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# Fetal load and the evolution of lumbar lordosis in bipedal hominins

Katherine K. Whitcome[1], Liza J. Shapiro[2] & Daniel E. Lieberman[1]

As predicted by Darwin[1], bipedal posture and locomotion are key distinguishing features of the earliest known hominins[2,3]. Hominin axial skeletons show many derived adaptations for bipedalism, including an elongated lumbar region, both in the number of vertebrae and their lengths, as well as a marked posterior concavity of wedged lumbar vertebrae, known as a lordosis[4–6]. The lordosis stabilizes the upper body over the lower limbs in bipeds by positioning the trunk's centre of mass (COM) above the hips. However, bipedalism poses a unique challenge to pregnant females because the changing body shape and the extra mass associated with pregnancy shift the trunk's COM anterior to the hips. Here we show that human females have evolved a derived curvature and reinforcement of the lumbar vertebrae to compensate for this bipedal obstetric load. Similarly dimorphic morphologies in fossil vertebrae of *Australopithecus* suggest that this adaptation to fetal load preceded the evolution of *Homo*.

Until recently, hominin females spent most of their adult lives either pregnant or lactating[7]. Pregnancy augments the mass of the human female abdomen by as much as 31% (6.8 kg)[8], translating the position of the maternal COM forward and increasing the torque exerted by the upper body around the hip joints. Although this shift in mass does not disrupt postural stability in quadrupeds (Fig. 1a, b), it uniquely destabilizes bipeds whose supporting joints and two-footed support base lie solely under the hips (Fig. 1c, d). Such gravid instability can be counteracted by muscles, but sustained recruitment risks muscle fatigue and increases the likelihood of spinal injury[9].

Pregnant mothers habitually compensate positionally to fetal load by extending the lower back. Our longitudinal study of 19 pregnant human females shows that adjustments to lumbar lordosis permit mothers to maintain a stable anteroposterior position of the COM as gestation progresses and fetal mass increases (Fig. 1e). Although full-term females extend their hips only slightly (about $5.6° ± 2°$ (mean ± s.d.)), they extend their lower back by as much as $28°$ ($18° ± 10°$), which realigns the COM above the hips and support base (Fig. 1e). When gravid females are experimentally constrained from exaggerating their lumbar lordosis, the COM translates by $3.2 ± 1.1$ cm ($P < 0.0001$) by the end of gestation, increasing the upper body's torque around the hip roughly eightfold (Fig. 1c, d). However, when free to self-select their positional alignment, pregnant females naturally increase their lumbar lordosis, limiting anteroposterior translation of the COM within a narrow range, less than $0.3 ± 0.7$ cm ($P = 0.5695$) by term (Fig. 1e). Once obstetric load has reached a threshold of about 40% of the expected term fetal mass (Fig. 2a), this lordotic adjustment increases in relation to fetal mass ($r = 0.9732$, $P = 0.0011$), thus maintaining a stable position of the COM throughout pregnancy (Fig. 2b). Extension of the lower back helps control COM position but exerts a biomechanical cost to gravid mothers in the form of shearing forces caused by the nearly 60%

increase in lumbar lordosis, from a mean angle of $32° ± 12°$ in early pregnancy to $50° ± 12°$ at term (Fig. 2b). Two measures of the deleterious effects of spinal shearing are the increased risk of forward displacement of the lumbar vertebrae[9,10] and the higher incidence of lower back pain in pregnant women[11,12]. Greater shearing occurs because increases in lordosis transmit relatively more spinal load
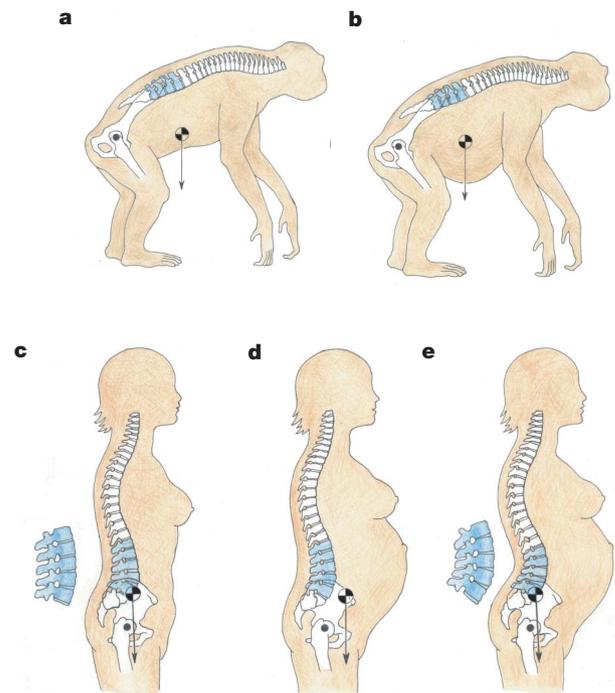

