Morphology, pathology, and the vertebral posture of the La Chapelle-aux-Saints Neandertal

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Although the early postural reconstructions of the Neandertals as incompletely erect were rejected half a century ago, recent studies of Neandertal vertebral remains have inferred a hypolordotic, flat lower back and spinal imbalance for them, including the La Chapelle-aux-Saints 1 skeleton. These studies form part of a persistent trend to view the Neandertals as less "human" than ourselves despite growing evidence for little if any differences in basic functional anatomy and behavioral capabilities. We have therefore reassessed the spinal posture of La Chapelle-aux-Saints 1 using a new pelvic reconstruction to infer lumbar lordosis, interarticulation of lower lumbar (L4-S1) and cervical (C4-T2) vertebrae, and consideration of his widespread age-related osteoarthritis. La Chapelle-aux-Saints 1 exhibits a pelvic incidence (and hence lumbar lordosis) similar to modern humans, articulation of lumbar and cervical vertebrae indicating pronounced lordosis, and Baastrup disease as a product of his advanced age, osteoarthritis, and lordosis. Our findings challenge the view of generally small spinal curvatures in Neandertals. Setting aside the developmentally abnormal Kebara 2 vertebral column, La Chapelle-aux-Saints 1 is joined by other Neandertals with sufficient vertebral remains in providing them with a fully upright (and human) axial posture.

human evolution | Late Pleistocene *Homo* | lumbar lordosis | spino-pelvic morphology | paleopathology

Late 19th and early 20th century postural reconstructions of Neandertals (1, 2), and particularly the extensive one of the La Chapelle-aux-Saints 1 Neandertal skeleton by Boule (2), created persistent images of these late archaic humans as primitive and incompletely erect. Neandertals were inferred to lack modern human lumbar and cervical lordosis, along with a faint thoracic kyphosis, habitually bent hips and knees, and divergent halluces. Combined with their perceived combination of ancestral and uniquely derived features (2), plus their temporal proximity to early modern humans, this postural reconstruction served to distance ourselves from these Late Pleistocene humans.

Through the mid-20th century, a series of reassessments (3–5) highlighted the errors of earlier reconstructions, with one (5) focusing attention on the osteoarthritic nature of the La Chapelle-aux-Saints remains. Together, these and later analyses (6–9) provided Neandertals with a fully erect (human) posture with normal spinal curvatures. However, a series of recent papers (10–16) have argued that the Neandertals, including La Chapelle-aux-Saints 1, possessed lumbar vertebrae and pelvic incidence angles indicating reduced lumbar lordosis, flatter cervical lordosis and thoracic kyphosis than modern humans, and little of the pelvic tilt associated with bipedal posture (and lumbar lordosis) in recent humans. Such a flat spinal curve in recent humans is associated with an anterior shift of the line of gravity and instability leading to chronic back pain (17), raising questions about its appropriateness for the Neandertals.

The aim here is therefore to reassess the pathology and the posture of one of the key specimens in these considerations, the "vieillard" from La Chapelle-aux-Saints. The focus is initially on his pelvic incidence determined from a pelvic reconstruction, to provide a measure of lumbar lordosis before the development of his extensive spinal osteoarthritis. It is combined with an evaluation of his pelvic tilt based on the distribution of degenerative changes in the hip joint. The alignment of the cervical and lumbar vertebrae based on their osteoarthritic changes is then employed as an alternative means to deduce spinal curvature in his later life. These assessments have implications for both the upright posture of Neandertals and for our perceptions of behavior in these nonmodern humans in their Late Pleistocene context.

Results

Pelvic Incidence and Posture. The virtual reconstruction of the La Chapelle-aux-Saints 1 pelvis (*SI Appendix*, Fig. S2) shows that the nonpathological portions of the two sides are entirely symmetrical. The pelvic incidence angle (the angle in the sagittal plane between a ray from the hip joint center to the superior sacral surface and the perpendicular to the sacral surface; ref. 18) is not affected by the left acetabular degenerations, given the symmetrical matching of the equivalent left and right acetabular portions and hence an accurate location of the femoral head centroid. The resultant pelvis displays a pelvic incidence angle of 56° (Fig. 1), which is trivially above the mean (52.4° ± 11°, $n = 131$) of a modern human sample and well within its range of 27°–82° (18).

