper body to a vertebra depend in part on wedging properties of the vertebral body. A non-wedged body experiences pure compression in orthograde postures, (c) a lordotically wedged body experiences the non-coplanar forces of compression and shear. (d) The lordotic and kyphotic curves of the lumbar spine are more complex than depicted here because the points that comprise the arcs are articulated vertebrae whose connections are secured through parallel curved pillars of dorsal zygapophyses and ventral vertebral bodies.

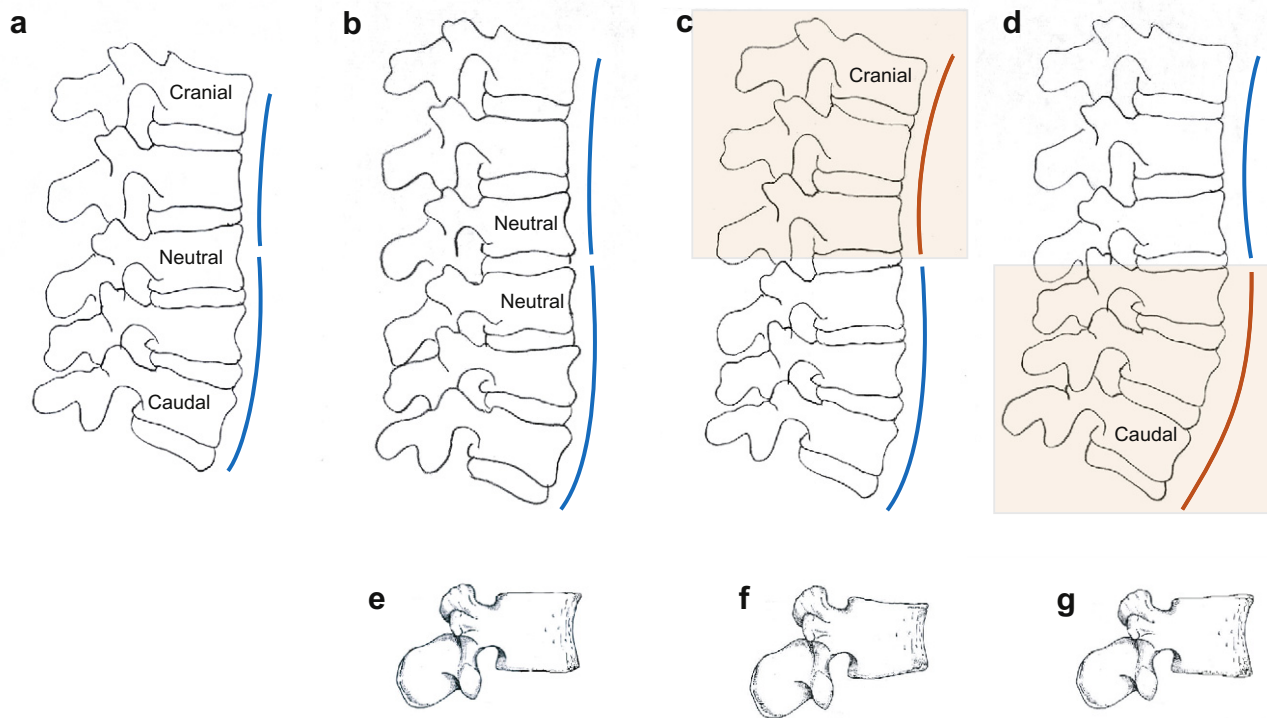


Figure 3. Model of spinal curvature. (a) Modal L5 lumbar spine showing midsection position of neutral (non-wedged) vertebra, (b) Extra-modal L6 spine by addition of a neutral, non-wedged vertebra in the mid lumbar region, generating moderate kyphotic and lordotic curves consistent with the Modal L5 spine, (c) Extra-modal L6 spine with cranial position of extra-modal vertebra enhancing kyphotic curvature, (d) Extra-modal L6 spine with caudal position of extra-modal vertebra augmenting lordotic curvature, (e) Neutral vertebra (non-wedged), (f) Kyphotic vertebra (ventral wedged), (g) Lordotic vertebra (dorsal wedged).

scenarios of modified lumbar curvature, that L6 either lengthens the column cranially, increasing lumbar kyphosis (Fig. 3c) or lengthens the column caudally, increasing lumbar lordosis (Fig. 3d).

If the extra-modal element is incorporated into either the cranial origin or the caudal terminus of the lumbar region, spinal curvature will be modified, as a cranial position enhances kyphosis increasing anterior load on the vertebral bodies (Fig. 3c), while a caudal position augments lordosis elevating posterior load along the zygapophyses (Fig. 3d). Both scenarios (Fig. 3c and d) increase differential loading between the ventral and the dorsal pillars: the ventral pillar comprised of vertebral bodies and intervertebral discs and the dorsal pillar comprised of neural arch components and articular zygapophyses (Pal and Routal, 1986, 1987). Should the additional lumbar vertebra attain positional identity within the true lordotic concavity where vertebral bodies are dorsally wedged, it will increase the posterior load that must be resisted by the zygapophyses (Fig. 3d). However, positional identity of the sixth element may fall within the neutral region, preserving the modal lordotic curve, thus minimizing shear effect, indicating that a longer lumbar spine need not alter the Euler defined functional curvature.