Figure 1 | **COM and lumbar lordosis during pregnancy. a**, Quadrupedal chimpanzee, non-pregnant. **b**, Quadrupedal chimpanzee, pregnant with no change in sagittal position of the COM with respect to the postural support base. **c**, Bipedal human female with typical lumbar lordosis and COM in approximate sagittal alignment with the hip. At a given 0.005-m COM distance from the hip, a 409-N upper body generates 2 N m torque at the hip. **d**, Pregnant human female with anteriorly translated COM, lacking positional adjustment of lumbar lordosis. The force of gravity, when more distant from the hip, generates a larger hip moment and an unstable upper body. With pregnancy, a 511-N upper body and a COM at 0.032 m from the hip increases the torque to 16 N m. **e**, Typical pregnant human female with naturally extended back and recovered COM by means of increased lumbar lordosis, a stable positional alignment with reduced hip torque (1.5 N m) but with exacerbated spinal shearing load. Open circle with cross hairs, COM in sagittal plane; filled circle, hip position in sagittal plane; arrow, direction of gravitational force.

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along the dorsal pillar of the spine comprising the zygapophyseal joints[13] (Fig. 3d). Typical bipedal posture directs only 16% of the total compressive load through these joints[14], and slight extension of the lower back redirects another 12% to the zygapophyses[15]. During pregnancy the mean lordotic excursion of 18° shifts even greater loads onto the zygapophyses, as much as 20–40% according to published models[15,16].

Given the demands of fetal load and the importance of pregnancy for fitness, one predicts that natural selection has operated on the unique anatomy of the hominin lumbar region to mitigate the bio-mechanical problems that females confront. Our analyses show that
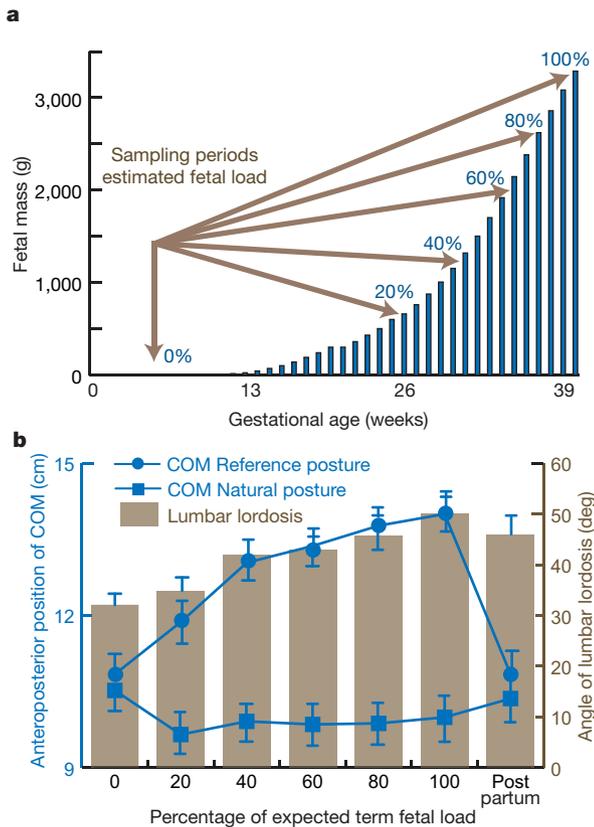
Figure 2 | Maternal COM and lumbar lordosis relative to fetal load.
a, Increase in fetal body mass by weeks of gestation, showing six prepartum sampling sessions of sequential periods of 20% fetal load (estimated fetal mass from ref. 20). Note the increasing rate of increase in fetal mass within the second trimester and the maximum increase in the third trimester.
**b,** Angle of lumbar lordosis and position of the COM with respect to human pregnancy. Means are plotted against stages of fetal growth and an approximate eight-week postpartum period. Results support the predicted relationship between COM reference posture (circles) and lordosis (bars), their strong correlation ($r = 0.9732$, $P = 0.0011$) and the constancy of COM natural posture (squares) when gravid females self-select their angle of lumbar lordosis. Circles plot the mean forward position of the COM recorded in a reference posture (see Methods) in which pregnant females were constrained from self-selecting their postural alignment. In the absence of positional adjustment, COM translates 3.2 cm from 11 cm at 0% fetal mass to 14 cm at 100% fetal mass. Note the return to the baseline position postpartum. Bars plot the mean angle of lumbar lordosis self-selected by pregnant females in natural stance. Lumbar lordosis increases from an angle of 32° at 0% fetal mass to 50° at 100% fetal mass, late in pregnancy. The angle of lumbar lordosis begins to decrease postpartum. Squares plot the resultant forward position of the COM self-selected by pregnant females in natural posture, when postural alignment was not artificially constrained. As women naturally increased their lumbar lordosis, their COM remained relatively stable, translating by no more than 1 cm during pregnancy. The difference in forward position of the COM from early pregnancy to term was 0.3 cm. $n = 19$. Data are means ± s.e.m.