The left acetabulum exhibits a series of degenerative changes reflecting advanced osteoarthritis. There is a massive periarticular growth along the dorsal acetabular margin and new bone formation

Significance

Fully upright and balanced posture is one of the hallmarks of humanity, and it has long been seen as present among all members of the genus *Homo*. However, recent considerations of Neandertal vertebrae have concluded that these late archaic humans, who were both behaviorally and phylogenetically close to ourselves, lacked fully developed spinal curvatures and must therefore have had precarious postures. Reassessment and virtual reconstruction of the La Chapelle-aux-Saints 1 Neandertal skeletal remains provides direct anatomical evidence that he, and by extension other Neandertals, possessed the usual human lower back and neck curvature (lordosis). It is therefore time to move beyond making Neandertals less human and focus on the subtle shifts in Late Pleistocene human biology and behavior.

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on the lunate articular surface, but most importantly, there is a strip of eburnation 10–12 mm wide extending from the area of the anterior inferior iliac spine (AIIS) to the middorsal border (Fig. 2), or from sectors ~2–5 following the division of the lunate surface of the acetabulum into seven anatomically defined sectors (19) (*SI Appendix*, Fig. S5). The extent of this degeneration provides a midpoint of 3.5, which is close to the median (3.25) of a recent human cadaver sample and well within its range (2.75–3.75, $n = 81$). The more restricted but distinct depression in the right superior acetabulum (Fig. 2) extends from just dorsal of the AIIS to the middorsal margin, or 2.5–4.5, providing a midpoint of 3.5. All of these fossil and recent human values indicate a midpoint for weight-bearing joint reaction force through the hip joint near or modestly dorsal of the AIIS, the area in which acetabular pressures are greatest during static or dynamic loading in normal human upright posture and locomotion (e.g., refs. 20–24; *SI Appendix*, *section V*).

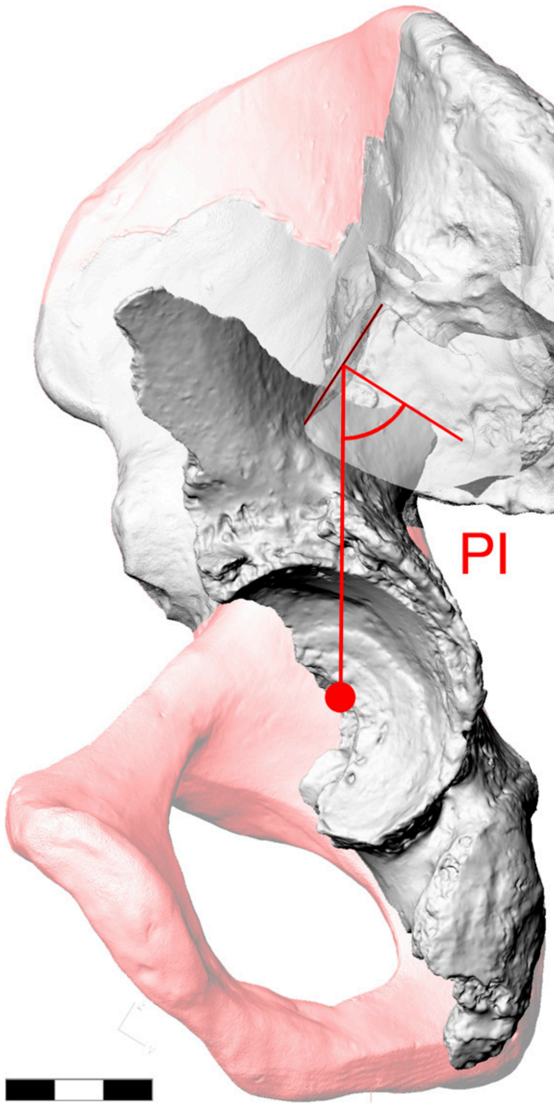

Fig. 1. Left lateral view of the La Chapelle-aux-Saints 1 left acetabulum, medial view of the right hip bone and midsagittal section of the sacrum. (Scale bar, 3 cm.) The pelvic incidence angle (PI) = 56°. Pink: the portions of the right hip bone reconstructed in plaster by Boule (11–13). Note that the reconstructed sacral promontory projects the S1 body more superiorly than the preserved portion; the reconstruction is therefore conservative, because the preserved portion alone would provide a higher PI.

