Lumbar lordosis of Extinct Hominins

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ABSTRACT The lordotic curvature of the lumbar spine (lumbar lordosis) in humans is a critical component in the ability to achieve upright posture and bipedal gait. Only general estimates of the lordotic angle (LA) of extinct hominins are currently available, most of which are based on the wedging of the vertebral bodies. Recently, a new method for calculating the LA in skeletal material has become available. This method is based on the relationship between the lordotic curvature and the orientation of the inferior articular processes relative to vertebral bodies in the lumbar spines of living primates. Using this relationship, we developed new regression models in order to calculate the LAs in hominins. The new models are based on primate group-means and were used to calculate the LAs in the spines of eight extinct hominins. The results were also compared with the LAs of modern humans and modern nonhuman apes. The lordotic angles of australopithecines (41° ± 4), H. erectus (45°) and fossil H. sapiens (54° ± 14) are similar to those of modern humans (51° ± 11). This analysis confirms the assumption that human-like lordotic curvature was a morphological change that took place during the acquisition of erect posture and bipedalism as the habitual form of locomotion. Neandertals have smaller lordotic angles (LA = 29° ± 4) than modern humans, but higher angles than nonhuman apes (22° ± 3). This suggests possible subtle differences in Neandertal posture and locomotion from that of modern humans. Am J Phys Anthropol 000:000–000, 2011. ©2011 Wiley-Liss, Inc.

The lordotic curvature of the lumbar spine (lumbar lordosis) in humans is a critical component in the ability to achieve upright posture. Along with pelvic tilt and the angulation of the sacrum within the pelvis, lumbar lordosis brings the upper body over the lower limbs and allows the load from the upper body to be applied via the vertebral column and sacrum to the pelvis and legs (Gracovetsky and Iacono, 1987; Farfan, 1995; Whitcome et al., 2007). These three characteristics act in tandem to locate the line of gravity of the body close to the acetabulum. Lumbar curvature influences, and is influenced by, the morphology of the anterior pillar (formed by the vertebral body and intervertebral disks) and posterior pillar (formed by the articular processes and the laminae) of the spine, the pelvis, and the thoracic cavity (Sanders, 1998; Harrison et al., 2002; Lovejoy, 2005; Jang et al., 2009; Been et al., 2010a).

When lordosis is out of sync with the other features, allowing the line of gravity to deviate from its alignment near the acetabulum, people can have substantial complications, including functional issues such as a reduction in stride length and walking velocity and spinal pathologies. For instance, people with LAs below the normal range of 30–80° exhibit a short stride and slow walking speed (Grasso et al., 2000; Sarwahi et al., 2002; Hirose et al., 2004). Because of the flattening of their normal lordosis, their line of gravity lies anterior to the acetabulum, necessitating hip and knee flexion. On the other side of the lordosis continuum, people with hyperlordosis (lordotic curvature greater than the normal range) have a higher tendency to develop spondylolisthesis (Antoniades et al., 2000), a potentially debilitating condition where one vertebra slides forward relative to adjacent vertebrae. This relative movement between vertebrae can compromise spinal nerve function. Consequently, it seems clear that an appropriate amount of lumbar lordosis is important to normal function in humans.

Lordotic curvature is defined herein as the angle between the superior endplate of the first sacral vertebra and the superior end plate of the fifth presacral vertebra. Only general estimates of the LA of extinct hominins are available today, usually based on the wedging of the vertebral bodies. These descriptions of the LA of the fossils indicate where the specimen’s morphology
resembled or differed from that of modern humans (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1998; Ward, 2002; Whitcome et al., 2007; Weber and Pusch, 2008). For instance, the vertebral specimens of Australopithecus africanus (STS 14) have been described as having vertebral body wedging similar to that of humans (Whitcome et al., 2007). On the basis of these estimates from vertebral wedging, most researchers agree that both australopithecines and H. erectus had lumbar LAs within the normal range of modern humans (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1998; Ward, 2002; Whitcome et al., 2007), presumably in response to constraints similar to those apparent in humans.

However, since the discovery of the nearly complete skeleton of La Chapelle-aux-Saints in 1908 (Bouyssonie et al., 1908), an ongoing debate over the LA of Neandertals (H. neanderthalensis) has existed. On the one hand, Trinkaus (1983), Arensburg (1991), and Cleuvenot (1999) have argued that the LA of Neandertals is within the normal range for modern humans. On the other hand, other scholars have found that the LA of Neandertals is smaller than that of modern humans (Boule, 1911–1913; Weber and Pusch, 2008; Been et al., 2010a). Definitive understanding of the degree of lumbar lordosis in Neandertals requires more than simple description of vertebral wedging.

Recently, a new method for calculating the LA in skeletal material has become available (Been et al., 2010a). This method is based on the relationship between the lordotic curvature and the orientation of the inferior articular processes in the lumbar spines of living human and nonhuman primates. Because the method uses a measurement taken within each vertebra, articulation of the entire lumbar spine is not required. This work demonstrated that 89% of the variation in the lordotic curvature in living primates is related to the orientation of the inferior articular process (Been et al., 2010a) and not dependent on soft tissue morphology. Thus, this method should be a reliable predictor of the lumbar LA in disarticulated hominin spines, as long as extinct hominins exhibit the same relationship as do living primates.

The aims of this study are, therefore, first, to calculate a specific statistical model for calculating the lordotic curvature for each extinct hominin specimen. This is necessary because the fossil specimens vary in the number of preserved vertebrae. The second aim is to calculate the lordotic curvature of the lumbar spines of extinct hominins using these statistical models. Finally, based on our results, we will examine the evolution of lordotic curvature in hominins.