humans are characterized by a strong, derived pattern of lumbar sexual dimorphism that is evident in several aspects of the lumbar vertebrae. One major feature of human lumbar sexual dimorphism is the degree and pattern of dorsal wedging that forms the lumbar lordosis and results from a disproportionately short dorsal margin of the vertebral body. Vertebral wedging differs significantly between human sexes from L1 to L4 ($P < 0.0001$ to $P < 0.008$; Fig. 3a). The complete lordotic sequence of dorsal wedging in males spans just two vertebrae, the penultimate and last lumbar vertebrae. In contrast, the female pattern of dorsal wedging includes three vertebrae, the pre-penultimate, penultimate and last lumbar vertebrae (Fig. 3a, d). This 3:2 wedging dimorphism occurs regardless of variation in the total number of lumbar elements, whether variant L4, modal L5 or variant L6, but is entirely absent in chimpanzees (Supplementary Tables 1 and 2). Females benefit from the third wedging level during pregnancy because it enables them to increase the lordosis with less inter-vertebral rotation. An equivalent angular excursion between L3 and L4 results in greater extension of the upper body in females than in males (Fig. 3e). In this way, females minimize shear force across lumbar vertebral joints by about 30% (Supplementary Information).

Two additional key features of human lumbar sexual dimorphism are present within the dorsal pillar. First, the zygapophyseal surface area is 14% ± 3% ($P < 0.01$) larger relative to vertebral size in females than in males (Fig. 3b), which is consistent with the redirection of a larger proportion of spinal load along the dorsal structures during human pregnancy. Second, female prezygapophyseal joint surfaces are oriented more coronally by an average of 13% ± 5% ($P < 0.05$) than those of males (Fig. 3c), enhancing resistance to large shearing forces imposed by fetal mass and back extension. As in wedging, these zygapophyses are not significantly dimorphic in chimpanzees (Supplementary Table 2). In bracing the zygapophyses more coronally, human female vertebrae achieve greater buttressing against anterior displacement of vertebral bodies within the deep lumbar curve.

The evidence for lumbar sexual dimorphism in humans which improves maternal performance in posture and locomotion suggests that the distinctive hominin lumbar curve has been subject to strong selection pressures. If so, one expects these adaptations to be present in the genus *Australopithecus*, which is known to have been habitually bipedal at least two million years after the earliest bipedal homi-nins[2,3]. It is intriguing that, of the two nearly complete known aus-tralopith lumbar segments, Sts 14 and Stw 431, the former has the typical human female pattern with three dorsally wedged vertebrae, whereas the latter has a more male-like pattern with fewer lordotic vertebrae (Fig. 4a). One possible explanation for this difference is that one female and one male *A. africanus* are sampled. This inference is supported by the observation that the prezygapophyses of Sts 14 (L1–L6) are angled 9–12° more coronally than the measurable facets of Stw 431 (L3, L5 and L6; Fig. 4b), as is typical of the human female and male patterns, respectively (Fig. 3c). Australopiths not only had a lumbar lordosis with human-like wedging patterns, but they also had relatively large zygapophyseal facets[5] with angular dimorphism sim-ilar to that in modern humans. Because these features have a fun-damental role in resisting shear force[14], similar patterns of lumbar dimorphism in *Australopithecus* and *Homo* indicate that spinal shear was also a major challenge in australopiths in general, and especially for gravid females. Similarities in body size and life history between australopiths and chimpanzees suggest that term mass and duration of gestation for australopiths was chimpanzee-like (1,590 g at 230 days)[17,18] rather than human-like (3,200 g at 290 days)[19,20]. Even so, term mass of the australopithecine fetus would easily have exceeded the 40% load trigger of 1,200 g in human pregnancy for a substantial period of pregnancy, approximately the last trimester (Supplemen-tary Information).