The bony contribution to lumbar lordosis derives primarily from vertebral body shape (Cheng, 1998; Been et al., 2010) and is determined by relative differential length in the ventral and dorsal aspects of the centrum (Fig. 3). Ventrally wedged vertebral bodies predominate in the thoracic region cranially adjacent to the lumbar spine (Fig. 3f) (Cunningham, 1886; Latimer and Ward, 1993). Sequentially, they decrease in degree of ventral wedging cranio-caudally (Rose, 1975; Latimer and Ward, 1993; Sanders, 1998; Whitcome et al., 2007), flattening to some extent the kyphotic arc of the thoracic spine. Vertebral body wedging then transitions from

the kyphotic state to a lordotic dorsal-wedge configuration (Fig. 3g). Collectively, a sequential decrease in kyphotic wedging combined with an increase in lordotic wedging give the human lumbar spine its distinctive structural lordosis.

Cumulative wedging across lumbar vertebrae produces a measurable radius of lordotic curvature. Although adding a sixth lumbar vertebra to the L5 modal spine holds the potential to deepen the lordotic curve and therefore alter the biomechanical environment of the lower spine, radial stasis of the lumbar curve is possible. Mass applied to a deeply curved vertical pillar generates a longer moment arm than the same mass applied to a pillar of equal length but of shallower curvature (Fig. 2a and b). Because deep curves produce large torques loading the pillar constituents with a high shear force (Tveit et al., 1994; Kingma et al., 2007) (Fig. 2b), lengthening of the modal L5 spine by additional vertebrae should prevent an increase in the radius of curvature.

Because the zygapophyses of bipeds become sequentially more coronally oriented from the cranial to the caudal boundaries (Odgers, 1933; Latimer and Ward, 1993; Sanders, 1998; Masharawi et al., 2004; Whitcome et al., 2007), the rotational effect is similar in each modal manipulation regardless of position within the series increasing the range of sagittal flexion and extension in the lumbar spine. A six-element lumbar spine will introduce, in a step-wise manner, greater obliquity in the lower lumbar region.

Hypotheses

This study uses a biomechanical model of lumbar number effect on lordotic function to evaluate the human L6 variant as a model for reconstructing early hominin modal number and spine function, highlighting shared principles of Euler column strength and sagittal

spine flexibility among early and modern hominins. Based on the Euler model of lumbar curvature and loading, four explicit hypotheses addressing the functional role of vertebral number in both the modal (L5) and the extra-modal (L6) lumbar spines are tested:

Hypothesis 1. If column strength is a fundamental role of the lumbar curve, the positional identity of the sixth lumbar vertebra should fall in the mid lumbar region where its effect on the lordotic spine will be predominantly neutral. Thus, the extra-modal L6 variant will be similar to the L5 mode, preserving the functional length of the lumbar Euler curve.

Hypothesis 2. If preservation of the lumbar Euler curve requires stasis in the wedging geometry of the true lumbar vertebrae, the kyphotic and lordotic wedging geometry of the modal and extra-modal lumbar spines will remain equal.

Hypothesis 3. If Euler strength is maintained across the modal and extra-modal variants, the radius of curvature in both will be equal.

Hypothesis 4. Given that human lumbar facets in craniocaudal sequence become increasingly oblique, the facet angle of the last lumbar within the extra-modal variant will be more oblique than the modal variant, with implications for load resistance and movements within the lumbar spine.

Materials and methods

The sample

Complete series of lumbar vertebrae for 60 modal and 21 extra-modal individuals of known age and sex were drawn from skeletal archives of the Hamann-Todd Osteological Collection, Cleveland Museum of Natural History and the Terry Collection, National Museum of Natural History in Washington DC. Although the L6 variant is present in both sexes (Schultz and Straus, 1945), this study sample included only males in order to: 1) control for lumbar vertebral sexual dimorphism that might otherwise confound a pooled sex sample (Whitcome et al., 2007); and 2) obtain a robust sample population, as the L6 variant occurs with greater frequency in males than in females (Bornstein and Peterson, 1966; de Beer Kaufman, 1974). An informal survey of the skeletal collections demonstrated a higher representation of L6 males than L6 females,

consistent with the published reports. Morgue records providing general biological profiles for specimens, including sex, age and gross pathologies support each collection. Sex noted in collection documents was reassessed for all individuals according to a suite of pelvic indicators established by Phenice (1969) and Ubelaker and Volk (2002). Chronological age within 20–40 years at death was further evaluated by visual confirmation of epiphyseal closure in the postcrania. Individuals whose sex or age was ambiguous according to either collection records or observer assessment were excluded. Ancestry-related differences within the sample population (morgue identified and morgue parlanded as black or white) were tested for ethnicity effect using paired samples Student's *t*-test. No significant ethnicity response was obtained.

Lumbar vertebral identification

Vertebrae were classified as lumbar according to their zygapophyseal orientation (Washburn and Buettner-Janusch, 1952). This facet-based designation differs from the non-rib-bearing convention in its functional emphasis on the range of motion between vertebral elements, as movements in the lumbar column are largely determined by zygapophyseal morphology (Bogduk, 1997). Parasagittally oriented facets guide sagittal flexion and extension, yet they resist rotation in other planes (e.g., Rockwell et al., 1938; Hildebrand, 1974; Yamamoto et al., 1989; Guan et al., 2007; Busscher et al., 2009). In caudal progression the zygapophyses of bipeds open coronally and therefore buttress against shear stress along the lumbar spine, reducing the risk of ventral displacement inherent in the lordotic portion of the column (Latimer and Ward, 1993; Bogduk, 1997). For these reasons, the functional relevance of the facet-based designation of a vertebra to the lumbar spine as an alternative to the non-rib-bearing designation becomes apparent. This is particularly meaningful with respect to the resulting difference in lumbar vertebral numbers between the early and more recent bipeds given by the facet designation.