**Materials and Methods**

### Materials

**Radiographic analysis**

A total of 106 lateral radiographs of modern humans (after Been et al., 2010a) and 76 lateral radiographs of nonhuman primates were examined. All radiographs met the following criteria: (1) from adult living subjects with no detectable radiographic abnormalities (e.g., degeneration or reduced disk height) and (2) high resolution with a clearly visible lumbar spine. The modern human sample included 106 adult humans (56 men and 50 women) from Israel. The radiographs were taken when the subjects were standing with arms flexed across their chests.

The nonhuman primates included the spinal (lumbar) radiographs of Macaca fascicularis and Macaca fuscata.

### Methods

**Angular measurements**

The modal number of lumbar vertebrae varies among primate species. For example, the lumbar spine of Lemur and Macaca has seven lumbar vertebrae, whereas the lumbar spine of Pan has only four lumbar vertebrae (Schultz, 1961). The difference in vertebral number is not only restricted to the lumbar segment but also present in the thoracic and sacral regions (Pilbeam, 2004).

Because LA is dependent on the number of vertebrae included in the calculation (Harrison et al., 2001; Vialle et al., 2005), comparison of results among genera with different numbers of lumbar vertebra requires standardization. Thus, we have chosen a presacral segment of five vertebrae which is the number of lumbar vertebrae in human sample included 106 adult humans (56 men and 50 women) from Israel. The radiographs were taken when the subjects were standing with arms flexed across their chests.

The nonhuman primates included the spinal (lumbar) radiographs of Macaca fascicularis and Macaca fuscata.
Modern and fossil *H. sapiens*, Neandertals, and *H. heidelbergensis* (McCown and Keith, 1939; Trinkaus, 1983; Arensburg, 1991; Haeusler et al., 2002; Pilbeam 2004; Gómez-Olivencia, 2009; Bonmatí et al., 2010). *Australopithecus* and *H. erectus* could arguably have six rather than five lumbar vertebrae (Robinson, 1972; Walker and

<table>
<thead>
<tr>
<th>Individual</th>
<th>Species</th>
<th>Vertebrae used</th>
<th>Observations</th>
<th>Additional references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stw 431</td>
<td><em>Australopithecus</em></td>
<td>PS₁-PS₄ (n = 4)</td>
<td>Adult male. Fifth (PS₁) and fourth (PS₂) lumbar vertebrae show pathological signs: spondylosis deformans following Staps (2002) also interpreted as brucellosis by D’Anastasio et al. (2009).</td>
<td>McHenry, 1992; McHenry and Berger, 1998a,b; Haeusler et al., 2002</td>
</tr>
<tr>
<td>Sts 14</td>
<td><em>Australopithecus</em></td>
<td>PS₂-PS₄ (n = 3)</td>
<td>Young adult (Bonmatí et al., 2008). Five (Haeusler et al., 2002) or six lumbar vertebrae (Robinson, 1972). The inferior articular processes in PS₁ and PS₅ are reconstructed.</td>
<td>Haeusler, 2002</td>
</tr>
<tr>
<td>KNM WT-15000</td>
<td><em>H. erectus/H. ergaster</em></td>
<td>PS₁-PS₃ (n = 3)</td>
<td>Subadult male; five (Brown et al., 1985, Haeusler et al., 2002) or six (Walker and Leukoy, 1993; Latimer and Ward 1993) lumbar vertebrae. Possible spinal pathology, related to infant malnutrition (axial dysplasia); small vertebral canal (Latimer and Ohman, 2001; but see Schiess et al., 2006).</td>
<td></td>
</tr>
<tr>
<td>Shanidar 3</td>
<td><em>H. neanderthalensis</em></td>
<td>PS₂, PS₃, PS₅ (n = 3)</td>
<td>35–50–year-old male (Stewart, 1977; Trinkaus 1983). It shows articular facets for lumbar ribs attached to the first lumbar vertebra, Baastrup disease on the spinous processes, and marked degenerative changes at the body of the first and second lumbar vertebra (PS₁,PS₂) (Ogilvie et al., 1998).</td>
<td></td>
</tr>
<tr>
<td>Kebara 2</td>
<td><em>H. neanderthalensis</em></td>
<td>PS₁-PS₅ (n = 5)</td>
<td>20–30–year-old male; lumbar rib attached to the first lumbar vertebra and nonossification (pseudoarthrosis) of the spinous processes of the last four lumbar vertebra (PS₁,PS₅) (Duday and Arensburg, 1991);Weber and Pusch (2008) further report mild degenerative changes of the vertebral bodies (PS₂-PS₃) and facet joint (PS₁).</td>
<td>Arensburg, 1991</td>
</tr>
<tr>
<td>La Chapelleaux-Saints</td>
<td><em>H. neanderthalensis</em></td>
<td>PS₁, PS₂, PS₅ (n = 3)</td>
<td>&gt;40 year old male; Baastrup disease in the spinous processes (Ogilvie et al., 1998).</td>
<td>Boule, 1911–1913; Dawson and Trinkaus, 1997.</td>
</tr>
<tr>
<td>Cro-Magnon 1</td>
<td><em>H. sapiens</em></td>
<td>PS₁, PS₂, PS₃, PS₅ (n = 4)</td>
<td>Middle aged male; degenerative changes on PS₃ and PS₄.</td>
<td></td>
</tr>
<tr>
<td>Cro-Magnon 3</td>
<td><em>H. sapiens</em></td>
<td>PS₁-PS₅ (n = 5)</td>
<td>Adult male.</td>
<td></td>
</tr>
</tbody>
</table>

