Fetal Load and the Evolution of Lumbar Lordosis in Bipedal Hominins

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Supplementary Information

Supplementary Table 1. Human lumbar vertebral wedging angle in degrees for females and males in three numeric variants: L6 Variant (6 lumbar vertebrae); Modal (5 lumbar vertebrae); L4 Variant (4 lumbar vertebrae). Complete series of dorsally wedged lumbar vertebrae (lordotic) are enclosed by boxes, according to sex. Note that regardless of variant numeric length, females present three dorsally wedged lumbar vertebrae while males present just two. Means for each sample group are reported with (standard deviation).

	Female			Male		
Vertebral Level [1]	L6 Variant *n = 12*	Modal *n = 59*	L4 Variant *n = 8*	L6 Variant *n = 20*	Modal *n = 59*	L4 Variant *n = 7*
a	**3.55 *** **(2.07)**			**5.57** **(2.73)**		
b	**1.89 *** **(2.62)**	**2.21 ***** **(1.83)**		**3.54** **(1.66)**	**4.26** **(1.86)**	
c	-0.33 (2.18)	**0.09 ***** **(2.46)**	**1.2 *** **(1.54)**	1.1 (2.90)	**2.42** **(2.30)**	**3.32** **(1.50)**
d	-2.25 (2.81)	**-1.17 *** **(2.46)**	-0.77 (2.22)	-0.46 (2.48)	**0.15** **(2.47)**	1.87 (2.48)
e	-2.81 (2.48)	**-3.17 **** **(2.19)**	-2.5 (2.21)	-2.56 (2.04)	**-1.60** **(2.42)**	-1.25 (2.78)
f	-7.56 (2.75)	-5.54 (2.96)	-7.15 (1.24)	-7.39 (2.35)	-6.65 (2.88)	-3.41 (1.32)

Vertebral Level[1:] levels are listed in order from cranialmost to caudalmost position.
Boldface indicates significant result. Wilcoxon Rank Sums Test, Bonferroni adjusted.
* indicates P < 0.01, ** indicates P < 0.001, *** indicates P < 0.0001.
Positive angles are kyphotic. Negative angles are lordotic. Vertebrae are transitional, neither kyphotic not lordotic, when -0.5° > angle < 0.5°.
Lordotic vetebral series enclosed by boxes.

Supplementary Table 2. Male and female differences in lumbar vertebrae in the common chimpanzee (*Pan troglodytes schweinfurthii*), magnitude (probability) and results of Wilcoxon Rank Sums test on size-adjusted vertebral variates.

Pan troglodytes schweinfurthii difference in male and female lumbar vertebrae

Variable	(n) (M,F)	Lumbar vertebral level L1		L2		L3		L4	
Centrum Wedging Angle	(14, 10)	-0.746	(ns)	-0.746	(ns)	0.797	(ns)	-1.054	(ns)
Prezygapophyseal Area	(14, 10)	-0.439	(ns)	-1.363	(ns)	-0.23	(ns)	-0.694	(ns)
Prezygapophyseal Angle	(14, 10)	-0.792	(ns)	-0.026	(ns)	-1.78	(ns)	0.180	(ns)

Two-tailed Wilcoxon Rank Sums test of significance, Bonferonni adjusted.
M, male; F, female; ns, $P > 0.05$

Supplementary Table 3. Comparison of cast and fossil datasets for lumbar vertebrae of *Australopithecus africanus* Stw 431. **a** vertebral body linear dimensions. **b** prezygapophyseal angle. Variates differ by less than 2.5%.

a Vertebral body

	dorsal height (mm)			ventral height (mm)		
	cast [1]	fossil [2]	difference	cast [1]	fossil [2]	difference
L1 [3]	-	-	-	-	-	-
L2	24.0	24.0	0.0	22.2	22.0	0.0
L3	24.8	24.4	0.4	23.6	23.5	0.1
L4	23.7	24.0	0.3	22.8	23.0	0.2
L5	22.7	22.7	0.0	22.1	22.7	0.6
L6	19.7	19.7	0.0	21.9	21.7	0.2

[1] Measurements taken by KW on first generation cast generated by the Sterkfontein Research Unit Laboratory, Witwatersrand

[2] Measurements taken by William Sanders directly from fossils, unpublished

[3] Incomplete preservation of variate landmarks precludes measurement

b Prezygapophysis

	facet angle (degrees)		
	cast [1]	fossil [2]	difference
L1 [3]	-	-	-
L2 [3]	-	-	-
L3 [4]	24	24	0
L4 [5]	-	-	-
L5	44	44	0
L6	50	50	0

[1] Measurements taken by KW on first generation cast generated by the Sterkfontein Research Unit Laboratory, Witwatersrand

[2] Measurements taken by William Sanders directly from fossils, unpublished

[3] Incomplete preservation of variate landmarks precludes measurement

[4] Measurement taken from right prezygapophysis

[5] Although at least one prezygapophysis is present, separation from vertebral body precludes identification of lumbar level

4. Supplementary Notes

1. Shearing. Spinal shear force produces a tendency for translational movement of vertebrae with respect to one another. Two factors are particularly relevant to spinal shear: 1) any force (axial or nonaxial) transmitted along a curved column generates a shearing component, and 2) anterior loading generates additional shear, e.g., fetal loading in the maternal abdomen during bipedal postures and locomotion. The lumbar region of bipeds is vulnerable to anterior sagittal translation due to the posterior concavity of the lordotic curve as the angle of lordosis increases, so too does the shearing component. Resistance to shear load is provided by hard and soft tissues, the former comprised of lumbar zygapophyses, the latter of intervertebral disks and ligaments. Viscoelasticity of the joint disk between articulating zygapophyses allows slowly applied and constant shear load to transfer through the facet joints. Since our evolutionary study of lumbar lordosis in hominin taxa is performed on comparative samples of modern humans and australopithecines, we focus on just hard tissue anatomy, which is preserved in fossils such as Sts 14 and Stw 431. We employ a model of human spinal shear using a free body technique for coplanar (shear and compression) forces[43], simplifying load to just two forces; one produced by upper body mass induced moment (including fetal load) and another produced by the erector spine muscles resisting the maternal center of mass moment. The counter torque of the erector spinae is the product of the calculated muscle force magnitude based on the equilibrium equation (using our computed upper body mass and calculated COM position) and the muscle lever arm (0.066 m)[44]. Trigonometric calculation of shearing and compressive forces: shear = upper body mass*sin(theta); and compression = upper body mass *cos(theta) + muscle magnitude. Sample n = male 59, female 54. Mean shear force (sd) with an increase of 4^{o} extension: female 0.14 N/mm^2 (0.12), male mean 0.21 N/mm^2 (0.14). P = 0.026, alpha 0.05.

2. Measurements. Sts 14 measurements used were taken by W. Sanders on the original specimen (see Ref. 5). For Stw 431, measurements were taken by K.W. on first generation casts provided by the Sterkfontein Research Unit, Witwatersrand Medical School. Our cast data are consistent with measurements taken directly on the Stw 431 fossils by William Sanders, unpublished (see Supplementary Table 3).

3.Fetal growth. The chimpanzee fetus reaches 1200 g at week 28[45] followed by the parturition event at week 33[46,47], resulting in a mean five week period of fetal mass/growth exceeding 1200 g. Note that 1200 g is the trigger for modern human females whose typical nongravid body mass is 42 - 73 kg[48]. Body mass of the adult nongravid female chimpanzee is 34 - 46 kg[48], depending on the subspecies. Australopithecines may have had a fetal mass trigger below 1200 g and a critical period of fetal load challenge greater than five weeks in duration.

5. Supplementary References

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