Variables

Linear variables of Centrum Dorsal Length (CDL), Centrum Ventral Length (CVL) and Anteroposterior Length (APL) illustrated and defined in Fig. 4 were measured on each lumbar vertebra using

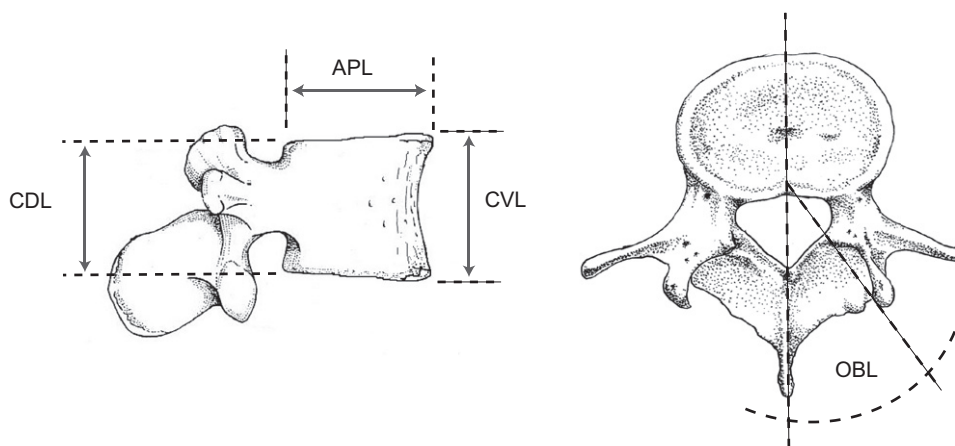


Figure 4. Linear and angular variables recorded for lumbar vertebrae. Left: lateral view of lumbar vertebra showing linear measurements of centrum dorsal length (CDL, greatest craniocaudal distance along the dorsal margin of the body), centrum ventral length (CVL, greatest craniocaudal distance along the ventral margin of the body) and anteroposterior length (APL, greatest anteroposterior distance on the cranial surface of the body). Right: cranial view of lumbar vertebra showing angle of zygapophyseal obliquity (OBL, taken as the angle formed by the sagittal midline of the vertebral body (independent of spinous process skew) and a line determined by the two opposing transverse margins of the right zygapophyseal facet).

a Mitutoyo 500-171 digital-sliding caliper accurate to ± 0.02 mm then used to calculate a trigonometric variable of vertebral body wedging, following Digiovanni et al. (1989):

$$\text{Wedging angle} = 2 \text{ arc tangent } \left[\frac{[\text{CDL} - \text{CVL}]/2}{\text{APL}} \right] \quad (3)$$

A vertebra was determined to be neutral, neither kyphotic nor lordotic, within the range $+0.5^\circ$ to -0.5° . Positive angles indicate kyphosis, while negative angles indicate lordosis. Unlike the hard tissue vertebral bodies that remain rigidly kyphotic or lordotic through a range of postures and movements, the soft tissue intervertebral discs undergo significant deformation in response to spinal movement (Adams et al., 1994). In fact, healthy discs function as thin-walled pressure vessels that are highly malleable, due primarily to the annulus fibrosus that reduces in anterior height as much as 35% and increases in posterior height as much as 90% during sagittal flexion (Kanayama et al., 1995). Thus, discs appear to contribute little to the inherent configuration of spinal curves and are not assessed in this study. Positional identity of the extra-modal vertebra was determined by comparison of the wedging sequences in the L5 and L6 variants. Radius of curvature was obtained mathematically in MATLAB using vertices and midpoints of fused quadrilateral polygons derived from vertebral body dimension to best fit circles through midpoints. For the purpose of isolating the bony contribution of vertebral bodies to the lordotic curve, the vertebra of neutrality (non-wedging) defines the start position of the lordotic arc and the caudalmost dorsally wedged vertebra delimits the regional end position. Zygapophyseal angle OBL (Fig. 4) was measured as the parasagittal angle of the right facet using an SPI 30-394-1 protractor accurate to $\pm 1^\circ$.

Statistical analyses

In order to examine structure and function associated with variation in hominin lumbar vertebral count, I collected both linear and angular dimensions of vertebrae among the L5 modal and the L6 extra-modal groups within modern humans. Linear data were tested for normal distribution using the Kolmogorov–Smirnov–Lillefors test (Thode, 2002). To test the null hypothesis of no difference between groups in positional identity and radius of curvature, a test of homogeneity of variance was performed using the Scheffé–Box test (Sokal and Rohlf, 1995). The distribution of linear data within both groups did not uniformly meet the statistical assumptions of normality and equal variance. Thus, comparisons between the two groups were performed with the nonparametric Wilcoxon Rank Sum test (Sokal and Rohlf, 1995). The measured angle of zygapophyseal obliquity and the calculated angle of vertebral body wedging have circular distributions that require directional statistical methods for analysis (Batschelet, 1981). The polar and rectangular coordinates of all angular variates along with their respective sine and cosine values were processed through a custom Matlab

script in order to calculate mean angle, mean angular deviation, and 95% confidence limits for both the L5 modal and the L6 extra-modal groups. Comparisons between the two groups were performed with The Watson and Williams Two-Sample Test, a circular analog of a one-factor ANOVA using the critical value $F_{0.05(1),1,N-2}$ (Zar, 2010).