* PS₁(4289), PS₂(4266), PS₃(4286), PS₄(4285). We attribute these four vertebrae to Cro-Magnon 1 based on the presence of degenerative pathology. The number between parentheses is the label of the individual vertebral specimens.

b These associations of vertebrae belonging to the same individual differ from those published by Vallois and Billa (1965).

c PS₁(4281), PS₂(4280), PS₃(4287), PS₄(4268), PS₅(4282). We attribute these five vertebrae to a male, younger than Cro-Magnon 1, and thus it could belong to Cro-Magnon 3 or 4. The number between parentheses is the label of the individual vertebral specimens.
<table>
<thead>
<tr>
<th>Species</th>
<th>Individual</th>
<th>Source</th>
<th>Articular process angle (AP)</th>
<th>Vertebral body wedge angles (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>PS₅</td>
<td>PS₄</td>
</tr>
<tr>
<td><em>H. sapiens</em></td>
<td>Cro-Magnon 1</td>
<td>Radiograph</td>
<td>100</td>
<td>93</td>
</tr>
<tr>
<td><em>H. sapiens</em></td>
<td>Cro-Magnon 3</td>
<td>Radiograph</td>
<td>99</td>
<td>108</td>
</tr>
<tr>
<td><em>H. sapiens</em> average</td>
<td></td>
<td></td>
<td>99.5</td>
<td>100.5</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>Kebara 2</td>
<td>Radiograph</td>
<td>88</td>
<td>87</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>La Chapelle-</td>
<td>Radiograph</td>
<td>87</td>
<td>M</td>
</tr>
<tr>
<td>aux-Saints</td>
<td>Shanidar 3</td>
<td>Radiograph</td>
<td>89</td>
<td>F</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td></td>
<td></td>
<td>88.0</td>
<td>87</td>
</tr>
<tr>
<td><em>H. erectus</em></td>
<td>KNM WT-15000</td>
<td>Photograph</td>
<td>F</td>
<td>F</td>
</tr>
<tr>
<td><em>Australopithecus</em></td>
<td>STS - 14</td>
<td>Radiograph</td>
<td>F</td>
<td>101</td>
</tr>
<tr>
<td>africanus</td>
<td>Stw - 431</td>
<td>Photograph</td>
<td>F</td>
<td>99</td>
</tr>
<tr>
<td><em>Australopithecus</em></td>
<td></td>
<td></td>
<td>100</td>
<td>96</td>
</tr>
<tr>
<td>average</td>
<td>Modern <em>Homo sapiens</em> (n = 106)</td>
<td>Radiograph</td>
<td>x ± SD</td>
<td>94 ± 5</td>
</tr>
<tr>
<td>Modern <em>Homo sapiens</em> (n = 52)</td>
<td>x ± SD</td>
<td>Radiograph</td>
<td>87 ± 4</td>
<td>87 ± 5</td>
</tr>
<tr>
<td><em>Ape</em> (n = 9)</td>
<td>x ± SD</td>
<td>Radiograph</td>
<td>95 ± 5</td>
<td>95 ± 3</td>
</tr>
<tr>
<td><em>Lemur</em> (n = 8)</td>
<td>x ± SD</td>
<td>Radiograph</td>
<td>83 ± 3</td>
<td>85 ± 3</td>
</tr>
<tr>
<td><em>Saimiri</em> (n = 4)</td>
<td>x ± SD</td>
<td>Radiograph</td>
<td>91 ± 3</td>
<td>90 ± 4</td>
</tr>
<tr>
<td><em>Saguinus</em> (n = 3)</td>
<td>x ± SD</td>
<td>Radiograph</td>
<td>83 ± 6</td>
<td>88 ± 7</td>
</tr>
</tbody>
</table>

M, vertebra missing; F, vertebra present but fragmentary. After Been et al. (2010a).

b The sample is composed of four chimpanzees (*Pan troglodytes*), two gorillas (*Gorilla gorilla*), two orangutans (*Pongo pygmaeus*), and one gibbon (*Hylobates sp.*).

c Vertebral body wedge angles (B): Negative value indicates kyphotic wedging; Positive value indicates lordotic wedging.
Leakey, 1993), although this vision is contested by other scholars (Haeusler et al., 2002).

Nonetheless, in order to be able to compare LA among species, we define LA as that of the last five presacral vertebrae. This approach creates a lumbar region that is intermediate in vertebral number between the longer lumbar spines of monkeys and (potentially) early hominins and the shorter lumbar spines of modern great apes. This approach is justified, because no correlation exists between the number of lumbar vertebrae and the degree of lordosis in primate species. For example, humans have five lumbar vertebrae with lordosis of >50°, apes have four lumbar vertebrae with ~20–25° of lordosis, and macaque monkeys have seven lumbar vertebrae with lordosis of ~14° (Been et al., 2010a).

To facilitate comparison among the different hominin groups and between hominins and nonhuman primates, we numbered the vertebrae in relation to the sacrum, as have others that compared the lumbar vertebrae of nonhuman primates, early hominins, and modern humans (Latimer and Ward, 1993; Abitbol, 1995). The vertebra just above the sacrum is denoted PS1 (first presacral) in all of the spines; the vertebra above PS1 is denoted PS2, and so forth.