Since the discovery of the first australopithecine postcrania[4] there has been a concerted study of the evolution of hominin locomotion, yet without consideration of the biomechanical challenges posed by
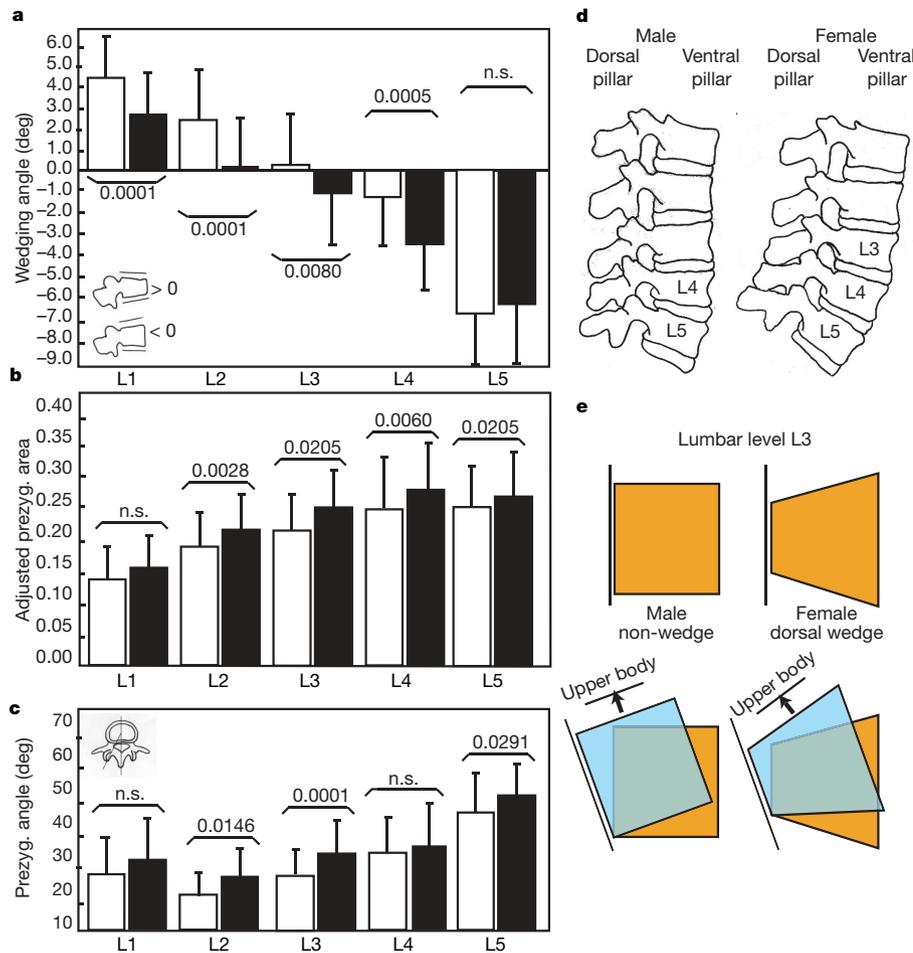
Figure 3 | Sex differences in the lumbar vertebral column of human males and females. Female values are shown by filled bars, male values by open bars. **a**, Wedging angle of vertebral bodies, angles greater than $0°$ are kyphotic (thoracic-type wedging), whereas angles less than $0°$ are lordotic (lumbar-type wedging). Females present a longer series of dorsally wedged vertebrae; L3, L4 and L5, whereas males are lordotic at only two levels, L4 and L5. **b**, Prezygapophyseal (prezyg.) area, adjusted by geometric mean for overall vertebral size. The female area is significantly larger than the male area at L2, L3, L4 and L5, indicating that females bear a greater proportion of spinal load along the dorsal pillar, which is consistent with fetal loading patterns identified during pregnancy. **c**, Prezygapophyseal angle. The female facets are significantly more oblique at L2, L3 and L5, conferring greater resistance to forward displacement of lumbar vertebrae. In **a**–**c**, $n = 59$ males, 54 females. Data are means and s.d. **d**, Diagram of lumbar region in males and females, showing contrasting mean wedging patterns and anatomical structures within the dorsal pillar (including zygapophyses) and ventral pillar (vertebral bodies). **e**, Difference in vertebral body shape in males and females at L3. There are equivalent angles of excursion yet there is greater upper body extension in the female spine. The inherent dorsal wedging shape of the female L3 relative to the non-wedged male L3 generates less shearing force when the upper body is repositioned by means of lower back extension, as occurs during fetal loading.

pregnancy. Our analyses not only show that the derived dimorphism of the lumbar lordosis in modern humans helps mothers to mitigate the shearing forces generated by fetal load, but also indicate that the biomechanical demands of pregnancy exerted an early selection pressure on the evolution of lumbar lordosis in bipedal hominins. These

results highlight the vulnerability of the lumbar vertebrae to various forms of loading in bipeds, and the importance of adaptations in both the lumbar vertebrae and the dimensions of the pelvic canal[21–23] to female reproductive success. It is reasonable to hypothesize that fatigue and pain in the lower back muscle affected early hominin mothers just as they do modern mothers, possibly limiting foraging efficiency and the ability to escape from predators, leaving the gravid female at risk of nutritional stress and injury or death. Later hominins underwent a reduction in the number of lumbar vertebrae, from six to five modal vertebrae[5,24,25], along with relative increases in vertebral body size[26] possibly for carrying[5], increased trekking[27] and/or endurance running[28]. Regardless of the varied selection pressures behind these shifts, fetal load remained a persistent selection factor in the evolution of lumbar sexual dimorphism in hominins.
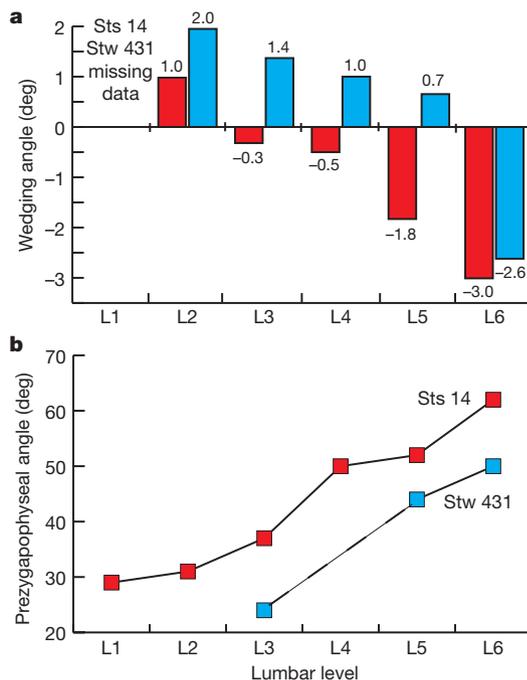
Figure 4 | Australopithecine lumbar lordosis and prezygapophyseal angle. a, Angle of lumbar vertebral wedging for *Australopithecus africanus* specimens Sts 14 (red) and Stw 431 (blue). Sts 14 shows a wedging pattern similar to that in modern human females, comprising the three caudalmost lumbar vertebrae, column L4, L5 and L6. Although the preserved lumbar column of Stw 431 is less complete than that of Sts 14, the caudalmost levels are preserved well enough to identify a different wedging pattern. The dorsal wedging sequence of Stw 431 includes only one lumbar vertebra, at the last lumbar level. In this manner, Stw 431 is unlike Sts 14 and modern human females and is more similar to modern human males in having a shorter region of lordotic lumbar vertebrae. **b**, The prezygapophyseal angle of the preserved lumbar region for Sts 14 and Stw 431. The larger angles of Sts 14 relative to those of Stw 431 mirror the modern human female–male pattern in that Sts 14 presents more oblique angles and therefore greater coronal orientation of the prezygapophyseal facets than Stw 431 (see Supplementary Information).