Statistical significance for the analyses was determined according to a modified Bonferroni correction advocated by Jaccard and Wan (1996). Significance values for all tests were rank-ordered from smallest to largest and matched with adjusted levels of significance determined as $0.05/n$, where n is sequentially reduced by the number of remaining variables. This correction retains an overall Type I error rate of 5% (Jaccard and Wan, 1996). Statistical analyses were performed on angular variables only, that is, angles recorded directly from vertebral elements and angles calculated from recorded linear dimensions. Because angular variables are independent of body size, no adjustment for allometric scaling effect was required. All linear statistical analyses were performed using JMP 8.0 software package. Circular statistical analyses were conducted entirely in Matlab.

Results

Positional identity

The extra-modal vertebra assumes the positional identity of L1 (Table 1), lengthening the kyphotic region of the lumbar spine. It lies at the thoraco-lumbar boundary adding a third ventrally wedged lumbar vertebra of 25.2 mm (± 1.5 mm) ventral length and 28.2 mm (± 1.3 mm) dorsal length with a kyphotic wedging angle of 5.6° ($\pm 2.7^\circ$). Among the six vertebrae within the extra-modal spine, it has the smallest ventral dimension and greatest ventral wedging angle.

Vertebra wedging (lumbar lordosis)

Mean raw dimensions (\pm sd) of the lumbar vertebral bodies and the mean wedging angle (\pm angular deviation) for each vertebra in the L5 modal and L6 extra-modal groups are presented in cranio-caudal order (Table 2). The variants differ in wedging angle from 1° to 4° when paired by vertebral level. Although the transitional (non-wedged) vertebra of each occurs at a different lumbar level, L3 in the modal variant and L4 in the extra-modal variant, two dorsally wedged vertebrae configure the lordosis of both groups equally at their penultimate and last lumbar levels. Even though the extra-modal variant is numerically longer, its lordotic sequence is numerically identical to the modal pattern having two elements that are paired in the same caudalmost position. Thus, the constituents of true lumbar lordosis in L6 do not include the extra-modal vertebra.

Table 1

Raw dimensions of vertebral body length for human L5 modal and L6 extra-modal variants.^a

Lumbar level	L5 modal			L6 extra-modal		
	Ventral length ^b	Dorsal length		Ventral length	Dorsal length	
L1	26.1	28.6	Kyphotic ^c	25.2	28.2	Kyphotic
L2	27.3	28.7	Kyphotic	26.7	28.7	Kyphotic
L3	28.3	28.4	Neutral ^d	28.2	28.8	Kyphotic
L4	28.4	27.4	Lordotic ^e	28.5	28.3	Neutral
L5	28.8	24.9	Lordotic	28.4	26.9	Lordotic
L6	–	–	–	28.7	24.3	Lordotic

^a Sample comprised of adult males, L5 modal $n = 60$, L6 extra-modal $n = 21$.

^b All values are means reported in mm.

^c Vertebral body shape in which dorsal length exceeds ventral length.

^d Vertebral body shape in which ventral length approximates dorsal length.

^e Vertebral body shape in which ventral length exceeds dorsal length.

Table 2
Lumbar vertebral wedging angle in modern human L5 modal and L6 variant groups.^a

Lumbar level	Variant	CVL		CDL	APL	Wedging
		Ventral height ^b		Dorsal height	A-P length ^c	Angle ^d
		Mean (sd)	Mean (sd)	Mean (sd)	Mean (sd)	
L1	L5 modal	26.1 (1.5)	28.6 (1.4)	34.3 (2.3)	4.3 (1.9)	
	L6 extra-modal	25.2 (1.7)	28.2 (2.0)	30.0 (2.9)	5.6 (2.6)	
L2	L5 modal	27.3 (1.8)	28.7 (1.5)	34.8 (2.3)	2.4 (2.3)	
	L6 extra-modal	26.7 (2.2)	28.7 (2.1)	31.1 (2.9)	3.6 (1.7)	
L3	L5 modal	28.3 (1.8)	28.4 (1.7)	35.5 (3.4)	0.1 (2.5)	
	L6 extra-modal	28.2 (2.0)	28.8 (2.0)	32.2 (3.1)	1.0 (2.7)	
L4	L5 modal	28.4 (1.8)	27.4 (1.7)	35.2 (2.5)	-1.6 (2.4)	
	L6 extra-modal	28.5 (2.0)	28.3 (2.1)	32.5 (2.7)	-0.3 (2.3)	
L5	L5 modal	28.8 (2.1)	24.9 (1.9)	34.7 (2.4)	-6.7 (2.9)	
	L6 extra-modal	28.4 (2.0)	26.9 (2.0)	33.0 (2.6)	-2.5 (1.9)	
L6	L5 modal	—	—	—	—	
	L6 extra-modal	28.7 (2.4)	24.3 (2.2)	34.0 (2.8)	-7.5 (2.2)	

Values in parentheses represent mean angular deviation.

Values > 0.5 indicate ventral wedging, values < -0.5 indicate dorsal wedging.

^a Variants comprised of adult males, L5 modal $n = 60$, L6 extra-modal $n = 21$.

^b Linear dimensions reported in mm.

^c A-P length = anteroposterior length centrum cranial surface.

^d Wedging Angle: $(2 \text{ arc tangent})[(\text{CDL} - \text{CVL})/2]/\text{APL}$, computed from raw data following Digiovanni et al. (1989), reported in degrees.