As described previously (Been et al., 2010a), lateral radiographs were used to measure LA of the five presacral vertebrae, vertebral body wedging and the orientation of the inferior articular processes relative to the vertebral body. For each of the five vertebrae (PS1-PS5), three lines were drawn (Figs. 1 and 2): along the cranial endplate of the vertebral body (including the first sacral vertebra); along the caudal endplate of the vertebral body; and along the ventral border of the inferior articular process. These lines were used to measure three angles:

1. The LA between the cranial endplate of PS5 and the cranial endplate of S1.
2. The vertebral body wedge angle (B) between the cranial and caudal end plates of the vertebral body.
3. The inferior articular process angle (AP) between the cranial endplate and the ventral border of the inferior articular process of the same vertebra, as seen in the lateral radiograph in the facet joint space.

Measurements B and AP were made for each of the five presacral segments. All measurements were taken by the same investigator (EB) using a 25-cm Jamar goniometer with a 360° scale in 1° increments. Summations of measurement B and AP were also calculated: \( \Sigma B \) equals the sum of the body wedge angles of vertebrae PS1–PS5; and \( \Sigma AP \) equals the sum of the inferior articular process angles of these vertebrae.

The body wedge angles were measured in order to compare our results to previously published data, because previous assessments of the LA in extinct hominins usually refer to the wedging of the vertebral bodies. The inferior articular process angles were measured to develop new regression models for calculating the LA in fossil hominins (Been et al., 2010a).

In order to determine if our measurements were reproducible, five radiographs of modern humans (65 measurements) were measured twice, 3 weeks apart, by one of us (EB). The intraclass correlation coefficients were 0.97 (P < 0.001) for LA and for B and 0.88 (P < 0.01) for AP. The mean angular deviation between trials was 2.4° for LA, 1.9° for B, and 2.85° for AP.

Developing regression models

New regression formulae for calculating LA in fossil hominins were developed based on primate group means (Table 3 and Fig. 3), using bivariate fit models (fit Y by X, JMP statistics software, SAS Institute, Cary, NC). For each primate group, the individual values for LA, B, and AP were averaged to produce the mean for the group. These models were specifically developed for each specimen based on the number of intact vertebrae present in the specimen. Our method yields standard errors of estimation (SEE) of greater than 10° when only one or two vertebrae are present. Consequently, we did not calculate the LAs for specimens with less than three intact vertebrae, which limit the available fossil sample.

We grouped the primates loosely based on phylogenetic relationship. For example, in the macaque group, we
combined the results for *M. fasicularis* and *M. fuscata*, whereas in the ape group, we combined the results for *P. troglodytes*, *G. gorilla*, *P. pygmaeus*, and *Hylobates* sp. (Table 3). We recognize that grouping nonhuman apes, but separating *Saimiri* and *Saguinus* might at first seem illogical, but we were constrained in our sampling ability. All of the nonhuman primates were captive animals, and the radiographs were obtained during veterinary exams, except for those from the macaques, which were obtained for research purposes. Consequently, our sample is one of convenience and we could neither obtain equal numbers of individuals of all species nor could we obtain all species that we would have preferred to have. Some genera (*Gorilla*, *Pongo*, and *Hylobates*) are represented by only one or two individuals, while other genera have more. All of the nonhuman apes had similar LAs (Table 3), but *Saimiri* and *Saguinus* are different. We created the primate groups, then, based on phylogeny, but influenced by the number of available individuals and the morphology of the lumbar region.

We evaluated the impact of the decision to use the primate group-mean method by eliminating the groupings and using all the primate individual values to develop statistical models. This method has its own flaws; however, in that it over-represents individuals in *Macaca* and *Homo* relative to the nonhuman apes. The all primate, individual-based method produced the same trends as the primate group-mean method (analysis not shown), allowing us to conclude that our primate group-mean models are robust.

Still, the possibility exists that SEEs and $R^2$s that are based on (6) group means could be misleading when predicting individual variation (Ruff, 2003). In order to test how well the group-mean model works to predict individual values, we calculated the LAs for all of our extant individuals (human and nonhuman primates) and then calculated the mean difference between the measured and calculated LAs.

We performed individual and sample comparisons of the calculated LAs between the fossil individuals and the modern human and ape sample using Z-scores and Mann-Whitney's U-test. Using the Bonferroni correction, the threshold value would be 0.0125, which is similar to that obtained by the Dunn-Šidák correction. The difference between these two correction methods is higher as the number of groups involved increases.

Finally, because it is possible that LA is influenced by locomotor form, we calculated the LAs of the extinct hominins using statistical models developed just from the angles measured from the radiographs of modern humans (See also Been et al., 2010a). As we had done for the group-mean method, we calculated the mean difference between the measured and calculated LAs of the humans in order to determine how well the statistical model predicted individual values.

### RESULTS

#### Regression models based on primate group-mean method

Regression models (that predict lordotic curvature) were developed from the sum of the inferior articulating process angles ($\Sigma$AP) in primates, using the mean value for each primate group. The regression models and the data used to develop them are summarized in Table 3 and Figure 3. All of the group-mean models have coefficients of determination $R^2 > 0.9$ between the sum of
articular process wedging and the lordotic curvature and low standard errors of estimation (SEE < 5; Table 3 and Fig. 3). The resultant lordotic curvatures of the fossil hominins and the formulae used to calculate them are summarized in Table 4.