METHODS SUMMARY

The anteroposterior position of the maternal COM was identified from ground reaction force vectors measured by a triaxial transducing force plate, following the zero-point-to-zero-point integration technique[29].

Angular excursions of the lumbar spine were calculated from three-dimensional positional data acquired from a Vicon motion analysis system capturing infrared reflections from surface markers that were externally adhered to palpable landmarks of the thoracic, lumbar and sacral vertebrae.

Comparative morphometrics were used to evaluate patterns of sexual dimorphism in the human lumbar spine. Linear and angular dimensions of lumbar vertebrae were measured to identify the relative size and shape of vertebral features subject to the biomechanical stresses generated by fetal load.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

1. Darwin, C. *The Descent of Man* (John Murray, London, 1871).
2. Galik, K. *et al.* External and internal morphology of the BAR 1002'00 *Orrorin tugenensis* femur. *Science* **305,** 1450–1453 (2004).
3. Zollikofer, C. P. E. *et al.* Virtual cranial reconstruction of *Sahelanthropus tchadensis. Nature* **434,** 755–759 (2005).
4. Robinson, J. T. *Early Hominid Posture and Locomotion* (Univ. of Chicago Press, Chicago, 1972).
5. Sanders, W. J. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *J. Hum. Evol.* **34,** 249–302 (1998).
6. Latimer, B. & Ward, C. V. in *The Nariokotome* Homo erectus *Skeleton* (eds Walker, A. & Leakey, R.) 266–293 (Harvard Univ. Press, Cambridge, MA, 1993).
7. Strassmann, B. I. The biology of menstruation in *Homo sapiens*: total lifetime menses, fecundity, and nonsynchrony in a natural-fertility population. *Curr. Anthropol.* **38,** 123–129 (1997).
8. Jensen, R. K., Doucet, S. & Treitz, T. Changes in segment mass and mass distribution during pregnancy. *J. Biomech.* **29,** 251–256 (1996).
9. White, A. A. & Punjabi, M. M. *Clinical Biomechanics of the Spine* (Lippincott, Philadelphia, 1990).
10. Bogduk, N. *Clinical Anatomy of the Lumbar Spine and Sacrum* (Churchill Livingstone, New York, 1997).
11. Ostgaard, H. C., Andersson, G. B. J., Schultz, A. B. & Miller, J. A. A. Influence of some biomechanical factors on low-back pain in pregnancy. *Spine* **18,** 61–65 (1993).
12. Dumas, G. A., Reid, J. G., Griffin, M. P. & McGrath, M. J. Exercise, posture, and back pain during pregnancy. Part 1. Exercise and posture. *Clin. Biomech.* **10,** 98–103 (1995).
13. Pal, G. P. & Routal, R. V. Transmission of weight through the lower thoracic and lumbar regions of the vertebral column in man. *J. Anat.* **152,** 93–105 (1987).
14. Adams, M. A. & Hutton, W. C. The effect of posture on the role of the apophyseal joints in resisting intervertebral compressive forces. *J. Bone Joint Surg. Br.* **62,** 358–362 (1980).
15. Lorenz, M., Patwardhan, A. & Vanderby, R. Jr. Load-bearing characteristics of lumbar facets in normal and surgically altered spinal segments. *Spine* **8,** 122–130 (1983).
16. Dunlop, R. B., Adams, M. A. & Hutton, W. C. Disc space narrowing and the lumbar facet joints. *J. Bone Joint Surg. Br.* **66,** 706–710 (1984).
17. Lee, D. R., Kuehl, T. J. & Eichberg, J. W. Real-time ultrasonography as a clinical and management tool to monitor pregnancy in a chimpanzee breeding colony. *Am. J. Primatol.* **24,** 289–294 (1991).
18. DeSilva, J. & Lesnik, J. Chimpanzee neonatal brain size: Implications for brain growth in *Homo erectus. J. Hum. Evol.* **51,** 207–212 (2006).
19. Institute of Medicine of the National Academies. *Nutrition During Pregnancy. Part 1. Weight Gain* (National Academy Press, Washington DC, 1990).
20. Alexander, G. R., Himes, J. H., Kaufman, R. B., Mor, J. & Kogan, M. A United States national reference for fetal growth. *Obstet. Gynecol.* **87,** 163–168 (1996).
21. Washburn, S. L. Sex differences in the pubic bone. *Am. J. Phys. Anthropol.* **6,** 199–207 (1948).
22. Schultz, A. H. Sex differences in the pelves of primates. *Am. J. Phys. Anthropol.* **7,** 401–423 (1949).
23. Rosenberg, K. & Trevathan, W. Bipedalism and human birth: The obstetrical dilemma revisited. *Evol. Anthropol.* **4,** 161–168 (1996).
24. Arensburg, B. in *Le Squelette Mousterien de Kebara 2* (eds Bar Yosef, O. & Vandermeersch, B.) 113–146 (Cahiers de Paléoanthropologie, Paris, 1991).
25. Trinkaus, E. *The Shanidar Neandertals* (Academic, New York, 1983).
26. Jungers, W. L. Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. *J. Hum. Evol.* **17,** 247–265 (1988).
27. Ruff, C. B. in *Primate Locomotion: Recent Advances* (eds Strasser, E., Fleagle, J., Rosenberger, A. & McHenry, M.) 449–469 (Plenum, New York, 1998).
28. Bramble, D. M. & Lieberman, D. E. Endurance running and the evolution of *Homo. Nature* **432,** 345–352 (2004).
29. Zatsiorsky, V. & King, D. An algorithm for determining gravity line location from posturographic recordings. *J. Biomech.* **31,** 161–164 (1998).