Further evidence of wedging equivalence is apparent in comparison of rate change within the lordotic sequence (Table 3). The largest increase in lordotic wedging occurs in the last–penultimate pair where the wedging angle increases 4.9° in both modal and extra-modal variants. Angular change across the suprajacent grouping of the penultimate–transitional (neutrally wedged vertebra) pair varies by just 0.3° and the means do not differ statistically ($p = 0.675$, $z\text{-score} = -0.4188$). The comparison of ventral and dorsal centrum lengths illustrates a similar regional progression (Table 1). These dimensions influence vertebral body wedging and therefore the curve of the lumbar spine. The boxed values highlight the relative constancy of centrum length throughout the lumbar region. At each lumbar level, craniocaudal length is conserved in either the ventral or dorsal aspect. Specifically, dimensions of the neutral vertebra fall within the range of 28.3–28.5 mm, and whether wedged vertebrae are kyphotic or lordotic, their vertebral bodies conserve the primary length of 28 mm. Wedging change in centrum shape results from either a decrease or an increase in length of the opposing side, and this pattern is mirrored precisely in the L5 and L6 variants. Along the lumbar spine, kyphosis is reduced through an increase in ventral centrum length. Alternately, lumbar lordosis derives from reduction in dorsal centrum length (see Sanders, 1995, 1998; Table 1). Although the extra-modal variant incorporates a longer series of cranially positioned kyphotic vertebrae than the modal variant (3 versus 2), they share a derived pattern of ventrodorsal proportional length, both in their single neutral level and within their two-tiered lordotic series at the penultimate and last lumbar positions. The functional lengths of the two variants (the distance between

Table 3
Rate of change in dorsal wedging angle from the last lumbar level proceeding cranially to the transitional vertebra for human L5 modal and L6 extra-modal variants.^a

Adjacent lumbar levels	L5 modal ($n = 60$)	L6 extra-modal ($n = 21$)	F-value ^b	Significance
Last–Penultimate	5.1 ± 2.7 ^c	5.0 ± 1.9	0.90	ns
Penultimate–Transitional	1.8 ± 2.1	2.2 ± 2.0	0.68	ns

^a Wedging Angle: $(2 \text{ arc tangent})[(\text{CDL} - \text{CVL})/2]/\text{CVD}$, computed from raw data following Digiovanni et al. (1989), reported in degrees.

^b Critical value for Watson-Williams test of two mean angles is $F_{0.05}(1,178)$.

^c Mean ± standard angular deviation.

inflection points) were equal, 57.2 mm and 57.1 mm for the modal and extra-modal variants, respectively (Table 1).

Wedging results show that the morphological pattern of lumbar lordosis present in each variant is strikingly similar. Most importantly, the extra-modal variant with its extended vertebral length attains its transitional wedging angle within the same pre-penultimate position as the shorter modal variant. Therefore, the functionally relevant difference in the two groups arises from structural incorporation of an “additional” kyphotic body, not a lordotic body, into the cranial reach of the L6 variant.

Radius of curvature

The mean radius of curvature (ROC) along the lordotic region of the lumbar spine of the modal L5 group is 843.5 mm (± 258.4 mm) with a range of 286.9 mm–1037.8 mm. The mean ROC of the extra-modal L6 group is 831.3 mm (± 253.9 mm) with a range of 302.5 mm–1032.9 mm. The variants' mean ROC differs by 1.5%, and this difference is non-significant, ($p = 0.869$, $z\text{-score} = 0.1640$), further indicating that lumbar lordosis is conserved across the numeric variants.

Zygapophyseal obliquity

When paired according to lumbar levels L1 through L5 the prezygapophyseal angles of the L5 and L6 groups are similar (Table 4). Values differ by less than 3° at any one level, and differences are statistically non-significant ($p = \text{range}, 0.21\text{--}0.94$). In this sense, the key progressive obliquity is conserved across the numeric variants. However, the presence of an additional lumbar vertebra in the extra-modal variant introduces into the progressively oblique series a sixth lumbar vertebra of extreme facet obliquity ($53^\circ \pm 10^\circ$) at the last lumbar position (Fig. 5).

Discussion

The model presented in this study investigates lordotic effects of adding a sixth element to the common lumbar series of five vertebrae in modern humans. Results of the model test support the major prediction that the lumbar lordosis of the L6 extra-modal variant matches the lordotic curve and lumbar constituents of the L5 mode. Specifically, findings show that both variants feature a single neutral midsection vertebra and a two-element series of lordotic vertebrae at the penultimate and last lumbar positions with similar radii of lordotic curvature (Fig. 6). Yet, despite this geometric conservation in lumbar lordosis, the human L5 and L6 variants differ in two key traits: 1) the L6 morph has an extended series of three kyphotic vertebrae at its cranial boundary; and 2) more strongly oblique zygapophyses at its caudal limit.

Lordotic shape and lumbar function

The four hypotheses addressed phenomena directly relating vertebral body shape to lumbar lordosis. Because the additional L6 vertebra assumed a kyphotic position there is no change in mid zone or lower lumbar wedging, and the radii of lumbar curvature and functional length are equal in L5 and L6 variants, achieving equivalent Euler column strength within the lower torso. Where lumbar spine strength is an issue, as it is among bipeds, preservation of a short lumbar curve consistent with Euler Buckling Theory appears to be principle. Whitcome et al. (2007) recently found that adult human females have a derived lumbar curvature that functions to compensate for obstetric fetal load. Whereas the complete lordotic sequence of dorsal wedging in human males spans two vertebrae, the lordotic sequence in human females extends along

Table 4
Prezygapophyseal obliquity in modern human L5 modal and L6 extra-modal variants.^a