Regression models based on modern human-only method
Regression models (that predict the lordotic curvature) were also developed from the sum of the inferior articular

Fig. 3. Correlation between lordotic angle (LA) and sum of inferior articular process (ΣAP), based on primate group means. Linear fit with 95% bivariate normal ellipse. These ellipses are both density contours and confidence curves. As confidence curves, they show where a given percentage of the data is expected to lie. ▲ = modern human; ▼ = Nonhuman apes; □ = Macaca; ● = Lemur; * = Saimiri; ○ = Saguinus.
TABLE 4. Calculated lumbar lordotic angles of extinct hominins

<table>
<thead>
<tr>
<th>Sample</th>
<th>Individual</th>
<th>Measured vertebrae</th>
<th>ΣAP</th>
<th>Regression model based on primate group-mean method</th>
<th>Calculated lordosis</th>
<th>Regression model based on modern human only method</th>
<th>Calculated lordosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fossil <em>H. sapiens</em></td>
<td>Cro-Magnon 1</td>
<td>PS₁, PS₂, PS₄, PS₅</td>
<td>402</td>
<td>LA = 0.645 × 402 – 215.6 (R^2 = 0.94,\ SEE = 4.22)</td>
<td>44 (LA = 0.63 \times \Sigma AP - 208) (R^2 = 0.55,\ SEE = 7.5)</td>
<td>46 (LA = 0.565 \times \Sigma AP - 237) (R^2 = 0.62,\ SEE = 6.8)</td>
<td>67</td>
</tr>
<tr>
<td>Fossil <em>H. sapiens</em></td>
<td>Cro-Magnon 3</td>
<td>PS₁,PS₅</td>
<td>538</td>
<td>LA = 0.528 × 538 – 220.5 (R^2 = 0.948,\ SEE = 4.04)</td>
<td>64 (LA = 0.63 \times \Sigma AP - 237)</td>
<td>67 (LA = 0.565 \times \Sigma AP - 237)</td>
<td>56.5 ± 15</td>
</tr>
<tr>
<td>Fossil <em>H. sapiens</em></td>
<td>average</td>
<td></td>
<td></td>
<td>(\bar{x} \pm SD) (54.0 \pm 14.1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>Kebara 2</td>
<td>PS₁,PS₅</td>
<td>465</td>
<td>LA = 0.528 × 465 – 220.5 (R^2 = 0.948,\ SEE = 4.04)</td>
<td>25 (LA = 0.63 \times \Sigma AP - 140) (R^2 = 0.42,\ SEE = 8.5)</td>
<td>26 (LA = 0.565 \times \Sigma AP - 237) (R^2 = 0.62,\ SEE = 6.8)</td>
<td>34</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>La Chapelle-aux-Saints</td>
<td>PS₁, PS₁, PS₅, PS₅</td>
<td>290</td>
<td>LA = 0.799 × 290 – 200 (R^2 = 0.96,\ SEE = 3.4)</td>
<td>32 (LA = 0.63 \times \Sigma AP - 140) (R^2 = 0.42,\ SEE = 8.5)</td>
<td>34 (LA = 0.693 \times \Sigma AP - 137) (R^2 = 0.40,\ SEE = 8.6)</td>
<td>33.3 ± 7</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>Shanidar 3</td>
<td>PS₂,PS₃, PS₅</td>
<td>283</td>
<td>LA = 0.911 × 283 – 226.7 (R^2 = 0.926,\ SEE = 4.8)</td>
<td>31 (LA = 0.63 \times \Sigma AP - 140) (R^2 = 0.42,\ SEE = 8.5)</td>
<td>40 (LA = 0.63 \times \Sigma AP - 140) (R^2 = 0.42,\ SEE = 8.5)</td>
<td>40</td>
</tr>
<tr>
<td><em>H. neanderthalensis</em></td>
<td>average</td>
<td></td>
<td></td>
<td>(\bar{x} \pm SD) (29.3 \pm 3.8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. erectus</em></td>
<td>KNM-WT 15000</td>
<td>PS₁,PS₂, PS₃</td>
<td>310</td>
<td>LA = 0.744 × 310 – 186.2 (R^2 = 0.964,\ SEE = 3.36)</td>
<td>45 (LA = 0.61 \times \Sigma AP - 144) (R^2 = 0.37,\ SEE = 8.8)</td>
<td>45 (LA = 0.61 \times \Sigma AP - 144) (R^2 = 0.37,\ SEE = 8.8)</td>
<td>45</td>
</tr>
<tr>
<td><em>A. africanus</em></td>
<td>STS - 14</td>
<td>PS₂,PS₃, PS₄</td>
<td>292</td>
<td>LA = 0.923 × 292 – 231.7 (R^2 = 0.929,\ SEE = 4.7)</td>
<td>38 (LA = 0.62 \times \Sigma AP - 136.4) (R^2 = 0.45,\ SEE = 8.2)</td>
<td>44 (LA = 0.62 \times \Sigma AP - 136.4) (R^2 = 0.45,\ SEE = 8.2)</td>
<td>44</td>
</tr>
<tr>
<td><em>A. africanus</em></td>
<td>Stw - 431</td>
<td>PS₁, PS₂, PS₃, PS₄</td>
<td>406</td>
<td>LA = 0.618 × 406 – 206.8 (R^2 = 0.95,\ SEE = 3.9)</td>
<td>44 (LA = 0.61 \times \Sigma AP - 203) (R^2 = 0.54,\ SEE = 7.5)</td>
<td>45 (LA = 0.61 \times \Sigma AP - 203) (R^2 = 0.54,\ SEE = 7.5)</td>
<td>45</td>
</tr>
<tr>
<td><em>Australopithecus</em></td>
<td>average</td>
<td></td>
<td></td>
<td>(\bar{x} \pm SD) (41.0 \pm 4.2)</td>
<td></td>
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process angles (ΣAP) using only the modern human data (Been et al., 2010a). These models have coefficients of determination (R²) ranging from 0.37 to 0.62 between the sum of articular process wedging and the lordotic curvature and standard errors of estimation (SEE < 9, Table 4). The resultant lordotic curvatures of the fossil hominins and the formulae used to calculate them are summarized in Table 4.