METHODS

Kinematic/kinetic sample structure. Nineteen pregnant women between the ages of 20 and 40 years participated in the longitudinal study, initiated at the third month of pregnancy and concluded in the third month of post parity. Study protocol received University of Texas at Austin IRB approval for human research. Volunteers were excluded if they demonstrated life histories characterized by joint illness/injury or previous pregnancy-related difficulties leading to medical treatment, restricted physical activity, or persistent discomfort. Maternal body weight was recorded each session and assessed by the Institute of Medicine standards[19], which recommend an increase of 1.36–1.81 kg in the first three months and 1.36–1.81 kg per month in the later trimesters. Subjects whose prenatal weight gain exceeded 12.75 kg would have been excluded from the analyses, but none eclipsed the parameter. To ensure that comparisons across subjects matched successive stages of fetal load, data collection sessions targeted seven parity windows of 0%, 20%, 40%, 60%, 80% and 100% fetal mass and a final session postpartum.

All kinematic and kinetic data were collected in the Developmental Motor Control Laboratory at the University of Texas at Austin. A Vicon motion analysis system (Vicon Peak) captured three-dimensional positional data (60 Hz sampling rate) of each subject during quiet stance and while walking freely though a 2 m³ viewing volume. Five infrared cameras recorded positional data and trajectories of lightweight 25-mm reflective markers externally adhered over spinous processes of vertebrae L1 (lumbar level 1), L4 (lumbar level 2) and S2 (sacral level 2), identified by palpation. The time reference of heel strike and toe-off was identified by the onset and cessation of vertical force, respectively, as registered on a triaxial transducing force plate (600 Hz sampling rate). Before each data collection session the viewing volume was calibrated by following static and dynamic protocols. Residuals for all cameras were consistently within a range of 0.400 to 0.594 mm, representing less than 0.1% of the 2 m³ viewing volume. The mean wand visibility approached 84.0%.

Kinematic/kinetic measurements. Vicon three-dimensional data files were transferred to a personal computer on which the lordotic angle was calculated algorithmically from positional data derived from lumbar vertebrae with BodyBuilder software (Vicon Peak). Angles were exported as ASCII to Microsoft Excel files for further analysis.

Three points defined by the vertebral markers L1, L4 and S2 allowed quantification of the lordotic angle between segments 1 and 2 defined by markers L1–L4 and L4–S2, respectively. Larger angles indicated more acute lumbar lordosis.

Kinematic and force-plate analogue data were captured to calculate the maternal total body COM in both the reference and self-selected postures. The static measure of COM taken in the consistent reference posture was needed to identify the translation of the resultant COM. Angular changes in lumbar lordosis were assessed functionally relative to the translation of this reference posture COM. To obtain as consistent a reference posture COM as possible, a portable plywood wall 3 feet × 6 feet (about 91 cm × 183 cm) was supported above the floor on a wheeled assembly spanning the force plate. Subjects stood with head, shoulders and buttocks in contact with the vertical panel. Once a stable posture had been attained, the portable wall was retracted. A second static measure of maternal COM was taken during natural stance to determine any self-selected kinematic repositioning of the COM. Reference posture COM was predicted to change significantly during pregnancy, as the segmental angles of lumbar lordosis and pelvic tilt were held constant from session to session through postural alignment with the reference panel. In contrast, the self-selected position of the maternal COM was expected to remain relatively constant throughout the study, its stability achieved through natural adjustments in lumbar lordosis.