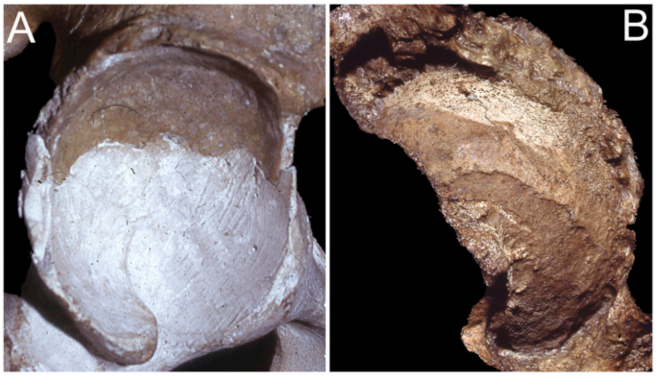

Fig. 2. Views of the La Chapelle-aux-Saints 1 right (*A*) and left (*B*) acetabula, oriented approximately anatomically. The depressed weight-bearing area is evident on the right one, and the broad band of eburnated articular bone in the weight-bearing area is evident on the left.

It is therefore apparent that La Chapelle-aux-Saints 1 had an overall pelvic posture well within the range of variation of modern humans through his life span. In addition, the orientation of the S1 cranial surface, which would have been established during development, was indistinguishable from those of recent humans.

Spinal Curvature and Vertebral Osteoarthritis. The pelvic incidence of La Chapelle-aux-Saints 1 predicts a well-developed lumbar lordosis angle of 52° with a 95% CI of 35° – 69°, following the regression equation of (15). A recent human sample (18) provides a mean of 55.6° (±11.2°, $n = 131$). The pattern and extent of his vertebral osteoarthritis reinforces this predicted normal human spinal curvature.

There are marked changes particularly in the lower cervical to upper thoracic spine, as well as the mid-to-lower thoracic region, comprising eburnation and telescoping facet joint subluxations (*SI Appendix*, Fig. S1; see also ref. 25). However, including minor changes indicates that all preserved facet joints were affected by osteoarthritis. In the cervical region, the tip of the C6 spinous process was flattened and a slight depression on its left inferior aspect matches the tip of the C7 spinous process, suggesting bony remodeling due to Baastrup disease (Fig. 3). Articulation of the cervical vertebrae also suggests reduced intervertebral disk spaces and close contact between the C4/C5 and C5/C6 spinous processes, but clear signs of osteophytic remodeling could not be observed. The articulation of the cervical vertebrae (Fig. 3) also provides a distinct C4 to T1 lordosis, also evident in the La Ferrassie 1 and Krapina 107 and 106/108–110 cervical vertebrae (26, 27).

Facet joint subluxation was also observed at L4/L5 and L5/S1, where it was associated with moderate osteoarthritic changes of the facets. These subluxations led to the formation of extra joints on the inferior sides of the bases of the right costal processes of L4 and L5 that articulated with notch-like nearthroses at the right superior articular processes of L5 and S1, respectively (Fig. 4). Moreover, the spinous processes of L4, L5, and S1 displayed signs of Baastrup disease with extensive osteophytic remodeling. Articulation of the lower lumbar vertebrae (Fig. 4) shows that the L4/L5 intervertebral space was markedly reduced, thus bringing the corresponding spinous processes into habitually close contact. The inferior L5 spinous process is eroded, but a small point of contact is present between the spinous processes of L5 and S1. A typical consequence of the asymmetric subluxations with nearthroses on the right side of L4, L5, and S1 is a right-convex degenerative scoliotic misalignment of these vertebrae (28, 29), which is to a lesser degree also present in the cervical spine.

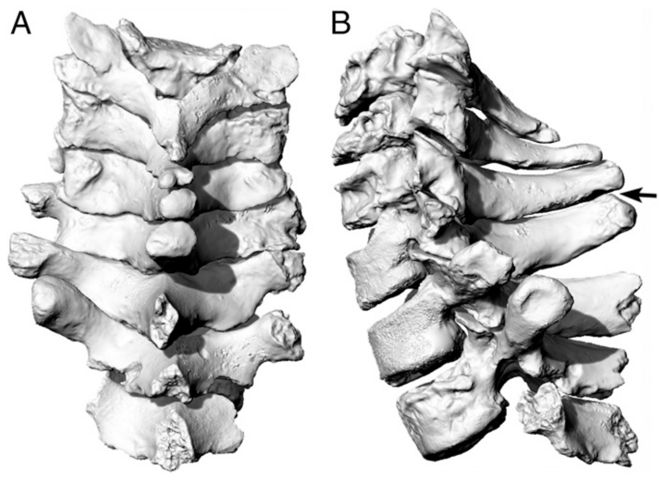

Fig. 3. The articulated cervical and upper thoracic series C4-T3 of La Chapelle-aux- Saints 1, surface-scanner generated models. (*A*) dorsal view, (*B*) lateral view. Note Baastrup disease of the spinous processes C6-C7 (arrow) and the mild degenerative scoliotic misalignment.