Validity of statistical models for predicting individual values

In order to determine the degree to which our statistical models were able to predict individual values, we calculated the mean individual prediction errors. We calculated the LA of all of our extant individuals (human and nonhuman primates) using the primate group-mean model and compared it with their measured LAs. The mean difference between the calculated and measured LA is ±5.92°. We repeated the process using the modern human-only model. The mean difference between the calculated and measured LAs in humans is ±5.93°.

Vertebral body wedging and articular process angles

The body wedge angles (B; negative value indicates kyphotic wedging; positive value indicates lordotic wedging) and the articular process angles (AP) for extant primates and for extinct hominins are shown in Table 2. Modern humans have a higher (more lordotic) sum of vertebral body wedging (ΣB = 6 ± 10, x ± SD) and a higher sum of articular process wedging (ΣAP = 510 ± 15) compared with nonhuman apes (ΣB = −13 ± 4, and ΣAP = 471 ± 7). Fossil H. sapiens show vertebral body wedging (ΣB = 18) and articular process wedging (ΣAP = 538) similar to modern humans. H. neanderthalensis shows vertebral body wedging (ΣB = −11) and articular process wedging (ΣAP = 465) that are smaller than that of modern humans and comparable with that of nonhuman apes. H. erectus shows vertebral body wedging and articular process wedging that are comparable with that of modern humans. Australopithecus shows vertebral body wedging (ΣB = 2) and articular process wedging that are comparable with modern humans, but below the average for modern humans throughout the spine (Table 2).

Although the overall articular process wedging of Neandertals is low compared with modern humans and similar to nonhuman apes, the Neandertal pattern of distribution within the spine of articular process wedging is similar to modern humans. Taking the mean values, vertebra closer to the sacrum in modern humans show an increase in articular process wedging, as do those of Neandertals. On the contrary, nonhuman apes show an approximately constant articular process wedging throughout the five presacral vertebrae. This pattern is difficult to ascertain, however, from single hominin individuals due to the fragmentary status of the record and, potentially, large intrapopulational variation.

Lordotic angles

The calculated LAs of the individual specimens are shown in Table 4 and Figure 4. The LA values for hominin groups and nonhuman apes are illustrated in Figure 5. Based on the primate group-mean models, the largest values of LA are in fossil H. sapiens (54° ± 14; 95% CI = 35–73). Australopithecus (41° ± 5; 95% CI = 35–47) and H. erectus (45°) show lower values. Neandertals show LAs (29° ± 5; 95% CI = 24–34) that are lower than all other hominins, but higher than modern nonhuman apes.

The modern human-only models show similar results: the largest values of LA are in fossil H. sapiens (57° ± 15). Australopithecus (44.5° ± 1) and H. erectus (45°) show lower values. Neandertals exhibit LAs (33° ± 7) that are lower than the other hominins, but higher than modern nonhuman apes. We should note that the modern human-only model calculates LAs that are on average 2° higher than the primate group-mean model.

Because of the similarity between the two methods, we report below only those analyses that used the values calculated from the primate group-mean method. We performed individual and sample comparison of the calculated LA between the fossil individuals and the modern human and ape sample using Z-scores and
Mann-Whitney’s U-test (Table 5). The individual specimens of fossil H. sapiens, H. erectus, and Australopithecus have LAs that are within the normal range for modern humans and above the normal range for extant nonhuman apes. Two of the three Neandertal specimens (La Chapelle-aux-Saints and Shanidar 3) have LAs that are at the lower end of the normal range for modern humans (Z-score between 1.5 and 1.96), but significantly above modern nonhuman apes. One Neandertal specimen (Kebara 2) has a very small LA (25°), which is below the normal range for modern humans and within the normal range for modern nonhuman apes.

Kruskal-Wallis tests between the LA values of modern H. sapiens, modern nonhuman apes, H. neanderthalensis, Australopithecus, and fossil H. sapiens indicate significant differences among these groups. To localize these significant differences, we performed Mann-Whitney pairwise tests (See Table 5). Both fossil H. sapiens and Australopithecus have LAs that are within the normal range for modern humans and above the normal range for modern nonhuman apes. It is interesting to note that the LA values of Neandertals are significantly below the values for modern Homo sapiens, but significantly above nonhuman ape values (Table 5). If we apply the Dunn-Sidák correction for multiple comparisons \(1 - (1 - \alpha)^{1/n}\) with an \(\alpha = 0.05\) and four groups considered (modern humans, nonhuman apes, Neandertals, and australopithecines), the threshold value obtained for significance is 0.0127, and Neandertals are significantly different from modern humans.

**DISCUSSION**

**Regression models**

The statistical models that were developed to calculate lordosis in fossil hominins (based on the primate group-mean method) have coefficients of determination between inferior articular processes angles and LAs of >0.9, as well as standard errors of estimation <7°. The LAs calculated with the primate group-mean method were confirmed by calculating models considering all primates as individuals and are consistent with the LAs calculated based on the modern human-only method.