Lumbar level	L5 modal		L6 extra-modal			Mean comparison	
	Angle ^b	Change from cranial level	Angle	Change from cranial level	Z-score	p-value	Significance
L1	26.4 ± 10.2c	—	28.2 ± 7.5	—	1.2501	0.21	ns ^d
L2	20.8 ± 6.0	−5.6	23.2 ± 11.2	−5.0	0.8884	0.37	ns
L3	25.3 ± 7.7	4.5	26.0 ± 8.57	2.8	0.5719	0.57	ns
L4	31.5 ± 9.6	6.2	32.3 ± 8.1	6.3	0.1224	0.90	ns
L5	42.7 ± 10.0	11.2	42.2 ± 8.7	9.9	−0.0714	0.94	ns
L6	—	—	53.3 ± 9.8	11.1	—	—	—

^a Sample consists of adult males, L5 modal $n = 60$, L6 extra-modal $n = 21$, left prezygapophyses.

^b Angle reported in degrees.

^c Mean ± angular deviation.

^d ns = non-significant p -value, Bonferroni adjusted Watson-Williams Test for 2 Samples.

three vertebrae. This wedging sequence, combined with relatively large zygapophyses, allows females to kinematically increase lumbar lordosis and subsequently align the increasingly large and anteriorly constrained fetal mass above the maternal hips and lower limb joints through extension of the torso (Whitcome et al., 2007). As a result, this positional shift also shortens the distance between the inflection points of the lordotic curve, thereby strengthening the lumbar spine. Although australopithecines and early *Homo* had six lumbar vertebrae and thus differed from later hominins, including modern humans, the Euler strength of their lumbar spines may have been similar, achieved either through wedging of the lumbar vertebrae or positional adjustment of the lumbar curve.

The key structural and functional feature of the extra-modal L6 variant, as predicted by the fourth hypothesis, is the presence of markedly oblique prezygapophyseal facets in the last lumbar position. In having an “extra” vertebral level, the L6 variant with its lumbar type zygapophyses allows a wide range of upper body flexion and extension, generating a long, sagittally dorsomobile spine. Moreover, greater facet obliquity at the last lumbar level provides increased resistance to anterior slippage of the vertebral bodies, a heightened risk given the greater range of upper body sagittal extension the L6 variant allows. This large prezygapophyseal angle at the last lumbar level buttresses against a shear displacement that is not inherently unique to the L6 variant since its bony lumbar lordosis is equivalent to that of the L5 variant. Rather, the added shear resistance in the extra-modal spine is likely to function during kinematic adjustments in posture and gait, particularly, greater extension of upper body allowed by the introduction of a lumbar type vertebra into the thorax of the mid torso.

Human L6 variant as model for australopith modal number and spine function

This study identifies two phenomena that are relevant to reconstruction of lumbar spine biomechanics in early bipeds, namely 1) an increase in the number of lumbar vertebrae does not require modification to the functional lumbar curve; and 2) lengthening of the lumbar region by increase in lumbar count impacts both structural and functional traits within the dorsal pillar, that is, the zygapophyses and not the vertebral bodies.

Sanders (1995, 1998) suggested that deep “capture” of the last lumbar vertebra within the iliac trough of *A. africanus* Sts 14 (similar to that of extant apes) renders the caudal lumbar vertebrae less mobile than in modern humans. Cumulative excursion across the long L6 column may have allowed Sts 14 and other early bipeds to achieve the same angular positions of modern humans despite limited mobility of the deep lumbosacral joint. Moreover, an L6 configuration would have facilitated finer nuanced sagittal flexion/

extension while walking and running, a compelling benefit to bipeds given the challenge of stabilizing the body center of mass over an alternating eccentric support base (Sanders, 1998; Crommert and Thorstensen, 2008).

A particular epaxial muscle affords fine incremental control of the lumbar spine. Because *m. multifidus* lies deep in the dorsal musculature and connects paired contiguous vertebrae with its high percentage of short muscle fibers by attachment to the zygapophyseal joints (Bogduk, 1997), it generates finer movements and stiffer scaffolding than muscles with long fibers spanning three or more vertebrae (McIntosh et al., 1986; Ward et al., 2009). Lumbar fascicles of *m. multifidus* exert a substantial proportion of the possible extensor moment (Yamamoto et al., 1989; Guan et al., 2007) and act predominantly in dynamic stabilization (Shapiro and Jungers, 1994; Schilling, 2009). This is due to high mechanical advantage gained by the muscle’s insertion on zygapophyses that extend dorsally in the lumbar region (Bogduk et al., 1992), further evidence of the importance of zygapophyses in lumbar spine function and strong rationale for defining lumbar vertebrae according to the zygapophyseal criterion. Australopiths and early *Homo* had relatively large lumbar zygapophyses with respect to their estimated body mass and notably larger zygapophyses than those of humans corrected for body mass (Latimer and Ward, 1993; Shapiro, 1993b; Sanders, 1995, 1998). This derived morphology suggests that australopiths loaded the spine’s dorsal pillar more heavily than modern humans, and thus implies different positional mechanics in early bipedalism.

Assuming the lumbar spines of the L5 and L6 morphs share the same flexural stiffness (EI), their critical loads as defined by

$$P_{cr} = \frac{4\pi^2 EI}{L^2} \quad (4)$$

are equal. This is because their functional lengths (L^2), assessed independently as the lordotic wedging sequence (2 vertebrae, 2 vertebrae), vertebral body height (57.1 mm, 57.2 mm) and radius of curvature (843.5 mm, 831.3 mm) do not differ. Therefore, according to Euler Buckling Theory, the human modal L5 and extra-modal L6 variants are of equal column strength.