The segmental lordosis angle of his L4 to S1 (55.5° ± 2.3°) predicts a very high mean lumbar lordosis angle of 73° – 79° based on his articulated vertebrae (SEest = 3.4°, r = 0.721; *SI Appendix*, Fig. S4). In combination with the lordosis angle predicted from his pelvic incidence, these considerations confirm the presence of a distinctly human lumbar lordosis for La Chapelle-aux-Saints 1.

Articulation of the lower lumbar vertebrae also demonstrates that the facet joint subluxations with the resulting nearthroses at L4/L5 and L5/S1, in combination with Baastrup disease of these vertebrae, must have led to a lordotically fixed and virtually immobile lower lumbar spine, incapable of extension and with a very limited capacity for flexion and lateral bending to the left side. It is likely that this lumbar rigidity led to the previously noted (25) lesser degree of lumbar facet degeneration compared with the marked cervical and thoracic changes.

Discussion

La Chapelle-aux Saints 1 has played a prominent role in discussions of the Neandertal posture since its initial analysis by Boule (2). Our assessment corroborates the presence of well-developed cervical and lumbar lordosis in this individual, as suggested previously (3, 5, 8, 9). It challenges recent reconstructions inferring limited Neandertal spinal curvature (10–16). We base our finding on two lines of evidence, (*i*) a pelvic incidence, associated with a normal human pelvic posture, close to the mean of modern humans, and (*ii*) the articulation of the cervical and the lower lumbar vertebrae. Additional inferences from the La Chapelle-aux-Saints 1 basicranium and other Neandertal vertebrae (*SI Appendix, section IV*) corroborate this conclusion.

Pelvic Incidence and Posture. La Chapelle-aux-Saints 1 provides the only sufficiently complete Neandertal pelvis that is both undistorted and nonpathological in the relevant portions. It therefore allows an accurate determination of his pelvic incidence. That incidence is not only fully modern, it is also significantly larger than the pelvic incidences of 34° reported for the Kebara 2 (15) and the 28° in the Atapuerca-Sima de los Huesos (AT-SH) pelvis 1 (11).

However, the Kebara 2 posterior ilia and sacrum were crushed and needed extensive reconstruction (30), and the L2 to L5 sustained a suite of developmental spinal dysraphism malformations and (probably secondary) degenerative abnormalities (31, 32). The AT-SH pelvis 1 individual also suffered from spinal dysraphism malformation of L5 leading to developmental dysplastic spondylolisthesis, and had an extensive suite of osteoarthritic degenerative changes (11). The resulting dome-shaped superior sacral surface of AT-SH pelvis 1 precludes proper measurement of its pelvic incidence. In addition, both the Kebara 2 and AT-SH pelvis 1 sacra exhibit lumbosacral transitional anomalies; lumbosacral transitional vertebrae are known to lead to erroneously small pelvic incidence angles and thus incorrect estimations of lumbar lordosis (18, 33, 34).

The Kebara and Atapuerca pelves are therefore inappropriate for assessing the pelvic incidence, and by correlation lumbar curvature, of the broader Neandertal (or Middle Pleistocene) populations. The pelvis of La Chapelle-aux-Saints 1 provides at least one Neandertal with a fully normal human configuration, in posture, angulation and implied lumbar curvature.

Additional support comes from the locations of milder degeneration in other Neandertal hip bones that parallel the location of the La Chapelle-aux-Saints 1 acetabular osteoarthritis. The Feldhofer 1, Kebara 2, and Krapina 208 and 209 acetabula have the midpoint of surface degeneration at sector 3, La Ferrassie 1 at 3.25, and Krapina 207 at 3.5 (27). All of these midpoints for weight-bearing degeneration are distinctly dorsal of the AIIS, indicating that the pelvic posture of the Neandertals generally was the same as that of recent humans.