The fore–aft vectors of the ground reaction force and centre of pressure from which COM values were calculated were recorded with a Bertec K70501 type 4550-08 force plate located in the centre of an open laboratory space, allowing subjects to achieve natural postures. Maternal body mass was recorded from the force plate as the z force component adjusted for the plate's baseline measure taken during the corresponding session.

To obtain the maternal COM during both reference posture and natural stance, the horizontal position of the static centre of gravity was calculated from vectors measured by the force plate by using the zero-point-to-zero-point integration technique introduced by Zatsiorsky & King[29], with the formula

$$X_{\mathrm{GLP}}(t) = \left[\iint_{t_n|-\delta < F_x < \delta}^{t_n+1|-\delta < F_x < \delta} \ddot{X}(t) \right] + \dot{X}(t_n)t + X_{\mathrm{COP}}(t_n)$$

where $X_{\mathrm{GLP}}(t)$ is the horizontal position of the static centre of gravity, t_n is time n, the vertical bar stands for 'under the condition that', F_x is the horizontal ground reaction force, δ is the incremental value, $\ddot{X}$ is acceleration, $\dot{X}$ is velocity and X_{COP} is the centre of pressure location along the x axis.

The method is based on the postulation that the horizontal position of the total body line of gravity and the total body centre of pressure on the force plate coincide when the horizontal ground reaction force, F_x, is zero. At this instant the torque about the intersection between the vertical axis through the ankles and the supporting substrate is either zero or negligible. The algorithm used to calculate the position of the COM was validated by Zatsiorsky and King[29] with videography-based segment mass. There was no significant difference (at the 0.05 level) and coefficients of correlation were high (0.79–0.96) (ref. 29).

The position of the maternal COM in both the reference posture and the natural stance was determined relative to a point of reference. The reference posture served to target a rigid anatomical reading of the position of the COM. The C7 marker was expected to be the most relevant and accurate body marker for calculation of the reference posture COM position, because it is the marker least likely to shift directionally in anatomical position relative to the location of the COM (among the non-dependent variable markers). Because the torso is a relatively solid segment, the C7 marker, adhered to the external palpable spinous process of the seventh cervical vertebra, provided a consistent reference for determining the fore–aft position of the maternal COM in the experimental condition on the reference board. In order to calculate the position of the COM during natural stance, the heel marker representing the base of support was used as a point of reference.

Repeated-measures analysis of variance (ANOVA, time × condition) was used to assess whether maternal gait kinematics and maternal COM differed with incremental increases in fetal growth. Both linear and nonlinear models were included because mass increase during pregnancy is nonlinear[8]. Repeated-measures design is appropriate for longitudinal data of this type, by providing a more precise estimate of the experimental error. The technique identifies variability due to individual differences because the same subjects take part in each condition. Because the variance caused by differences between individuals is not helpful in deciding whether there is difference between occasions, the known individual differences can be isolated from the analysis by subtraction from the error variance. This step increases the power of the analysis. Repeated-measures ANOVA models correlation between the repeated measures, which is important because the longitudinal series violates assumptions of independence. To test for the presence of significant differences in dependent variables at early-stage fetal load and at term fetal load at the group level, the non-parametric Wilcoxon rank sums test was applied. Statistical significance for the analyses was determined a priori at a level of $P \le 0.05$ for the independent variable of fetal load and three dependent variables of maternal COM and maternal lumbar lordosis angle. Adjustments for repeated tests were made with the Bonferroni correction.

Morphometric sample structure. The sample population of 59 males and 54 females chosen to test the study hypothesis was drawn from two well-studied twentieth-century osteological archives of known age and sex: the Hamann–Todd collection, curated at the Cleveland Museum of Natural History, and the Terry collection, housed at the National Museum of Natural History in Washington DC. Ancestry-related differences within the sample population (morgue identified) were tested for ethnicity effect by using ANOVA cross (sex and ethnicity). No significant ethnicity response by sex was obtained.

Autopsy records and morgue photos were examined to identify sex. All specimens were further assessed for sex in accordance with the modified Phenice method[30,31]. Individuals whose sex was ambiguous according to either collection records or observer Phenice assessment were excluded.

Specimens were selected within an adult age range of 20–40 years. This criterion targeted individuals whose skeletal development had reached maturity but whose ageing effects had not yet eclipsed osteophytic deposition, typical in synovial and symphyseal joint margins with ageing, for example spondylosis deformans[10]. Chronological age was obtained through morgue records and further evaluated by visual confirmation of postcranial epiphyseal fusion. If skeletal age was found to fall outside the inclusion range, the specimen was omitted from the study. Pathological specimens, whether determined by collection records or gross observation, were not analysed.