A deep capture of the australopith lower spine by the iliac trough would have restricted lateral flexion/extension excursions within the coronal plane. In contrast, sagittal and axial movements would have been less constrained, permitting the long six-element lumbar spine greater rotation in the transverse and sagittal planes than either a four-element or five-element spine, despite its deep capture. Such increased movement would have been advantageous for a biped with upper and lower body segments otherwise coupled by close approximation of the thorax and iliac crests. Although shape preservation of the second rib in KSD-VP-1/1n *A. afarensis* suggests that the thorax of this hominin may not have been funnel

Modal Series L1-L5 Extra-Modal Series L1-L6

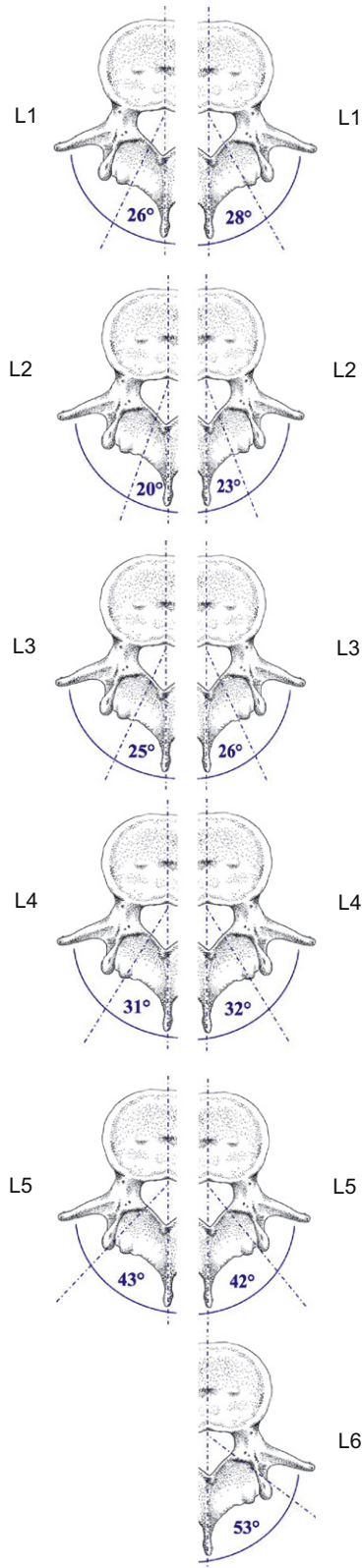


Figure 5. Prezygapophysyal angle (mean°) of numeric variants Modal L5 and Extra-modal L6 contrasted at each lumbar level (see Table 4 for sd of the mean). Vertebrae of the Modal and Extra-modal spines are paired in craniocaudal sequence from lumbar level L1 through lumbar level L5 demonstrating similarity in the mean prezygapophysyal angles. Because a sixth lumbar level is present in the Extra-modal L6 variant yet absent in the Modal L5 variant, the L6 lumbar level is shown unpaired, and the extreme facet obliquity of the last lumbar vertebra in the Extra-modal lumbar spine is evident.

shaped, the australopith's inferior thorax is described as mediolaterally broad (Haile-Selassie et al., 2010). Given both a broad lower thorax (Haile-Selassie et al., 2010) and a wide bi-iliac base (Schmid, 1983; Lovejoy, 1988), the upper and lower bodies of australopithecines were closely tethered, forming a compact torso unlike that of modern humans. Decoupling of the upper and lower bodies is thought to be a derived trait of *Homo* (Bramble and Lieberman, 2004). Furthermore, among australopiths, the craniocaudal length of lumbar vertebral bodies relative to estimated body mass was shorter than that of humans and similar to that of extant large bodied apes (Sanders, 1995). This morphology, along with a "deep capture" of the lumbar spine in australopiths (Sanders, 1995), is consistent with the notion of greater approximation between thorax and iliac crests in australopiths when compared to modern humans. The derived anatomical suite of australopiths/early *Homo*, combining a six-element lumbar sequence and a last lumbar position (L6) of marked zygapophysyal obliquity, promotes sagittal and axial rotations, respectively. However, if as some propose, locomotor evolution in early bipeds involved no increase in the number of lumbar vertebrae (Haeusler et al., 2002; McCollum et al., 2010; Haeusler et al., 2011), australopithecines would have been somewhat constrained in stabilizing the upper body over the alternating pendular movements of the lower body during bipedal gait.

Evolutionary implications: L6 mode in australopiths and early *Homo*

Homeotic shift in serial elements such as vertebrae and ribs arises readily with a change in *Hox* gene expression (Burke et al., 1995; Pilbeam, 2004; Gomez and Pourquié, 2009). Although the number of cervical vertebrae in mammals is highly conserved, lumbar count is remarkably labile (Slijper, 1946; Gambaryan, 1974; Galis, 1999). Clearly, among the extant primates, lumbar modal numbers reflect adaptations to the diverse positional behaviors different species typically engage (e.g., Hildebrand, 1959; Rose, 1974; Shapiro, 1995; Johnson and Shapiro, 1998; Shapiro and Simons, 2002). Given both the polymorphisms on which natural selection may act and the relevance of lumbar number in locomotor behaviors, not withstanding hominin bipedalism, variation in modal number among primate species is unsurprising. Furthermore, intraspecific variation is also prevalent as clearly exemplified within *H. sapiens* where three numeric variants occur, L4, L5 and L6, with the extra-modal series of higher frequency than the short sequence, regardless of which identifying criteria one applies (de Beer Kaufman, 1974; Shapiro, 1993a; Pilbeam, 2004). This within species variation combined with the interspecific difference in modal number between australopiths (L6) and modern humans (L5) indicates there is weak evolutionary constraint in hominin vertebral patterning.