Previous reports of the vertebral wedging, (Latimer and Ward, 1993; Sanders, 1998; Ward, 2002; Whitcome et al., 2007), are also consistent with the LAs found using the primate group-means method. Nonhuman apes have small LAs [22° ± 2°, (Abitbol, 1995); 22° ± 3° current study] and kyphotic lumbar vertebral bodies [\(\Sigma B = -19°\) (Latimer and Ward, 1993); \(\Sigma B = -13° ± 4°\), current study]. Neandertals also have small LAs (29° ± 3°) and kyphotic lumbar vertebral bodies [\(\Sigma B = -11°\), current study]. Species with high LAs (LA > 40°) have lordotic wedging of their vertebral bodies: modern humans [\(\Sigma B = 6°\) (Vialle et al., 2005); \(\Sigma B = 6° ± 10°\) current study], fossil H. sapiens [\(\Sigma B = 18°\) current study] and Australopithecus [\(\Sigma B = 1°\) (Whitcome et al., 2007); \(\Sigma B = 2°\), current study].

All of these comparisons yield the same pattern among the hominin species, providing us with confidence that the pattern we have reported is robust. Although it is possible that fossil hominins could exhibit a relationship between articular process angle and LA that is different from that found among all primates sampled or among only modern humans, it seems unlikely.

**Lordotic angle**

This study is the first to publish angular values for the LAs of extinct hominins. Australopithecines (LA = 41° ± 4°, 95% CI = 35–47°), H. erectus (LA = 45°), and fossil H. sapiens (LA = 54° ± 14°, 95% CI = 50–57°) have LAs that overlap the range of lordosis in our modern human sample (LA = 51° ± 11°, 95% CI = 49–53°). The finding of human-like LAs in australopithecines and H. erectus is in agreement with previously published data (Robinson, 1972; Latimer and Ward, 1993; Sanders, 1998; Ward, 2002; Whitcome et al., 2007). Lordotic curvature, in combination with pelvic tilt on the leg and sacral tilt within the pelvis, allows the upper body to be balanced above the acetabulum. It has also been suggested, based on pelvic morphology, that the lordotic curvature of Ardipithecus ramidus was already greater.
than that of nonhuman apes (Lovejoy, 2009); however, no lumbar vertebra of this species has been described. Our analysis supports the assumption that human-like lordotic curvature was a morphological change that took place during the acquisition of erect posture and bipedalism as the habitual form of locomotion.

Neandertals depart from this hominin trend, having smaller LAs (LA = 29° ± 4, 95% CI = 24–34) than do all other hominins, but higher angles than do nonhuman ape (LA = 22° ± 3, 95% CI = 20–24). The relatively small LAs of Neandertals are in agreement with Boule (1911–1913), Weber and Pusch (2008), and Been et al. (2010a), but contradict the results of Trinkaus (1983), Arensburg (1991), and Cleuvenot (1999). The less lordotically curved lumbar column of Neandertals could be inherited from their presumed middle Pleistocene ancestors—H. heidelbergensis—as is suggested by the kyphotic lumbar vertebral body wedging and the horizontal sacral endplate of the specimens from the Sima de los Huesos site (Arsuaga et al., 1999; Gómez-Olivencia, 2009; Bonmati et al., 2010).

**Limitations**

Our study is limited by several issues. First, even though we have used all the fossils available to us, the fossil sample is small and that lessens the power of any inferential statistical methods. Consequently, we have had to rely mostly on descriptive analysis. New findings, especially of lower Pleistocene H. erectus sensu lato, should help us to better understand the evolution of lumbar lordosis in hominins.

Second, some of the fossil specimen show marked pathologies such as degenerative changes (Cro-Magnon 1, Shanidar 3), spondylisis or brucellosis (Stw-431), Baasstrup disease (La Chapelle-aux-Saints and Shanidar 3), and nonossification of the spinous processes (Kebara 2). These pathologies are typically found in most modern human populations, and there is no evidence to indicate that these pathologies affect the degree of lordotic curvature (Maes et al., 2008; Papadakis et al., 2010).

Third, one of our specimens (KNM-WT 15000) is a juvenile with a suspected axial dysplasia (Latimer and Ohman, 2001), and therefore, it might exhibit different LAs than a fully adult specimen. We include it because the fossil record of lumbar spinal elements is sparse for early genus Homo but recognize that future work might render any evidence from it moot. In any case, elimination of it from our sample would not change our conclusions.

Finally, reconstructing LA without soft tissue requires that we understand the relationship between the intervertebral discs and lumbar lordosis. Fortunately, the models we employ are based on radiographs of the lumbar spines of living individuals, that is, that possessed both the vertebral bodies and the intervertebral discs (Been et al., 2010a), and intervertebral discs do not contribute to differences in overall lordosis as much as does vertebral wedging (Been et al 2010b). This suggests that the absence of intervertebral discs would not change the conclusions presented herein.

**Evolutionary Perspective on Lumbar Lordosis**

Given that Neandertals exhibit less lumbar curvature than other hominins, a critical question obtains: do Neandertals retain the primitive configuration of small LAs as seen in extant nonhuman apes? This proposition seems unlikely as parsimonious considerations exclude it. It is our contention that with the acquisition of bipedalism lordosis increased—from a degree similar to that of modern nonhuman apes (small lordosis) to the high lordosis seen in australopithecines, H. erectus and H. sapiens. The Neandertals, then, represent a reversal in this morphological trend.