Baastrup Disease and Osteoarthritis. Another important guide for the reconstruction of spinal posture is the presence of Baastrup disease in La Chapelle-aux-Saints 1 (see also ref. 35). It is present at C6/C7, L4/L5, and L5/S1. Baastrup disease ("kissing spines"; ref. 36) is caused by the contact of adjacent spinous processes during upright posture and repeated strains on the interspinous ligament. Initially, this leads to interspinous bursae and, with prolonged stress, to osteophytically enlarged spinous process tips. They become flattened and sclerotic, and nearthroses develop between them (37–39). Clinically it may be associated with tenderness in the midline and back pain during upright posture that worsens with spinal extension and subsides with flexion. L4/L5 is most often affected, but in more severe cases also L3/L4 (not preserved in La Chapelle-aux-Saints 1) and L5/S1, and the entire lumbar spine as well as the cervical vertebrae might be involved (39, 40). Often (in up to 50% of the patients with advanced Baastrup disease; ref. 37), a degenerative scoliotic misalignment of the lumbar spine can be observed, as the spinous processes try to swerve the strains. Such a scoliotic misalignment is implied by the unilateral nearthroses between L4/L5 and L5/S1 of La Chapelle-aux-Saints 1 and to a lesser degree it appears to have been present in the cervical spine.

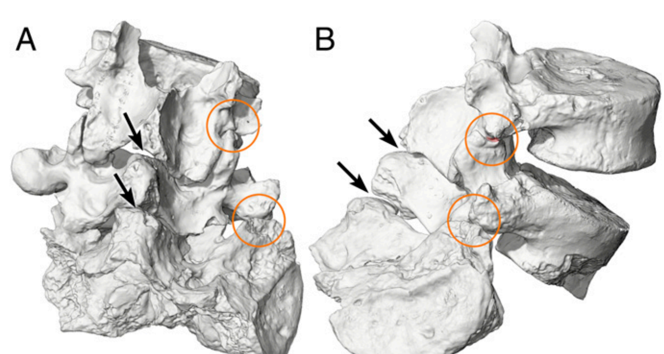

Fig. 4. Articulated lower lumber spine and sacrum of La Chapelle-aux-Saints 1, (*A*) dorsal view, (*B*) lateral view. Note the notch-shaped nearthroses between L4 and L5 as well as between L5 and S1 (circles) leading to degenerative scoliotic misalignment and Baastrup disease between the spinous processes of L4-L5 and L5-S1 (arrows; the inferior aspect of the L5 spinous process is eroded).

Risk factors for Baastrup disease include large spinous processes, increased lordosis (e.g., as compensation for increased thoracic kyphosis during advanced age), reduced intervertebral space, and other degenerative changes in the aging spine (37–41). In La Chapelle-aux-Saints 1, the L5 spinous process is not exceptionally large, and the degree of thoracic kyphosis cannot be assessed. However, reduced intervertebral spaces are evinced by the telescoping subluxation of the cervical and lower lumbar vertebrae. Moreover, articulation of the lower lumbar vertebrae with the sacrum suggests that the lordosis angle is in the upper range of modern humans if the nearthroses between the spinous processes and those at the bases of the costal processes are taken into account. In addition, La Chapelle-aux-Saints 1 is one of the oldest of the known Late Pleistocene specimens, both Neandertals and early modern humans.

Age-at-Death and Pathology. A reassessment of the age-at-death of La Chapelle-aux-Saints using the best preserved age indicator (the right iliac auricular surface) provides an age in the sixth or even seventh decade (*SI Appendix*, *section II*). It is therefore likely that the extensive osteoarthritic changes in his vertebral column, as well as those evident in his sternoclavicular, glenohumeral, cubital, radiocarpal, coxal, and pedal interphalangeal articulations (8), are related to the accumulated effects of age and to a lesser degree his Pleistocene foraging existence (42, 43). The vertebral degenerations can therefore be employed as the products of normal age-related processes in the evaluation of his spinal posture.

Conclusions

After more than a century of alternative views, it should be apparent that there is nothing in Neandertal pelvic or vertebral morphology that rejects their possession of spinal curvatures well within the ranges of variation of healthy recent humans. The La Chapelle-aux-Saints 1 pelvic remains provide a pelvic incidence angle and posture indicating normal human configurations and, by extension, a well-developed lumbar lordosis in upright posture. The latter is reinforced by the articulation of his L4 to S1 vertebrae, which provide an elevated lordosis angle, due in part to facet subluxation, nearthroses, and Baastrup disease. The articulation of C4 to T3 provides evidence for a well-developed cervical lordosis. The osteoarthritic changes in his vertebrae and hip support this pelvic and vertebral posture, as they reflect normal human age-related degenerations. Other, nonpathological, Neandertal pelvic and vertebral remains reinforce the pattern evident in La Chapelle-aux-Saints 1.