Given a modal number of four lumbar vertebrae in living African apes and thus as one predicts for our last common ancestor (Pilbeam, 2004; although see McCollum et al., 2010), early hominins increased the number of lumbar elements while later hominins reduced the number. Whereas great apes resist the large compression loads associated with frequent vertical climbing and semi-orthograde quadrupedal walking via a rigid lumbar spine that is shortened both in number of vertebrae and length of centra (Schultz, 1938, 1961; Schultz and Straus, 1945; Benton, 1967, 1974; Ankel, 1972; Rose, 1975; Jungers, 1984; Ward, 1991; Shapiro, 1993a; Sanders, 1998), similar lumbar morphology would have been disadvantageous for australopiths who were primarily challenged to maintain a freestanding yet apelike upper body over two alternating hindlimbs (Sanders, 1998). Lumbar lordosis resolved the australopith locomotor challenge and similarly functions in living bipeds.

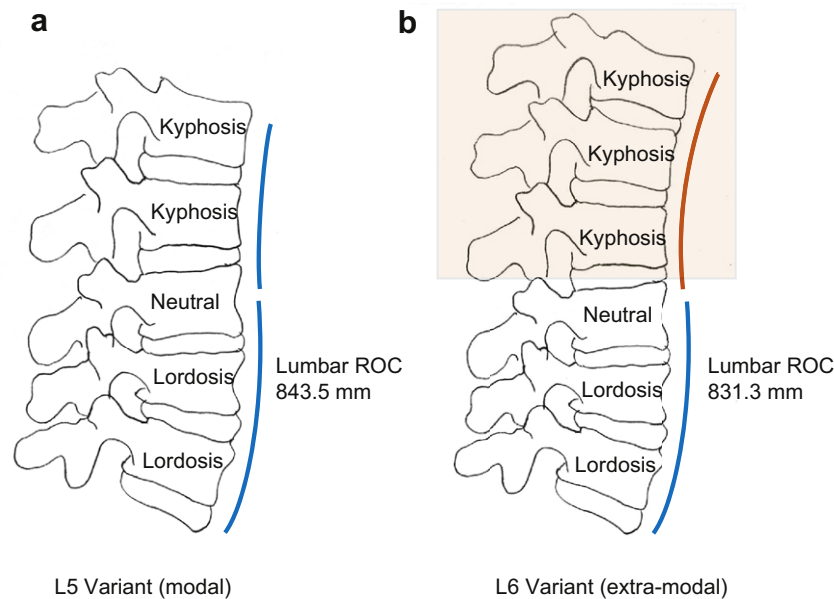


Figure 6. Human modal and extra-modal lumbar spines. (a) Modal variant series L1–L5, (b) Extra-modal variant series L1–L6. Both variants have a single neutral vertebra (non-wedged) in midsection and a two-vertebral series of lordotic vertebrae (dorsally wedged) in the lower lumbar spine expressing the same lordotic radius of curvature (ROC, non-significant). The L6 variant differs from the L5 mode in having a longer series of kyphotic vertebrae (ventrally wedged) at its cranial boundary and more oblique zygapophyses at the last lumbar level of the caudal boundary.

At least two derived spatial transformations, decoupling of upper and lower body segments and release of the lordotic curve from deep lumbar/iliac capture characterize lumbar spine mobility in later *Homo*. They appear as locomotor correlates of a behavioral shift toward high activity, range expansion and distance travel (Leonard and Robertson, 1997; Aiello and Wells, 2002; Bramble and Lieberman, 2004; Pontzer et al., 2010). These behaviors collectively drive repeated high impact loads on lumbar vertebrae that are resisted by a robust increase in vertebral centrum and disc size (e.g., Jungers, 1988; Shapiro, 1993b; Sanders, 1998). Reduction in lumbar vertebrae to a mode L5 in later *Homo* likely followed from the freed lower lumbar and increased centrum size providing optimal mobility, length and safety for lumbar lordosis function.

Conclusions

This study generated a model of the effect of lumbar vertebral number on lordotic function in human modal L5 and extra-modal L6 variants. Application of the biomechanical model in reconstructing australopith modal number and spine function highlights shared principles of Euler column strength and sagittal spine flexibility among early and modern hominins. Within modern humans the extra-modal L6 variant has an extended series of three cranially positioned kyphotic vertebrae and strongly oblique zygapophyseal facets at the last lumbar level. Although they share the same radius and length of lumbar curvature, the human L6 variant functionally differs from the human L5 mode in its expanded range of sagittal flexion/extension and enhanced resistance to shearing force. Given the modal number of six lumbar vertebrae in australopiths and early *Homo*, lumbar spine mobility and lumbar strength would have been key properties of vertebral function in early bipedalism. The intriguing transformations in lumbar modal number throughout hominin evolution, L4 to L6 followed by L6 to L5, represent a complex locomotor history not yet fully understood, one that awaits further fossil evidence and biomechanical study. Finally, although the likelihood of phylogenetic gain and reversal within hominins challenges our focus on parsimony, developmental ease

in homeotic shift should allay skepticism of such change in vertebral evolution, even among hominins.

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