The LA shows an increase in lordosis from the primitive condition, preserved in modern nonhuman apes (20° ~ 25°) to australopithecine and H. erectus (40 ~ 45) and then to H. sapiens (50 ~ 55), while Neandertals show a decreased lordosis (~30) when compared with other hominins (Fig. 6). The lack of fossil lumbar spines from early genus Homo is frustrating, because their morphology would provide important clues to understanding the evolution of lumbar lordosis.

A normal lumbar lordosis (within the range of 30° ~ 80°, see Bernhard and Bridwell, 1989; Jackson et al., 2000; Kimura et al., 2001; Harrison et al. 2001) plays a major role in bipedal walking in modern humans, as it serves as a shock absorber, helps maintain minimal perturbations of the head, and helps create the moment that moves the pelvis and the legs during bipedal walking. Although lumbar lordosis plays a role in the maintenance of an efficient upright posture, it also adds a certain amount of compliance for locomotion and protects the posterior
spinal ligament system from excess strain (Gracovetsky and Iacono, 1987; Bogduk, 1997; Vialle et al., 2005).

The events or selective pressures that generated smaller lumbar lordosis in the Neandertal lineage compared with other hominins are not immediately obvious. We can hypothesize that the lumbar lordosis is related to other distinctive Neandertal postcranial features like the lower limb, pelvic and thoracic morphology (Rak, 1991; Franciscus and Churchill, 2002; Polk, 2004; Gómez-Olivencia et al., 2009). These differences may indicate postural and locomotive differences in the Neandertal lineage compared with that of our species.

Lordotic curvature in humans appears to correlate with pelvic and thoracic morphology. Small LAs usually correlate with a vertical sacrum (horizontally oriented sacral endplate) and small thoracic kyphosis (Fig. 7; Harrison et al., 2002; Lovejoy, 2005; Boulay et al., 2006; Jang et al., 2009), although there are also cases of small LAs accompanied by normal or even hyperkyphotic thorax (Harrison et al., 2002). Examining the wedging of the Neandertal thoracic vertebrae may help to resolve that discrepancy (Goh et al., 1999).

Neandertals are known to have a larger thorax than modern humans. The shape of the thorax is also different: the uppermost and lowermost ribs are similar to those of modern humans but mid-thoracic ribs are significantly larger (Gómez-Olivencia et al., 2009). Some authors propose that Neandertals show a larger anteroposterior dimension compared with modern humans based on the ribs of Shanidar 3 (Franciscus and Churchill, 2002) or based on the clavicular proportions of several Neandertals. From the ribs of Tabun C1, Weinstein (2008) proposes that the thorax of this individual was expanded mediolaterally. Because of taphonomical distortion of ribs from Kebara 2 (and also Tabun C1), Gómez-Olivencia et al. (2009) did not propose in which direction (anteroposterior, mediolateral, or both) the Neandertal thorax was larger. In any case, it is reasonable to link the biomechanical differences that a larger thorax would impose to the spinopelvic balance and the presence of a less lordotic lumbar spine in Neandertals.

The Neandertal pelvis is wide (bilateral) with a long bi-iliac breadth, long and slender superior pubic rami, and the acetabulum is posterior relative to the pelvic inlet, compared with H. sapiens (Rak and Arensburg, 1987; Rak, 1990; 1993). Rak (1993) postulates that Neandertal gait is less efficient than that of modern humans and that the Neandertal pelvis lacks the shock-absorbing mechanism with which H. sapiens is equipped. A posteriorly situated acetabulum requires smaller LAs in order to adjust the weight of the upper body above the pelvis, but small LAs are less efficient at shock absorption, which is in accordance with Rak’s interpretation of the Neandertal pelvis.

Small LAs in humans are correlated with short stride length, slow walking velocity and an anteriorly flexed trunk (Grasso et al., 2000; Sarwahi et al., 2002; Hirose et al., 2004, Jang et al., 2009). Nonetheless, less-lordotic spines are clearly more stable and less mobile than more-lordotic lumbar spines (Scholten et al., 1988) and can carry heavy loads without developing high shear stress on the lumbar structures (Shirazi-Adl and Parianpour, 1999; Meakin et al., 2008). If this holds true for Neandertals, it might suggest, on the one hand, that Neandertals were better adapted to carry heavy loads and, potentially, to engage in generally more rigorous upper body activities (Pearson, 2000; Weaver, 2009). On the other hand, it might suggest that Neandertals had a short stride length and slower walking velocity compared with modern humans as has been suggested by Polk (2004). Nonetheless, if the upper body is more dorsally oriented, then less lordosis would be needed to

Fig. 7. Sacral and lumbar posture of modern humans (A) and Neandertals (B). Note the smaller lordotic angle and more horizontal sacral endplate of the Neandertal spine.
keep the center of mass in the same relative position. This would allow gait features such as knee flexion and stride length to be unaffected. Future biomechanical research should investigate the effect of these complex relationships on Neandertal gait.

CONCLUSIONS

If nonhuman apes are representative of the lumbar morphology of the last common ancestor between humans and nonhuman apes, then lumbar LA increased dramatically during hominin evolution from 20° to 25° as seen in nonhuman apes to >50° in H. sapiens. This change appeared early in hominin evolution, because the lumbar spines of australopithecines and H. erectus show human-like LAs of 40° to 45°. Neandertals are different from all other hominins (with the possible exception of the hominins from Sima de los Huesos, who are potentially Neandertal ancestors), exhibiting relatively small LAs (<30°). The reduced lordosis of Neandertals suggests postural and locomotive differences from the other hominins.

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LITERATURE CITED