Lumbar vertebrae were defined in accordance with their zygapophyseal orientation[32,33]. This facet-based designation differs from the widely used non-rib-bearing alternative[34] in its functional emphasis on the range of motion between vertebral elements; type and range of movement in the lumbar column are largely influenced by facet direction. The medial and lateral orientation of lumbar superior and inferior facets, respectively, guide sagittal flexion and extension while resisting both rotation[35] and ventral displacement[6,10].

Lumbar osteological measurements and analyses. Predictions of lumbar vertebral sexual dimorphism were tested on 14 vertebral variables at each lumbar vertebral level, chosen to define the relative size and shape of the lumbar vertebrae. Linear measurements were collected with a Mitutoyo 500-171 needle-point digital calliper and were recorded to the nearest 0.01 mm. Angular measurements were collected with an SPI 0–180° protractor.

Prezygapophyseal surface area was calculated from geometric mean adjusted linear variables using the equation for an ellipse. Linear measurements were used to calculate an angular variable of vertebral body wedging as described by Digiovanni et al.[36]:

$$\text{Wedging angle} = 2\arctan\{[(\text{centrum dorsal height} - \text{centrum ventral height})/2]/\text{centrum anteroposterior diameter}\}$$

Positive angles were kyphotic; negative angles were lordotic. A vertebra was determined to be neutral—neither kyphotic nor lordotic—when its value fell within the range $0.5°$ to $-0.5°$. JMP 5.0.1.2 (SAS Institute) and SPSS 12.0 (SPSS, Inc.) software packages were used for statistical analyses.

Without adjustment for body size variation within the sample population, any significant differences identified by contrasting males and females might reflect little more than stochastic distribution of body size differences within the samples. The representative measure of gross size used to remove the general isometric phenomenon[37,38] was the scale-free geometric mean[39,40] derived from the 48 linear variables of the lumbar vertebrae, 12 from each of the first, second, penultimate and last lumbar levels. Mosimann's[39] method removes the effects of size for each variable on an individual basis, using a directly measured index of individual size. Variates obtained for each individual were standardized by dividing the raw values by the geometric mean of the relevant specimen (the 48th root of the product of the variables).

In accordance with the biomechanical principles outlined in the two-pillar model of spinal force transmission[13] the variables represent the major load-bearing and load-resistant structures operating under conditions of bipedal obstetric load. Variables were tested for normality with the single-sample Shapiro–Wilk W test. A between-sex test for homoscedasticity was performed as a two-tailed F_{max} test with a 0.05 α. Because distribution assumptions of normality and homoscedasticity were not met for many of the variates, tests of significance in comparing male and female specimens were obtained with the Wilcoxon rank sums test using a multiple-comparisons adjustment to limit type I errors[41] as described by Jaccard and Wan[42], who advocated a modified Bonferroni procedure. The Wilcoxon rank sums test is a non-parametric test of the null hypothesis that both male and female samples for each variable derive from the same distribution.

30. Phenice, T. W. A newly developed visual method of sexing in the *Os pubis. Am. J. Phys. Anthropol.* **30,** 297–301 (1969).
31. Ubelaker, D. H. & Volk, C. G. A test of the Phenice method for the estimation of sex. *J. Forensic Sci.* **47,** 19–24 (2002).
32. Washburn, S. L. & Buettner-Janusch, J. The definition of thoracic and lumbar vertebrae. *Am. J. Phys. Anthropol.* **10,** 251–252 (1952).
33. Shapiro, L. in *Postcranial Adaptation in Nonhuman Primates.* (ed. Gebo, D.L.) 121-149 (Northern Illinois University Press, DeKalb, IL, 1993).
34. Schultz, A. H. The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* **2,** 303–438 (1930).
35. Rockwell, H., Gaynor Evans, F. & Pheasant, H. The comparative morphology of the vertebrate spinal column: its form as related to function. *J. Morphol.* **63,** 87–117 (1938).
36. Digiovanni, B., Scoles, P. & Latimer, B. Anterior extension of the thoracic vertebral bodies in Scheuermann's kyphosis: an anatomic study. *Spine* **14,** 712–716 (1989).
37. Corruccini, R. S. Shape in morphometrics: comparative analyses. *Am. J. Phys. Anthropol.* **73,** 289–303 (1987).
38. Jungers, W. L., Falsetti, A. B. & Wall, C. E. Shape, relative size, and size-adjustments in morphometrics. *Yb. Phys. Anthropol.* **38,** 137–161 (1995).
39. Mosimann, J. Size allometry: Size and shape variables with characterizations of the log normal and gamma distributions. *J. Am. Stat. Assoc.* **65,** 930–945 (1970).
40. Darroch, J. & Mosimman, J. Canonical and principal components of shape. *Biometrika* **72,** 241–252 (1985).
41. Sokal, R. R. & Rohlf, F. J. *Biometry: The Principles and Practice of Statistics in Biological Research.* 3rd Edition. (W.H. Freeman and Company, New York, 1995).
42. Jaccard, J. & Wan, C. K. *LISREL Approaches to Interaction Effects in Multiple Regression* (Sage, Thousand Oaks, CA, 1996).