This reconsideration of the La Chapelle-aux-Saints 1 remains, as related to vertebral posture and pathology, should emphasize what was accepted half-a-century ago but has been questioned as the relationship between the Neandertals and modern humans (44, 45) has become (uncomfortably to some) close. Despite the evident morphological contrasts, there is little, paleontologically or archeologically, to indicate differences in basic functional anatomy and behavioral capabilities between them and their Late Pleistocene modern human neighbors (46, 47). It is therefore hoped that this reassessment will substantiate what has long been evident.

Materials and Methods

The analysis is based primarily on the original La Chapelle-aux-Saints 1 partial skeleton (2, 48) (*SI Appendix*, *section I*). The right ilium is missing, and a cast [verified against measurements of the original; (49)] was employed. It represents an older male, with an age-at-death in the sixth or seventh decade (*SI Appendix*, *section II*).

The pelvic remains are undistorted. The sacrum includes the partial first and second sacral bodies, the right ala, and a displaced lamina. The left hip bone preserves the inferior ilium, the ischium, and the posterior half of the osteoarthritic acetabulum. The right hip bone retains most of the ilium with the auricular surface and the iliac acetabulum. Its missing portions were reconstructed in plaster on the original (2), and articulation with the sacrum indicates appropriate ischiopubic dimensions (49). Nineteen variably complete presacral vertebrae remain (50). They include C1 and C2, C4 to T2 (identified as C5 to T3 in ref. 2), two fragmentary upper thoracic vertebrae (T3 or T4 and T6 or T7), T8 to T12, L1, and L3 to S2 (*SI Appendix*, Fig. S1). Most vertebral bodies lack their ventral margins, but their dorsal bodies and neural arches are largely intact. C4 to T2 are intact with only minor damage.

High-resolution 3D surface scans of the vertebral and pelvic remains were acquired with a PT-M4c scanner (Polymetric). The scanner delivers 3D models with a maximum depth resolution of 0.006 mm at a scan field of 62 × 62 mm.

A virtual reconstruction of the pelvis (Fig. 1 and *SI Appendix*, Fig. S2) was performed using Geomagic Design X (3dsystems.com) and Amira 6.7 (fei.com). The sacrum was mirror imaged, and the reconstruction of the contour of the anterior portion of the superior sacral surface was guided by the outline of the preserved parts and checked against the dimensions of the L5 body. The eroded anterior sacral body with the promontory was fixed using the surface model of a modern human hemi-S1, which was warped onto the S1 body of La Chapelle-aux-Saints 1 using 167 landmark points; there was no warping of the fossil S1. The displaced lamina and median sacral crest were reduced. The missing caudal portion of the sacrum was not reconstructed. Mirror imaging the two hip bones allowed reassembly of the pelvis. The virtual reconstruction was assisted by a manual reconstruction of the pelvis using 3D prints of the elements. Based on the virtual reconstruction of the pelvis, we measured the pelvic incidence angle and estimated the lumbar lordosis following a regression equation that had been previously described (15).

To predict the spinal shape of La Chapelle-aux-Saints, its vertebral remains were digitally articulated using Rhinoceros 5.4 (rhino3d.com) so that the surfaces of adjacent facets showed maximal congruency while taking into account telescoping subluxations of the facet joints. Manual articulation of 3D prints of the vertebrae was used to assist the digital reconstruction.

The articulated L4 and L5 and the sacrum were used to estimate the lumbar lordosis angle (18) based on a least squares regression of the L4-S1 lordosis angle against the L1-S1 lordosis angle in 63 modern human upright standing lateral lumbar radiographs from the Balgrist University Hospital, Zurich (*SI Appendix*, Fig. S4). The lumbar radiographs were obtained according to standard protocols (51) (Ethics Committee of the Canton of Zurich Approval KEK-ZH-No. 2014–0309). The 95% prediction intervals were calculated as previously described (52).

The osteoarthritic changes were scored (following refs. 53 and 54) into absent, discrete-mild, moderate, and severe with eburnation. The distribution of the degenerative changes of the acetabula was scored according to the lunate surface divisions into seven sectors (19), in which the anterior and posterior extents of the degeneration are scored relative to the designated lines (2.5 centered on the AIIS) and the midpoint between these extents employed to reflect the primary area of the habitual joint reaction force.

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